



Drought-induced die-off triggers species composition shift at warmer and drier edges of climate gradient in *Pinus sylvestris* forests of Catalonia (NE Spain)

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Received: 15 October 2024 / Accepted: 9 April 2025
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Abstract

Climate change is increasing the frequency and intensity of drought episodes, with raising forest die-off events globally. Impacts of drought on tree growth and mortality have been extensively investigated, but studies on regeneration after these episodes and their consequences for tree diversity and potential plant composition shifts are still scarce, especially analysing climate gradients. We analyse the impact of drought-induced die-offs on woody plant diversity in *Pinus sylvestris* forests in Catalonia (NE Spain), considering local temperature and precipitation effects. We compared plots affected by die-off to non-affected ones, surveying tree layers in 2013, 2017, and 2022, and tree recruits in 2022. Die-off plots showed greater richness and diversity in tree layer after 5 and 10 years of die-off, particularly in drier sites, while higher evenness was observed in warmer sites. Such pattern indicated a vegetation shift towards a Mediterranean-type forest, with increasing ingrowths of *Quercus*, *Acer*, *Prunus*, and other broadleaf trees which incorporated to tree layer, potentially replacing dead *P. sylvestris*. In die-off plots, species richness and evenness of larger recruits were 36% and 42% higher, respectively, than in non-affected ones. Species in tree layer and recruiting communities showed a 29% higher similarity in die-off plots than in non-affected ones, supporting that die-off provide better opportunities for recruitment by incorporation into the tree canopy and successful establishment of new recruits. These results indicate that drought-induced die-off is triggering forests transition towards a more adapted plant composition to climate change concurrent with ongoing local climate conditions.

Keywords Biodiversity · Climate change · Mediterranean forest · Tree mortality · Vegetation shift

Introduction

Climate change is altering global temperature and precipitation patterns, increasing the frequency and severity of extreme weather events such as floods, heatwaves, windstorms, and droughts (IPCC 2023). Drought and heatwave episodes are driving large-scale forest die-off and tree mortality in many forest types across biomes (Allen et al. 2010, 2015). Drought-induced tree mortality is associated to plant water and carbon economy, when failure of water and carbohydrate transport (i.e., hydraulic and phloem failure, respectively) and carbohydrate depletion (i.e., carbon starvation) occur concomitantly (Mencuccini et al. 2015; Adams et al. 2017). This is often mediated by stand structure and competition among trees (e.g., stands with higher basal area experience more mortality), and biotic agents (i.e., pathogens and pests), all together interacting with

Communicated by Claus Bässler.

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climate (Anderegg et al. 2015; Jump et al. 2017; Jaime et al. 2019). The Mediterranean forest ecosystem is especially vulnerable to drought-related tree die-off and mortality events (Dorado-Liñán et al. 2019), raising concern about potential shifts or even forest collapse (Lloret and Batllori 2021). Indeed, widespread mortality episodes endanger the future of growth and dynamics of forest ecosystems (Babst et al. 2019; García-Valdés et al. 2021) and their services (Anderegg et al. 2013). However, our understanding on the effects of drought-induced mortality on forest regeneration and potential compositional changes remains largely unknown (Martínez-Vilalta and Lloret 2016; but see Batllori et al. 2020).

Episodes of drought-induced tree mortality provide opportunities to plant composition shifts as post-drought regeneration may follow uncertain successional trajectories during gap filling (Lloret and Batllori 2021; Lloret et al. 2022). The replacing individuals could correspond to the ingrowth of recruits (i.e., seedlings or saplings growing into the tree class) in the layer of dominant or co-dominant tree species of already existing recruits in the forest understory (i.e., advanced regeneration) or to propagules arriving from neighbouring forests and successfully establishing in the canopy (Lloret et al. 2022; Selwyn et al. 2024). Indeed, pre-drought dominant tree species can persist after mortality episodes provided their regeneration become successful, or, alternatively, new tree species recruits in the understory can achieve dominance after tree mortality (Batllori et al. 2020). Meanwhile, new species arrival in drought-induced die-off stands could also initiate new successional trajectories, resulting in novel community assemblages (Hobbs et al. 2006). Additionally, deadwood accumulation after tree mortality may assist in successful regeneration by increasing soil moisture, reducing seed predation, and protecting smaller seedlings from herbivores, while canopy opening alters microclimatic conditions by increasing the sunlight penetration (Schmidt et al. 2017; Thom et al. 2020). Therefore, drought die-off-induced sites provide conditions and resources for tree species turnover that could potentially induce changes in forest structure and composition, thus, determining short-and-mid-term resilience (Seidl et al. 2017; Lloret et al. 2022). Accordingly, in the aftermath of drought-die-off episodes, forest structure can become more complex and heterogenous (Chowdhury et al. 2024), while competition release may favour an increase of plant diversity (i.e., “disturbance paradox”, see Thom and Seidl 2016).

Indeed, compositional dynamics is largely determined by species-specific traits (Lloret et al. 2012; Batllori et al. 2020; García-Valdés et al. 2021). Generally, tree species having higher adaptability to drought, such as resprouting capacity and efficient water use strategy, are considered better self-replacers after drought (Zeppel et al. 2015). Meanwhile,

the advanced regeneration of shade tolerant recruits after canopy mortality potentially has better opportunities to become adults (Batllori et al. 2020). Therefore, gap creation in drought die-off sites may favour the germination and growth of seedlings and the ingrowth of shade-tolerant (Galiano et al. 2010, 2013) and drought-resistant species (Niinemets and Valladares 2006), which could maintain advanced regeneration in the understory. Overall, post-disturbance recruitment primarily sets the stage for long-term trajectory involving ecosystem recovery and community dynamics in forest stands; however, the outcome is difficult to predict as various factors simultaneously effect this successional process.

Plant compositional change during drought and post-drought periods is particularly influenced by local climate as the survival or the regeneration success of any given population is correlated with the species climatic requirements, reflecting species’ bioclimatic niche (Grubb 1977; Pironon et al. 2018; Pérez Navarro et al. 2019). In general, populations located close to species’ tolerance limits (i.e. experiencing lower climatic suitability or sited close to the edge of its bioclimatic niche) should exhibit lower regeneration levels, though alternatively may be more resistant to extreme drought episodes due to local acclimation or adaptation (Lloret and Kitzberger 2018; Solarik et al. 2018; Margalef-Marrase et al. 2020). In contrast, populations living in localities having historical suitable climate may become less tolerant to extreme climatic fluctuations because of higher demand for resources (Pérez Navarro et al. 2019; Elvira et al. 2021). However, they may maintain successful regeneration when climate become milder after an unfavourable climatic episode. So, compositional changes are expected to be influenced by climatic gradients, reflecting species’ environmental requirements (Batllori et al. 2020; Lloret and Batllori 2021). Yet, this compositional reorganization remains to be better documented at regional scale, considering local species adaptability and niche requirements, particularly across gradients of increasing dryness (Allen et al. 2015; Zhang et al. 2018).

Here we aim to elucidate the potential changes of woody species diversity and composition for a 10-years period following a drought-induced die-off and tree mortality episode (Jaime et al. 2019; Margalef-Marrase et al. 2023; Chowdhury et al. 2024), also considering the effects of local climatic factors through a gradient of precipitation and temperature. We studied woody plant diversity and composition immediately following the event and after 5 and 10 years in forest stands dominated by Scots pine (*Pinus sylvestris*) in Catalonia (NE Spain). We hypothesize that (i) plots affected by die-off will show a higher diversity of trees, recruits, and shrub species than non-affected ones over time, likely due to released competition and changes in environmental

conditions following tree death; and (ii) the increase in tree species diversity will be more prominent in the die-off affected plots that experience higher temperature and lower precipitation locally, where species other than *P. sylvestris* adapted to warmer and drier conditions would better resist the drought episode.

Methods

Study system and experimental design

We conducted this study in forests dominated by *Pinus sylvestris* in Catalonia (NE Spain) that had experienced die-off and tree mortality episodes due to a drought in 2012, exacerbated by bark beetle infestation (Jaime et al. 2019; Margalef-Marrase et al. 2023). In particular, we surveyed twenty different forest sites in 2013, 2017, and 2022 (Fig. S1a). The average distance between sites was $52.4 \text{ km} \pm 37.7 \text{ km SD}$ (Fig. S1a). Due to orographic variability, these *P. sylvestris* forests experience different temperature and precipitation conditions, with colder and wetter sites in the Pyrenees and drier and warmer conditions in the Catalan Coastal Range. Overall, the average annual temperature in the study sites is 10.6°C (range: 8.4 to 13.7°C), with annual precipitation accumulation of 734.1 mm (range: 552.0 to 822.6 mm) between 2012 and 2022 (Fig. S2).

In 2013, two paired circular plots with a 10-meter radius (about 314 square meters) were established in each site, ca. 50 to 150 m apart (Fig. S1b). Following a visual assessment of the occurrence of *P. sylvestris* mortality, one plot was established in a location affected by drought-induced die-off (hereafter, die-off plot) and the other plot was placed in a non-affected location (hereafter, control plot; see details in Chowdhury et al. 2024; Jaime et al. 2019; Margalef-Marrase et al. 2023). No salvage logging was carried out in the sites after the die-off episode.

To compute woody plant species richness, diversity (Shannon index), and evenness (Pielou index) in each plot, we surveyed species in the tree layer (i.e., alive trees with $\text{dbh} > 2.5 \text{ cm}$), and tree species in the community of recruits with $\text{dbh} \leq 2.5 \text{ cm}$ (i.e., comprising seedlings and saplings), as well as shrub species. Information of the tree layer were collected in all three surveys (2013, 2017, and 2022) from the whole plot, while recruits (seedlings and saplings) information was collected in 2022 by means of transect belts (2 m wide in each side) along two perpendicular transect lines 20 m long (Fig. S1b). Additionally, shrubs cover information was collected from two transect lines in 2022 (Fig. S1b).

Quantifying taxonomic diversity in tree layer, tree recruits, and shrubs

In 2013, tree layer species were identified and their dbh were measured (Fig. S1b, Table S1). We resampled each tree in all plots in 2017 and 2022 using the same standard procedures. In 2017 and 2022, new tree individuals with $\text{dbh} > 2.5 \text{ cm}$ incorporated in the tree layer (i.e., ingrowths) were also identified and measured by comparison to the previous survey (Table S1). We separately calculated tree richness in each plot for the three field-surveys while tree basal area was used as a proxy of abundance to compute diversity (Shannon index) and evenness (Pielou index) (Cruz-Alonso et al. 2021).

In 2022, we identified recruits at species level and counted them in the two transect belts (Fig. S1b, Table S1). The common area of the transect belts that intersect in the centre of the plot was surveyed only once to avoid duplicate counts. For this sampling, three developmental stages categories were considered: T1: seedlings under two years-old, T2: saplings older than two years with height $< 130 \text{ cm}$, and T3: saplings with height $> 130 \text{ cm}$ and $\text{dbh} < 2.5 \text{ cm}$ (see for a similar category in LIFE RedBosques 2018). For age estimation of recruits, we used morphological characteristics based on stem lignification. Specifically, for *Pinus* species, individuals with lignified shoots were classified as two years or older categories. Meanwhile, for broadleaf species, individuals with lignified stems or more than one shoot were classified on the same way. We then computed species richness for the total number of recruits (hereafter, all recruits) and for the three development categories (T1, T2, and T3) per plot. The count information of recruits was utilized to calculate diversity and evenness (Cruz-Alonso et al. 2021).

In 2022, shrub species were also surveyed in the two perpendicular transect lines (Fig. S1b). Each shrub species in contact with the transect lines that continuously covered at least 30 cm was identified and the cover length was recorded (Table S1). To eliminate duplication, shrub individuals that contacted with both transects were considered only once. In each plot, we also estimated shrub species richness, and the species cover information was used as a proxy of abundance to calculate shrub diversity and evenness.

Finally, to illustrate the precise species identity involved on species shifts, we recorded and plotted the species that appeared or disappeared in any site in the tree layer (2022 vs. 2013), recruits (2022), and shrub (2022) communities, considering plot condition and the temperature and precipitation gradients.

Similarity in tree species composition

We used the Sørensen similarity index (ranging from 0 to 1, indicating no similarity and exact similarity, respectively) to compare the composition of tree layer communities between the surveyed years (2013 vs. 2017, 2013 vs. 2022, and 2017 vs. 2022 comparisons) and between tree layer and recruiting communities in the die-off and control plots in 2022. Additionally, we computed species turnover and nestedness in these communities, which are two different components of β -diversity related to dissimilarity, as captured by Sørensen dissimilarity index (i.e., the opposite of Sørensen similarity index; Baselga 2010). These components explain two fundamental mechanisms: species replacement (turnover) and species overlap (nestedness), effectively disentangling overall changes in species composition. We also recorded and plotted the shared species between tree layer and recruiting community to pick their precise species identity in 2022, considering plot condition and the studied climate gradients.

Climate data

We used *easyclimate* package in R to extract daily minimum temperature, maximum temperature, and daily precipitation at 1×1 km resolution raster (Cruz-Alonso et al. 2023), for the forty plots (i.e., 20 sites \times 2 plot conditions, i.e., die-off and control plots) during the period since the drought episode (2012) to the survey data. When the survey was done at the beginning of the year, we considered the climate data until the previous year. So, for the 2013 survey we considered the 2012–2013 climatic data period, for the 2017 survey, we used the 2012–2016 climate data period, and for the 2022 survey we used the 2012–2021 climate data period. Furthermore, for the analysis of the similarity of tree species between 2017 and 2022, we also took the climate data of 2017–2021. Next, we calculated mean annual temperature, mean annual maximum temperature, mean annual minimum temperature, and mean annual precipitation using the daily climatic data. From this climatic dataset, we eventually selected mean annual temperature (hereafter, temperature) and annual precipitation (hereafter, precipitation) for further statistical analyses as these are the more comprehensive climatic variables (Fig. S2).

Statistical analyses

To examine the effect of die-off on basal area, species richness, diversity (Shannon index), and evenness (Pielou index) in the tree layer for a specific time, we constructed separate LMMs (Linear Mixed Models) for each response variable for 2013, 2017, and 2022, in which we included

plot condition as the sole explanatory variable and incorporated site as a random effect to account for the paired design.

To address the potential effects of the die-off episode and local climate (e.g., temperature and precipitation) across years on the tree layer, we separately applied LMMs, considering richness, diversity, and evenness as response variables. We also built a LMM considering plot tree basal area as response variable in order to analyse changes in forest structure over the years. In all these models, we used plot condition, year (2013, 2017, and 2022), temperature and precipitation as explanatory variables. Furthermore, interaction terms (plot condition, year, temperature, and precipitation) up to second order were also included as explanatory variables in the full model. For this analysis we included site and plot as random factors to account for the paired design (i.e., die-off and control plots) and repeated measures (i.e., 2013, 2017, and 2022 survey years), respectively.

Regarding tree species recruits, we separately applied LMMs, considering richness, diversity, and evenness indices as dependent variables. For these analyses we included plot condition, temperature, and precipitation as explanatory variables. The interaction terms plot condition \times temperature, plot condition \times precipitation, and temperature \times precipitation were also included as explanatory variables. We performed separate analyses for each recruit stage (T1, T2, and T3), and for all recruits. Similarly, LMM models were also constructed for shrub richness, diversity, and evenness. For both recruit and shrub analyses, we only used site as random factor to account for the paired plots design, while plot was not included as data were only available for the last year survey (2022).

Finally, we used LMMs to assess the similarity, turnover, and nestedness of the tree layer communities between years (2013 vs. 2017; 2017 vs. 2022; and 2013 vs. 2022, separately) as well as between the tree layer and the recruiting communities. In each case, the respective value of Sørensen index, turnover, and nestedness was separately used as the dependent variable. Then, we included plot condition, temperature, precipitation, and the second order interaction terms as explanatory variables. For these analyses, we used site as a random factor to account for the paired plots design.

We used the *lmer* function from the *lme4* package in R to construct the LMMs (Bates et al. 2024; R Core Team 2024; version 4.3.2). In each LMM, the continuous explanatory variables were scaled and *dredge* function from the *MuMIn* package was used to select the best model for each dependent variable based on AIC factor (Barton 2024).

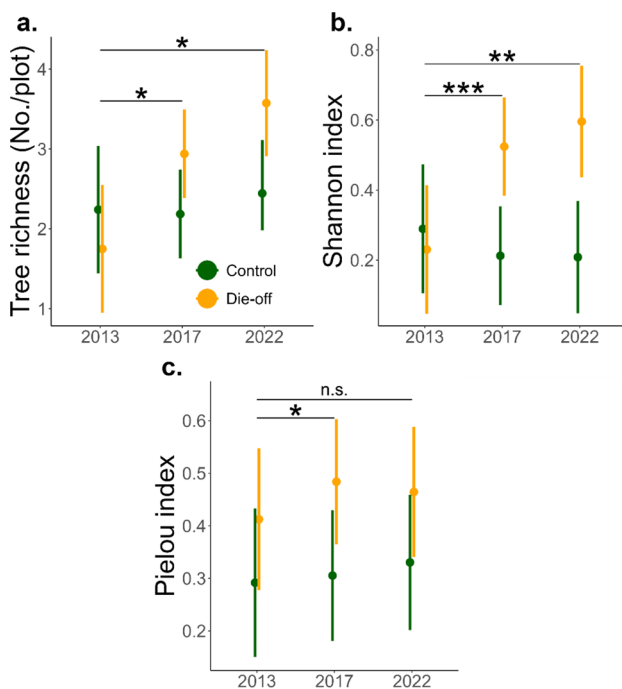


Fig. 1 Species richness (a), diversity (Shannon index; b), and evenness (Pielou index; c) in tree layer between the plot condition (die-off and control) and across years (2013, 2017, and 2022). Asterisk signs indicate significance of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$), while n.s. denotes not-significant ones

Results

Forest structural changes

Basal area was 54%, 53%, and 49% lower in die-off plots than in control ones in 2013, 2017, and 2022, respectively (Table S2). Across years, plot basal area increased by 15% in 2022 compared to 2013 across the study sites, but no significant differences existed between 2013 and 2017 (Table S3). Furthermore, we found that temperature negatively affected basal area. Interestingly, the interaction effects of temperature and precipitation indicated that basal area was higher in sites with lower temperature and higher precipitation (Fig. S3).

Changes in tree layer communities

Differences between die-off and control plots emerged through time. Thus, richness was 23% and 24% (marginally) higher in die-off plots compared to control ones in 2017 and 2022, respectively (Table S4), while diversity (Shannon index) was 77%, 114%, and 96% higher in die-off plots than controls in 2013, 2017, and 2022, respectively (Table S5). Interestingly, across the years, richness and diversity of the tree layer in die-off plots significantly increased in 2017 and 2022 compared to 2013, while control plots remained

Table 1 Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and local climate (temperature and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of the tree layer (in 2013, 2017, and 2022) in *P. sylvestris*-dominated forest in Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. $m.R^2$ and $c.R^2$ denotes to marginal R^2 (fixed effect) and conditional R^2 (fixed and random effect), respectively. Details of coefficients are given in supplementary materials (Table S6, S7, and S9)

Predictors	Estimates		
	Species richness	Shannon index	Pielou index
Year [2017]	-0.06	-0.08	0.01
Year [2022]	0.20	-0.08	0.04
Die-off	-0.49	-0.06	0.10
Temperature	0.46	0.18 **	0.03
Precipitation	0.12	0.07	-0.02
Year [2017]: Die-off	1.24 *	0.37 ***	0.06 *
Year [2022]: Die-off	1.62 **	0.45 ***	0.01
Die-off: Precipitation	-0.82 *	-0.23 **	
Die-off: Temperature			0.12 *
$m.R^2 / c.R^2$	0.29 / 0.83	0.39 / 0.93	0.27 / 0.97

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

steady across the 10-years period (Fig. 1a, b; Table 1, S6, S7). Regarding local climate, temperature showed a positive effect on diversity (Table 1). The interaction effects between plot condition (die-off and control) and local precipitation indicated that richness and diversity in tree layer in die-off plots was lower along the increasing precipitation gradient (Fig. 2a, b), while richness remained steady, and diversity increased slightly across the increasing precipitation gradient in control plots (Fig. 2a, b). However, evenness (Pielou index) in tree layer was 56% and 60% higher in die-off plots than in controls in 2017 and 2022, respectively (Table S8). Across years, evenness in die-off plots was only significantly lower in 2013 compared to 2017 (Fig. 1c; Table 1, S9) while in control plots remained steady across the years (Fig. 1c). The interaction between plot condition and temperature indicated that the evenness in tree layer was significantly higher in die-off plots compared to control ones only at the warmer edge of the temperature gradient (Fig. 2c). Specifically, *Quercus ilex*, *Quercus humilis*, *Acer monspessulanum*, *Crataegus monogyna*, *Fraxinus excelsior*, *Phillyrea latifolia*, *Prunus mahaleb*, and *Sorbus aria* appeared in new die-off affected plots in 2022 compared to 2013, mainly in drier and warmer sites (Fig. 3, S4, S5).

Changes in recruiting communities

We did not find any significant difference between plot condition or local climate in the richness, diversity, and evenness of tree recruits, when considering the three stages

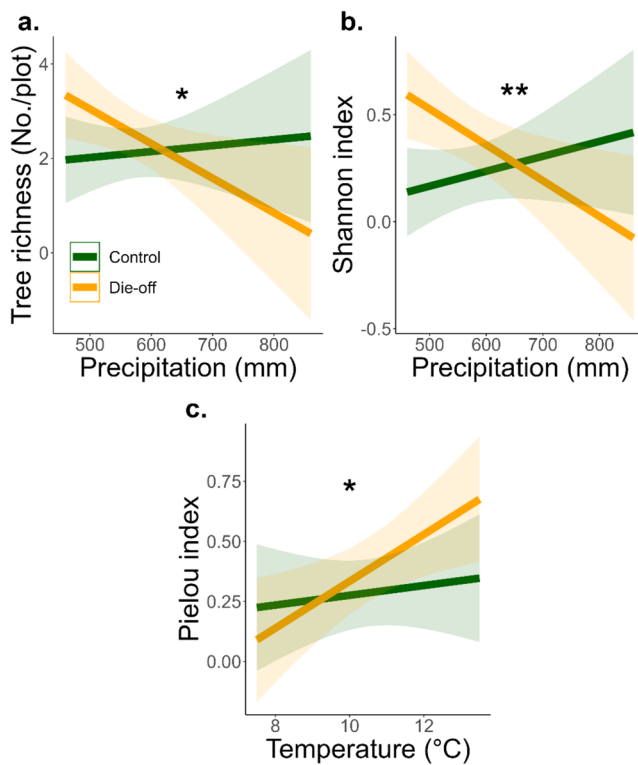


Fig. 2 Interaction effects of plot condition (die-off and control) and mean annual precipitation on adult tree species richness (a) and diversity (Shannon index) (b), and plot condition and mean annual temperature on tree evenness (Pielou index) (c), across 2013, 2017, and 2022. Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$). The envelopes around effect lines denote 95% confidence interval

of development together, and for the younger T1 and T2 stages, separately (Table 2; S10–S12). However, for the T3 stage (i.e., larger recruits), species richness and evenness were significantly higher in die-off plots compared to control ones, while no difference was observed for diversity (Table 2, S13). We also observed significant positive effect of temperature on richness, diversity, and evenness of these recruits (Table 2, S13). Specifically, larger recruit class of *Q. humilis*, *Q. ilex*, and *S. aria* newly appeared in the sites with warmer Mediterranean climate, thus promoting *Quercus* spp. to become dominant in about 35% of the total plots (Fig. S6). Meanwhile, the absence of the largest recruit class of *P. sylvestris* in warmer die-off plots was also apparent (Fig. S6). The absence of large recruits of *P. sylvestris* was recorded in approximately 50% of the die-off and control plots, separately, while the presence of recruitment (considering all recruits stages) was observed in only 25% of the die-off plots and 40% of the control ones, especially in drier sites (Fig. S6).

Changes in shrubs communities

Similar to recruits, shrub richness, diversity, and evenness did not show significant difference between die-off and control plots (Table 3, S14). However, there was a significant interaction between plot condition and precipitation (Fig. 4; Table 3, S14). The interaction indicated that die-off plots had significantly higher species richness, diversity, and evenness of shrubs compared to control ones at the drier edge of the precipitation gradient, while the differences disappeared as precipitation increases (Fig. 4a–c). Meanwhile, temperature negatively affected shrub evenness (Table 3, S14). Regarding composition, *Buxus sempervirens* was the dominating shrub species in die-off and control plots across the climate gradient (Fig. S7). However, several shrub species such as *Erica scoparia*, *Ligustrum vulgare*, and *Rosa* spp. newly appeared in sites having drier Mediterranean climate regime among the die-off plots (Fig. S7).

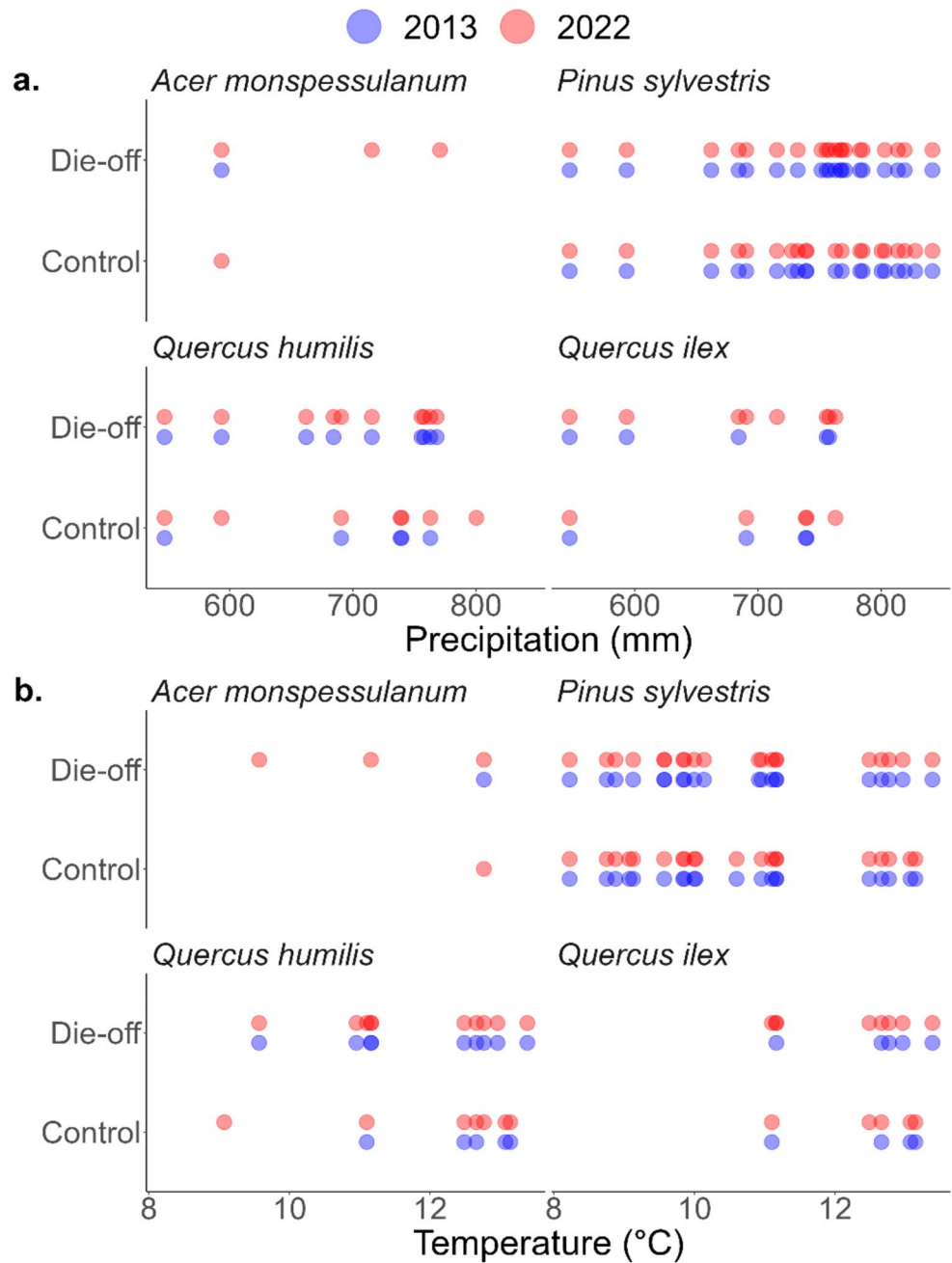
Similarity between tree layer and recruiting communities

We did not find any significant differences in the overall similarity, nestedness, and turnover of tree species composition between die-off and control plots across the three surveyed periods (i.e., between 2013 vs. 2017, 2013 vs. 2022, and 2017 vs. 2022; Tables S15–S17) indicating an overall high similarity of tree layer composition in affected and non-affected plots across the survey years. Local climate conditions did not have significant effects either. However, the similarity between tree layer and recruiting communities was higher in die-off plots than in control ones in 2022 (Fig. 5a, b; Table S18). Furthermore, temperature showed a positive effect on the similarity of tree layer and recruit composition between die-off and control plots, specifically due to the presence of *A. monspessulanum*, *Arbutus unedo*, *Prunus avium*, *Q. ilex*, and *Q. humilis* in both layers (Figs. 5a and 6, S8; Table S18). This pattern is consistent with the observation that the turnover component of Sørensen dissimilarity was significantly (but marginally) lower in die-off plots (0.21) than in control ones (0.39), while no differences were found for nestedness (0.25 and 0.20, respectively; see Fig. 5c, d).

Discussion

Here we report that forest stands of *Pinus sylvestris* that experienced die-off and tree mortality due to drought and associated bark beetle attacks (Jaime et al. 2019; Margalef-Marrase et al. 2023; Chowdhury et al. 2024) exhibited higher plant diversity, considering tree layer and large

Fig. 3 Presence of selected species in tree layer that showed changes across the precipitation (mm; **a**) and temperature (°C; **b**) gradients in die-off and control plots. Tree species that newly appeared in the edge(s) of climate gradients are shown here. Presence of all tree layer species are given at Fig. S4 and S5



recruits. Importantly, sites in the drier and warmer edges of Mediterranean-type climatic conditions showed higher diversity changes in tree layer, being this trend also present for shrub species. The opening of forest canopy due to die-off in drier and warmer sites likely provided better opportunities for advanced regeneration (i.e. suppressed tree saplings) belonging to species other than *P. sylvestris* to replace dead *P. sylvestris* trees, thus increasing diversity in the tree layer. The die-off episode affecting *P. sylvestris* thus triggered shifts of tree species composition favouring *Q. ilex*, *Q. humilis*, *A. monspessulanum*, *S. aria*, and other broadleaf trees. Additionally, the die-off plots also exhibited

higher richness and evenness of larger recruits likely due to an increase on survival, thanks to competition release after tree death. Also, the increase of habitat complexity, after the accumulation of standing and downed deadwood (Chowdhury et al. 2024), could aid tree seeds of different species to achieve successful germination and maintain their growth. Ultimately, this resulted in higher similarity between the tree layer and the recruiting community in die-off plots relative to control ones, pointing that the increased diversity driven by the die-off episode reflects to different life-history stages of tree species (i.e., canopy adults and recruits).

Table 2 Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and climate (temperature and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of recruiting tree species (all recruits, and T1, T2 and T3 stages; see more in Methods) in *P. sylvestris*-dominated forest of Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. $m.R^2$ and $c.R^2$ denotes to marginal R^2 (fixed effect) and conditional R^2 (fixed and random effect), respectively. Details of coefficients are given in supplementary materials (Table S10–S13)

Recruit components	Predictors	Estimates		
		Species richness	Shannon index	Pielou index
All recruits	Die-off	0.03	-0.04	-0.01
	Precipitation	-0.24	-0.17	-0.03
	Temperature	-0.17	-0.13	
	Die-off: Precipitation	0.09	-0.02	-0.07
	Die-off: Temperature	0.05	0.11	
	$m.R^2 / c.R^2$	0.05 / 0.81	0.08 / 0.72	0.07 / 0.73
Recruit in T1 stage	Die-off	-0.11	-0.03	0.09
	Temperature	-0.11	-0.11	-0.00
	Precipitation	-0.18	-0.21	-0.08
	Die-off: Temperature	0.08		
	Die-off: Precipitation	0.06		
	$m.R^2 / c.R^2$	0.04 / 0.75	0.07 / 0.64	0.10 / 0.53
Recruit in T2 stage	Die-off	0.25	0.534	-0.03
	Temperature	-0.65	0.340	0.06
	Precipitation	-0.87	0.200	-0.01
	Die-off: Temperature			-0.05
	Die-off: Precipitation			-0.03
	$m.R^2 / c.R^2$	0.08 / 0.73	0.06 / 0.67	0.07 / 0.23
Recruit in T3 stage	Die-off	0.68 *	0.18	0.35 *
	Temperature	0.50 *	0.20 **	0.25 *
	Die-off: Temperature			-0.16
	$m.R^2 / c.R^2$	0.19 / 0.45	0.22 / 0.35	0.33 / 0.51

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

Our findings indeed indicated a reduction of basal area in the die-off plots. This would correspond to open spaces and likely releasing competition. This facilitated previously suppressed tree individuals that maintained advanced regeneration and persisted in sub-canopy to grow (i.e. ingrowths), occupying the canopy layer in the following years after the event. Interestingly, the newcomers that fill the canopy gaps in die-off plots were often new tree species in the canopy compared to the pre-drought stand, resulting in higher diversity in the tree layer. Importantly, tree diversity also varied across the climate gradient. Higher tree diversity and evenness was found in the die-off plots located closer to the drier and warmer edges of the studied Mediterranean area. This may be attributed to *P. sylvestris* sensitivity towards drier-warmer sites (Bose et al. 2024; also see Fig. S3),

Table 3 Estimates of LMMs (Linear Mixed Models) determining the effect of drought-induced die-off (plot condition, die-off vs. control) and climate (temperature and precipitation) since the die-off episode on richness, diversity (Shannon index), and evenness (Pielou index) of recruiting shrub species in *P. sylvestris*-dominated forest of Catalonia (NE Spain). Temperature and precipitation correspond to mean annual temperature and mean annual precipitation, respectively. $m.R^2$ and $c.R^2$ denotes to marginal R^2 (fixed effect) and conditional R^2 (fixed and random effect), respectively. Details of coefficients are given in supplementary materials (Table S14)

Predictors	Estimates		
	Species richness	Shannon index	Pielou index
Die-off	0.36	0.02	-0.04
Precipitation	-0.22	-0.03	0.01
Temperature	-0.47	-0.18	-0.19 *
Die-off: Precipitation	-0.62 *	-0.18 *	-0.17 *
$m.R^2 / c.R^2$	0.13 / 0.64	0.19 / 0.58	0.30 / 0.41

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

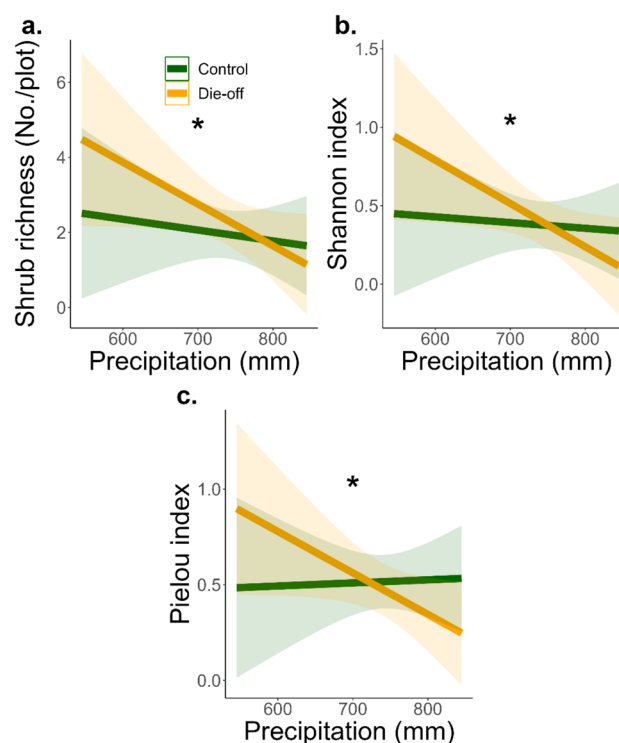


Fig. 4 Interaction effect of shrub species richness (a), diversity (Shannon index) (b), and evenness (Pielou index) (c) between plot condition (die-off and control plots) and mean annual precipitation. Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$). The envelopes around effect lines denote 95% confidence interval

which explain the sudden die-off-induced basal area reduction in 2013 (Table S3; also see Chowdhury et al. 2024). Ultimately, this is leading a community shift in the tree layer of the *P. sylvestris*-dominated forests with Mediterranean type climate.

Fig. 5 Estimates of the models of similarity of tree composition (Sørensen index) between tree layer and recruiting communities in relation to plot condition (die-off and control plots) and mean annual temperature (a), and box plot of Sørensen index (b), nestedness (c), and turnover (d) in die-off vs. control plots. Asterisk signs indicate the significance level of p-values (*: $p < 0.05$, **: $p < 0.01$, *** $p < 0.001$), while m.s. and n.s. denote marginal- and not-significant p-values, respectively. The $m.R^2$ and $c.R^2$ in denotes marginal and conditional R^2 of the model respectively (a). Details of coefficients tables are given in supplementary materials (Table S18)

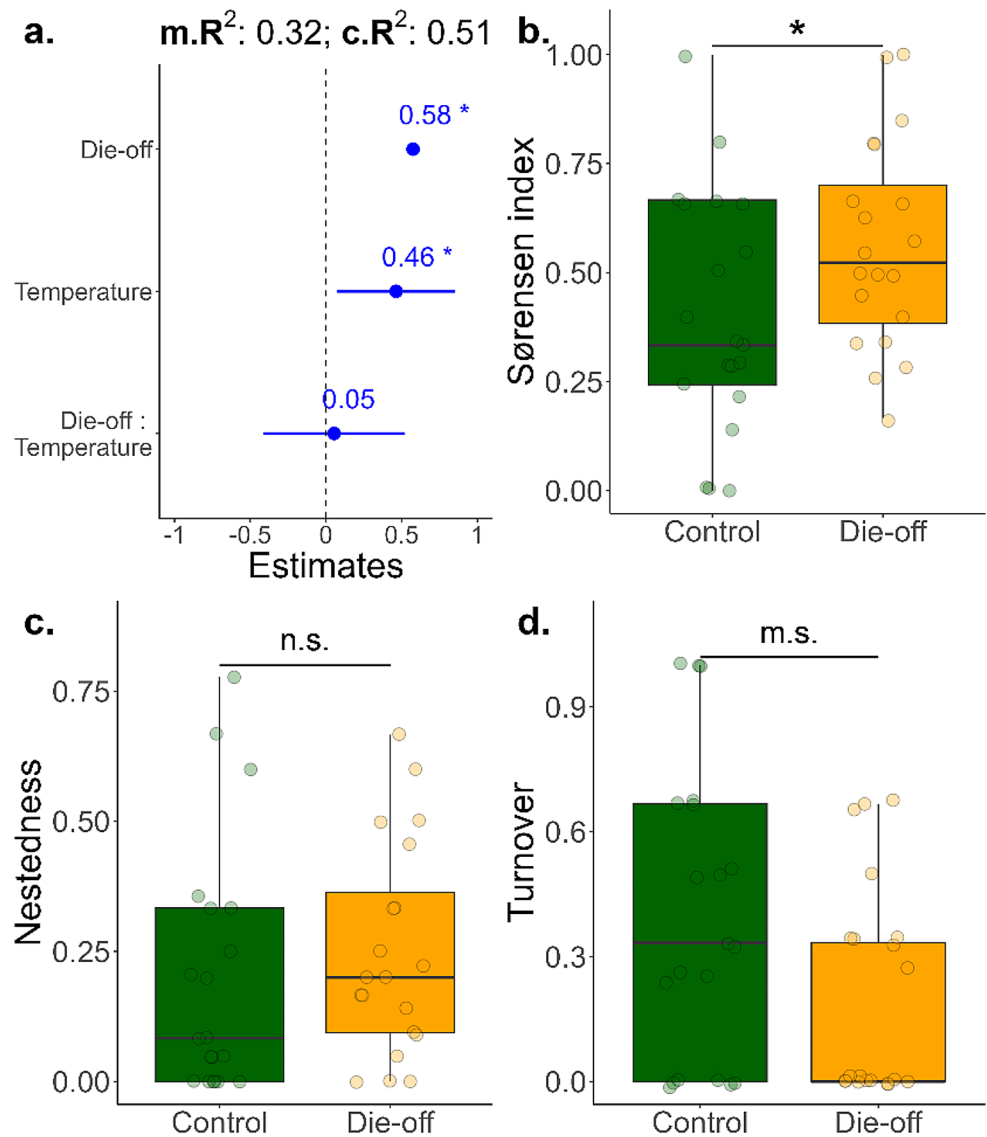
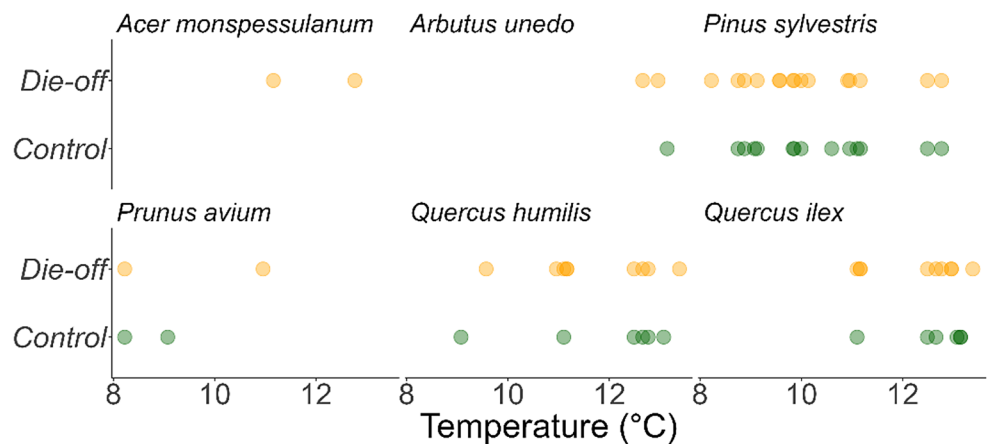


Fig. 6 Presence of selected tree species that appeared in both tree and recruiting communities across the temperature gradient in the die-off and control plots in 2022. Status of all tree species are given at Fig. S8



Indeed, shade tolerant species present in Mediterranean and Sub-Mediterranean forests, such as *Q. ilex*, *Q. humilis*, *A. monspessulanum*, and other broadleaf species were likely to stay in the understory before the die-off event. After the event, they got the resources and spaces to achieve the canopy, particularly in relatively drier sites, thus contributed to the increase the richness and diversity of tree layer (Fig. 3a, S4). These species were also growing abundantly in relatively warmer sites and increased tree evenness therein (Fig. 3b, S5). In fact, the increase of *Quercus spp.* co-dominance with *P. sylvestris*, agrees with previous observations in Mediterranean-type forests (Galiano et al. 2010, 2013; Rigling et al. 2013). Here we expand these observations to other species, mainly broadleaf trees (e.g., *A. monspessulanum*, *C. monogyna*, *F. excelsior*, etc.; see Fig. 3a, b, S4 and S5 for details) many of them relatively adapted to drought conditions. For instance, shade-tolerant species such as *Quercus spp.* and *A. monspessulanum* possess drought-related functional traits such as deep root systems, high specific leaf mass, and efficient water use strategies, enabling them to thrive in drier-warmer sites and contribute to the successful establishment in the canopy layer after the die-off event (González de Andrés et al. 2024; Italiano et al. 2024). On the other hand, wetter and colder sites that were affected by the die-off episode showed self-replacement of *P. sylvestris* and those sites remained less diverse and uneven.

When considering the different recruiting stages, exposed canopy trees that survived in die-off plots or those living closely had likely experienced better conditions for reproduction. Accordingly, they would have produced abundant seeds that can disperse and eventually germinate, thereby increasing the richness and evenness of tree species in the regeneration compartment where they were previously absent or scarce (Selwyn et al. 2024). However, differences between smaller seedlings and larger sapling were apparent. On one hand, similar abundance and richness of the smaller recruit categories in die-off and control plots were observed, likely because of a common species pool at the landscape-level. Furthermore, smaller seedlings are prone to die in both die-off plots and controls similarly as they have shallow and poorly developed root systems (Pratt et al. 2008); thus, being sensitive to climate stresses (Dobrowski et al. 2015; Canham and Murphy 2017). In contrast, the mortality-induced competition release likely favoured larger recruits because of their relatively well-developed root systems compared to smaller recruits (Lloret et al. 2009). More specifically, resprouting and drought-resistant capacity of larger recruits of *Q. humilis*, and *Q. ilex* in affected sites with warmer Mediterranean climate (Fig. S6), probably favoured these species, thus enhancing higher richness and evenness of largest recruits' category (Batllori et al. 2020). Conversely, *P. sylvestris* recruitment lowered in drier sites

(Fig. S6), also probably due to the reduction of seed cone production under this climatic condition (Clark et al. 2016).

The pattern of higher shrub richness, diversity, and evenness in drier die-off affected sites indicated that, similar to tree layer, several new shrub species occupy the vacant spaces. Specifically, shrub species such as *E. scoparia*, *L. vulgare*, and *Rosa spp.* with Mediterranean distribution tend to occupy the drier sites affected by die-off event. In turn, wetter sites provided favourable condition for *B. sempervirens* – a sub-Mediterranean shrub species that tends to become dominant in the study sites, lowering shrub richness, diversity, and evenness (Fig. S7). Interestingly, our findings about the positive influence of temperature on tree diversity and evenness (i.e., tree species in both canopy and recruiting community) contrasted with the declining of shrub evenness across the temperature gradient, suggesting that warmer sites favour the growth of larger tree recruits into the tree layer, potentially outcompeting shrub species.

Intense drought episodes can drive plant community shifts in forest through the replacement of dead trees of dominant species by recruits of a different species, which eventually become adults (Martínez-Vilalta and Lloret 2016). Interestingly, we observed higher similarity between tree layer and recruiting communities in die-off-affected plots. This could be explained by two co-existing successional processes. First, saplings of shade-tolerant tree species that remained suppressed under the tree layer prior to the drought event eventually incorporated into the canopy layer where the species was previously absent. Second, canopy trees belonging to species other than the dominant *P. sylvestris* got better opportunities for reproduction than in pre-die-off conditions becoming more abundant in the recruiting community. This is supported by the fact that die-off plots exhibited low species turnover between tree layer and recruiting communities, resulting in higher similarity. Conversely, unaffected plots showed lower similarity potentially due to the establishment of shade-tolerant recruits of different species arriving from outside the sampled plots and thriving under a more closed canopy (Selwyn et al. 2024). Overall, these simultaneous processes initiate a new successional trajectory that promotes plant community shift in die-off-induced *P. sylvestris* forests, especially in tree layer. Concomitantly, the available resources and the favourable microclimate produced after tree mortality would assist the germination and growth of new recruits, increasing tree species richness in the understory layer. Specifically, seedlings or resprouts of the shade-tolerant *Q. ilex* and *Q. humilis* may persist in the understorey until canopy opening (Espelta 2004), thanks to its resprouting and drought adaptive capacity (Zeppel et al. 2015). Furthermore, these features provide *Quercus spp.* some competitive advantages over *P. sylvestris* under drought stress conditions (Marañón

et al. 2004; Zeppel et al. 2015) across the studied climatic range, especially in warmer sites (Figs. 3 and 6). Meanwhile, the successional process that we observed in this study is accompanied by a reduced recruitment of *P. sylvestris* in drier-warmer sites (Figs. 3 and 6). In these sites, when experiencing extreme drought, the final regeneration success of *P. sylvestris* is jeopardized by the environmental requirements of juveniles (Galiano et al. 2010), which are stricter than for adults (Jackson et al. 2009). The result is an increase in the dominance of *Quercus spp.* in the study sites, pinpointing the need of protecting recruiting communities (e.g., from potential grazing by livestock), especially in the forest stands where *P. sylvestris* recruitment is vulnerable to climate change.

However, these inferences are subjected to the inherent limitations, including geographical factors, past forest management practices, and soil characteristics, when assessing the complex dynamics of forest ecosystems. Thus, experiments associated to gaps opened after die-off and long-term forest monitoring will be necessary to better understand the consequences of extreme climate events and their associated disturbances on forest composition, and particularly the eventual existence of shifts. Overall, this study on forest stands dominated by *P. sylvestris* highlights the importance of recruiting communities on this process. Also, it shows that local climate conditions combined with structural changes in forest stands due to drought-induced tree mortality and die-off episodes appear to operate as a filter in plant community that is leading to compositional shifting. These processes are expected to be exacerbated under climate change, thus accelerating forest adaption to the new conditions.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10342-025-01790-5>.

Acknowledgements We thank Miriam Selwyn, Raquel Díaz Borrego, Manto S. Kokolaki, Judit Caballé and Javier López for their assistance during field surveys in 2022.

Author contributions F.I.C., J.M.E., and F.L. conceptualized the idea. F.L. and J.M.E. supervised the research. F.I.C. analyzed and visualized the data and drafted the initial version of the manuscript. All authors contributed to the final version of the manuscript.

Funding Open Access Funding provided by Universitat Autònoma de Barcelona. The work was supported by “la Caixa” Foundation (ID 100010434, fellowship code: LCF/BQ/DI21/11860064), Spanish Ministerio de Ciencia e Innovación (PID2020-115264RB-I00), European Union RESONATE project (EH2020; GA: 101000574) and AGAUR, Generalitat de Catalunya (2021 SGR 00849 and SGR 00889).

Data availability Data will be made available on request.

Declarations

Competing interests The authors declare no competing interests.

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