

Climatic resilience to fire of the woody understory in Mediterranean seeder- and resprouter-dominated forests

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ABSTRACT

Fires can reshape Mediterranean forests and landscapes, yet their role in modifying the climatic disequilibrium (CD) of post-fire understory communities, quantified as the difference between species' climatic optimum and the observed climate, remains unclear. We assessed whether wildfires alter the CD of woody understory communities in forests dominated by two Mediterranean tree species with contrasting regeneration strategies: *Pinus halepensis*, a post-fire seeder, and *Quercus ilex*, a resprouter. We used burned plots from the Spanish National Forest Inventory sampled before and after fire, selecting forests clearly dominated by either species and burned once between the two most recent inventories. CD was quantified as the Euclidean distance between observed climate and community-inferred climate. We compared CD before and after fire, assessed changes in woody understory composition, and analyzed the influence on CD changes of fire severity, time since fire, CD peaks, regeneration traits, and forest structure. *Q. ilex* understories showed higher CD than *P. halepensis* understories, and wildfires did not significantly modify understory CD in either forest type, although the mechanisms underlying this stability differed. In *P. halepensis* forests, fire markedly altered understory composition, but post-fire regenerating species had similar climatic preferences. In *Q. ilex* forests, understory composition showed little post-fire variation, reflecting species persistence. Pre-fire climatic conditions were most relevant in explaining understory CD in *P. halepensis* forests, whereas forest structure was the most relevant factor in *Q. ilex* forests. Results suggested that Mediterranean understories are climatically resilient after fire, maintaining CD through compositional persistence or turnover among climatically similar species.

1. Introduction

In Mediterranean regions, wildfires are an integrated element in the dynamics of forest and shrubland plant communities (Bond and Keeley,

2005; He et al., 2019; McLauchlan et al., 2020; Pausas and Keeley, 2019; Pausas and Vallejo, 1999). Wildfires influence the shape and architecture of the landscape (Pausas, 2006) and can promote and accelerate renewal and change in the structure and composition of plant

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communities (Batllori et al., 2019; Traubad, 1994). These fire-driven changes are determined by fire severity and frequency (González-De Vega et al., 2016), climatic factors such as temperature and precipitation variability before and after the fire (Codina et al., 2026; Elvira et al., 2026, 2025, 2021; Ermitão et al., 2024; Viana-Soto et al., 2020), and by the characteristics of the vegetation prior to fire (Arnan et al., 2007; Lloret et al., 2016; Pausas et al., 2004a, 2004b; Puerta-Piñero et al., 2012). The role of species composition and stand structure is particularly relevant in these fire-prone forests, where many species show fire adaptations (Keeley et al., 2011; Tavşanoğlu and Pausas, 2018) that determine their post-fire recovery (Arnan et al., 2007; Lloret and Vilá, 2003; Pausas et al., 2004a, 2004b; Puerta-Piñero et al., 2012). Major plant adaptations for recovery after fire include abundant recruitment by germination, often through the massive release of seeds from serotinous fruits or cones - an ecological adaptation in which plants retain their seeds in protected structures until environmental cues, such as fire, trigger their release - after fire, and resprouting from vegetative structures that can survive burning (Bond and Midgley, 2001; Pausas et al., 2004a, 2004b).

Resprouting species produce new shoots after fire, relying on various types of protected organs, including epicormic buds that allow resprouting from trunks and branches, and buds in the lignotuber that enable resprouting from the base. In these plants, stored carbohydrate and nutrient reserves enhance the growth of new shoots and leaves (Bond and Midgley, 2001; Clarke et al., 2013; Paula et al., 2016; Pausas and Keeley, 2017). This strategy favors the persistence of the individual, as recovery occurs from surviving tissues and does not depend exclusively on the recruitment of new seedlings (Bond and Midgley, 2001; Pausas and Keeley, 2017). In ecosystems of the western Mediterranean basin, this response is very common in sclerophyllous woody species that dominate the later stages of forest succession (Verdú, 2000), and it is particularly representative in the genus *Quercus* and in shrubs or small tree species such as *Pistacia lentiscus* L., *Arbutus unedo* L., *Rhamnus* spp., and *Erica* spp. among others (Tavşanoğlu and Pausas, 2018). In contrast, post-fire seeder species are usually killed by fire, but their aerial or soil seed banks resist, allowing the recovery at the population level (Céspedes et al., 2012; Daskalidou and Thanos, 1996; Enright et al., 2007; Pausas and Lamont, 2022). In some cases, heat or smoke stimulates post-fire germination (Moreira et al., 2010). Many post-fire seeders are characterized by their pioneer nature, with abundant recruitment immediately after fire and generally rapid growth, frequently dominating community composition in the early stages of succession (Verdú, 2000). Some of the most representative seeder species in the western Mediterranean include serotinous pines such as *Pinus halepensis* Mill. and shrubs such as *Salvia rosmarinus* Spenn., *Ulex parviflorus* Pourr. and *Cistus* spp. (Lloret et al., 2003; Pausas and Vallejo, 1999; Santana et al., 2012; Tapias et al., 2001).

In the current context of climate change, intensity and recurrence of fire on plant communities in the Mediterranean basin are expected to increase (Alvarez et al., 2024; Grau-Andrés et al., 2024; Turco et al., 2018), with potential to exceed the species' regeneration capacity by limiting the recovery from seed banks and carbohydrate reserves required for resprouting despite their fire adaptations (Codina et al., 2026; Coop et al., 2020; Le Breton et al., 2022). For obligate-seeder species, vulnerability arises mainly because warmer and drier conditions can lower post-fire population densities, delay reproductive maturity and slow seed production and accumulation, while shorter fire intervals further increase immaturity risk. Together, these processes narrow the range of fire intervals compatible with population persistence, a phenomenon termed "interval squeeze" (Enright et al., 2015). By contrast, the greater persistence of resprouting species may buffer short-term fire impacts but also delay compositional adjustment to climate change, allowing climatic debt to accumulate and potentially impairing ecosystem functioning (Bertrand et al., 2016; Stemkovski et al., 2026), while extreme climatic conditions and their interaction with disturbances may trigger abrupt changes in plant communities

(Serra-Díaz et al., 2018; Williams et al., 2021).

At the same time, ongoing climate trends are altering the climatic suitability patterns of existing plant communities, resulting in an increasing in community climatic disequilibrium (CD) - i.e., the distance in the climatic space between the observed climate and the community inferred climate (the climate inferred from the climatic niche optimum of the species community composition, weighted by species' relative abundances) - (Díaz-Borrego et al., 2024, 2025; Pérez-Navarro et al., 2024a). This disequilibrium translates into poorer species performance and potentially lower resistance to disturbance (Díaz-Borrego et al., 2024; Pérez-Navarro et al., 2021), unless species modify their distribution or adapt to new climatic conditions. On the other hand, some disturbances such as extreme climatic episodes, can act as catalyst, reducing CD by favoring the establishment of species better adapted to the current climate (Pérez-Navarro et al., 2024b, 2021). Wildfires, due to their strong disruptive potential, could affect the CD of plant communities by producing changes in community composition after the burning. However, no studies have examined the effect of fire on community CD.

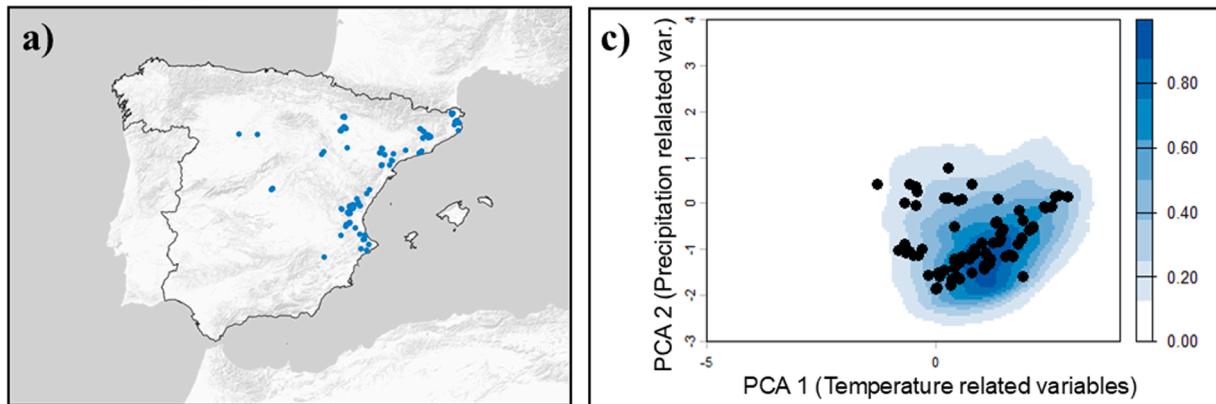
The general objective of this study is to assess the effect of forest fires on the CD of Mediterranean forests. Specifically, we aim to quantify the change in CD of understory communities (only woody species) before and after fire in forests dominated by keystone tree species in the western Mediterranean: *Pinus halepensis* (obligate seeder) and *Quercus ilex* L. (resprouter), which generally differ in their environmental position and successional status. *Pinus halepensis* forests are typical of drier localities and the species is considered as pioneer species in Mediterranean communities, while *Q. ilex* forests are typical of moister localities and are considered a more advanced successional stage (Folch i Guillen, 1981). To understand the variation in CD due to fire, we analyze post-fire changes in the composition of the understory woody plant community and their relationship with increases or decreases in CD. Finally, we examine the role of climate, forest structure and fire characteristics on the differences in CD after and before fire. We hypothesize that (H1) the CD of the understory of burned Mediterranean forests varies between forest types, with lower CD expected in *P. halepensis* forests than in *Q. ilex* forests, as their early-successional and disturbance-prone character may promote stronger climatic filtering of the understory community; (H2) the post-fire regenerative mechanisms of Mediterranean vegetation would allow the maintenance of forest understory CD after wildfire; and (H3) changes in understory CD after fire will be higher under more extreme pre- and post-fire climatic conditions, greater fire severity and lower structural diversity of the stand.

2. Material and methods

2.1. Study area and species

The study area comprises the Mediterranean region of the Iberian Peninsula (Fig. 1), a topographically diverse area with an extensive coastline, inland plateaus and several mountain ranges. The climate is generally characterised by hot, dry summers and cooler, wetter winters, although temperature and rainfall vary considerably across the region due to altitude, continentality and maritime influence (Rivas-Martínez et al., 2017). Geological and edaphic conditions are also heterogeneous, with siliceous and acidic substrates predominating across much of the western Iberian Peninsula, and calcareous and more basic substrates in the eastern Iberian Peninsula (Buira et al., 2021; Loidi, 2017). Specifically, we analyzed forest areas dominated by Aleppo pine (*P. halepensis*) and holm oak (*Q. ilex*). These two forest types are representative of the Iberian Mediterranean region and play a key role in forest successional dynamics and landscape ecology. They also reflect contrasting post-fire regeneration strategies: *P. halepensis* is a pioneer, colonizing species in most Mediterranean forests that establishes after fire from a seed bank remaining in semi-serotinous cones, whereas *Q. ilex* is a later successional and resprouting species, typically

Pinus halepensis



Quercus ilex

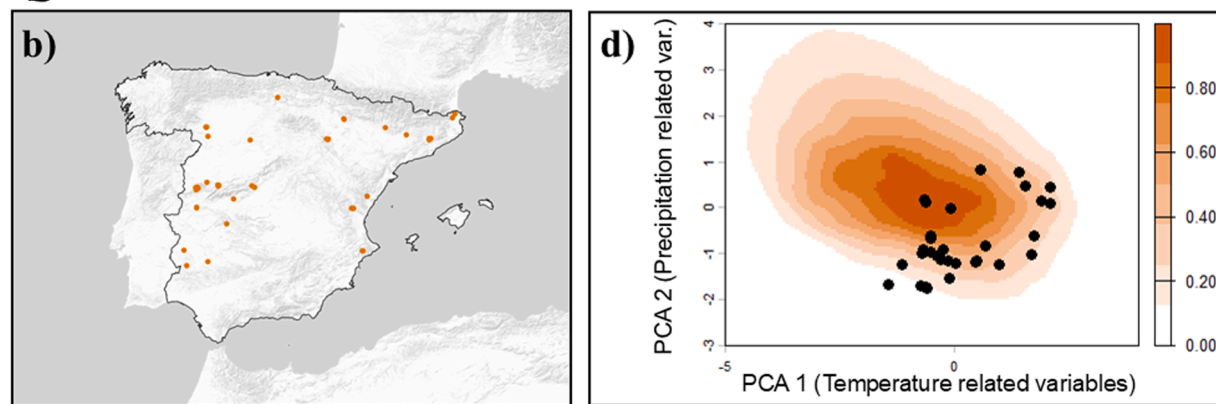


Fig. 1. Study region in the Iberian Peninsula (Spain). a) Location of burned Spanish National Forest Inventory (SNFI) plots dominated by *Pinus halepensis* as the main tree species (blue dots). b) Location of burned SNFI plots dominated by *Quercus ilex* as the main tree species (orange dots). For each species, the shaded areas (right panels) represent the climatic niche inferred from their European distribution range; points indicate the position of the studied plots within each species' climatic niche (c-d). Blue shading corresponds to *P. halepensis* and orange shading to *Q. ilex*. In the right subplots, the X-axis (PCA1) represents climate variables related to temperature and the Y-axis (PCA2) variables related to precipitation; positive values indicate higher temperature or precipitation values, and negative values indicate lower ones. A detailed description of niche calculation is provided in [Section 2.4.2 Climatic niche characterization](#).

associated with more mature forests ([Lookingbill and Zavala, 2000](#)).

We studied permanent plots from the Spanish National Forest Inventory (SNFI) located in peninsular Spain that were affected by wildfires between the two most recent available inventory cycles (SNFI3 and SNFI4) (IFN3; [Ministerio de Medio Ambiente, 2007](#); IFN4; [Ministerio para la Transición Ecológica y el Reto Demográfico, 2024](#)). The region of Andalusia was excluded because complete SNFI4 information was not available at the time of the study. Despite belonging to the same Mediterranean climatic region of the Iberian Peninsula, marked differences in climate and vegetation occur across the study area, determining the distribution of the studied forests. Forests dominated by *P. halepensis* ([Fig. 1A](#)) are mainly located within the dry mesomediterranean and thermomediterranean bioclimate ([Rivas-Martínez et al., 2017](#)). In contrast, *Q. ilex* forests ([Fig. 1B](#)) show a broader distribution: those in the eastern half of the Iberian Peninsula correspond mainly to the dry mesomediterranean bioclimate, whereas western holm oak forests occur within dry and subhumid mesomediterranean and supramediterranean bioclimate.

The differences in dominant tree species and their distribution along the bioclimatic gradient concur with the composition of the understory community. In general, *P. halepensis* forests tend to have more open canopies than *Q. ilex* forests, which allow greater exposure and light availability in the understory. In the studied SNFI *P. halepensis* forests, the understory community is mainly composed of *P. halepensis* saplings and shrub species such as *Salvia rosmarinus*, *Quercus coccifera* L., and

Juniperus oxycedrus L. ([Table S1](#)). The SNFI *Q. ilex* forests included in this study correspond to sites characterized by relatively dry and/or warmer conditions of their climatic niche ([Fig. 1](#)), as reflected by the presence of *Cistus* spp., *S. rosmarinus* or *Lavandula stoechas* L. ([Table S2](#)), which are commonly associated with open, early-successional stages in Mediterranean ecosystems ([Santana et al., 2011, 2012a; Siles et al., 2008](#)). Specifically, the eastern *Q. ilex* forests show an understory composition similar to pine forests, dominated by shrubs such as *Q. coccifera*, *S. rosmarinus*, *Genista scorpius*, and *Q. ilex* saplings ([Table S3](#)). In contrast, western holm oak forests are characterized by understories dominated by *Cistus ladanifer* L. and *Lavandula stoechas*, together with *Q. ilex* regeneration ([Table S4](#)). This difference reflects the greater presence of siliceous and acidic soils in the western part of the Iberian Peninsula, which favor acidophilous understory shrub communities ([Quinto Canas et al., 2021](#)).

2.2. Forest understory data

We used data from the two most recent editions of the SNFI corresponding to the sampling periods of the study areas (IFN3; [Ministerio de Medio Ambiente, 2007](#); IFN4; [Ministerio para la Transición Ecológica y el Reto Demográfico, 2024](#)), processed using the *forestables* R package ([Tovar et al., 2024](#)). Surveys of the SNFI are performed using permanent circular plots positioned at the intersections of a 1×1 km² UTM grid covering all forested areas of the study region. Each SNFI circular plot

encompasses four concentric variable-radius subplots from 5 to 25 m radius, wherein trees are inventoried based on their species identity and size characteristics. For this study, to define forest type, SNFI data on tree species identity and diameter at breast height (DBH) were considered for every living tree with a DBH > 7.5 cm within each plot. We selected plots with a distinct dominance of one of the two target species in the tree layer, defined as at least 70% of relative abundance in terms of basal area. In addition, for forests dominated by *P. halepensis* in the tree layer, we applied a second filter to exclude plots in which the abundance of *Q. ilex* regeneration exceeded the combined abundance of *P. halepensis* regeneration and adult pine trees, as these plots are likely to represent pine stands currently undergoing transition towards *Q. ilex* forests. Such pine–oak transitions reflect forest succession and historical changes in land use and management, with *Q. ilex* establishing beneath pine canopies and progressively limiting pine regeneration (Carnicer et al., 2014; Guirado et al., 2008; Navarro-González et al., 2013; Sheffer, 2012). Regeneration was defined according to the SNFI criteria as live individuals recorded in the regeneration layer, ranging from seedlings shorter than 30 cm to saplings taller than 130 cm with a normal diameter below 7.5 cm.

After this filtering procedure, we retained only those plots that had been burned only once between the SNFI3 and SNFI4 inventories, to ensure that the observed response was not driven by fire frequency and to better isolate the effect of climate, and with a minimum interval of four years between the fire event and the SNFI4 resampling, to allow sufficient time for initial post-fire vegetation recovery. Fire occurrence was determined using a georeferenced wildfire database for the period 1985–2018 obtained from Álvarez et al. (Álvarez et al., 2024). Following these criteria, we selected a total of 80 plots dominated by *P. halepensis* and 35 plots dominated by *Q. ilex*.

To characterize the composition of the woody understory community before and after fire, we used SNFI data on cover and abundance of shrub species and regeneration of tree species (IFN3; Ministerio de Medio Ambiente, 2007; IFN4; Ministerio para la Transición Ecológica y el Reto Demográfico, 2024). Woody shrub species were surveyed within fixed 10-m-radius subplots, where the projected cover of each species was independently estimated as a percentage of the sampled area. Tree regeneration was surveyed within fixed 5-m-radius subplots. To allow comparison between shrub species and tree regeneration and to estimate total understory cover, we converted tree seedling and sampling abundance into cover values using the allometric equations (De Cáceres et al., 2019) that produced projected crown area as a percentage of the 5-m-radius subplot. Thus, both shrub and tree-regeneration data were expressed as species-level percentage cover before being combined. Total understory cover was calculated as the sum of species-level cover values and could therefore exceed 100% (or 1 when expressed as a proportion), because species may overlap vertically and occupy different vegetation layers.

Across all selected plots, the understory community comprised a total of 108 species. To reduce model complexity and increase the representativeness of the data, we excluded rare species occurring in less than 5% of plots, resulting in a final dataset of 34 woody species. Of these, 32 species were present in *P. halepensis* forests (Table S1) and 30 in *Q. ilex* forests (24 in eastern holm oak forests and 13 in western holm oak forests; Table S2–S4). Eastern and western *Q. ilex* plots were classified according to their longitudinal position, using the longitude of the boundary plot separating both geographic subsets as the threshold (3.44° W).

Functional trait data related to post-fire regeneration strategies, including resprouting ability (RespFire) and seedling establishment ability (Seedl), were obtained for each understory woody species from BROT, a plant trait database for Mediterranean Basin species (Tavşanoğlu and Pausas, 2018).

2.3. Fire data

Fire severity was calculated from Landsat-based fire severity maps using the Google Earth Engine (GEE) platform following Parks et al. (2018). As described in Álvarez et al. (2024), we applied the relativized delta normalized burn ratio (RdNBR) (Miller and Thode, 2007), that analyzes the vegetation state before and after fire with satellite images, using the mean compositing approach, where all cloud-free pixels from September to October for the year previous to the fire and the year of the fire are stacked, and the mean value for each pixel over the stack is used to compute fire severity. When September–October images were not available, we expanded the period to November. We used RdNBR because it incorporates pre-fire vegetation characteristics through the use of pre-fire NBR values, and is not too sensitive to spatial variation in vegetation type, structure, and canopy cover, an essential property for heterogeneous Mediterranean landscapes (Botella-Martínez and Fernández-Manso, 2017; Miller and Thode, 2007; Parks et al., 2014).

The rest of the fire variables considered here are fire ID and years between fire and SNFI, calculated from the fire year and the SNFI3 and SNFI4 sampling year, as provided by the SNFI database (Ministerio para la Transición Ecológica y el Reto Demográfico, 2024).

2.4. Climatic disequilibrium

2.4.1. Climatic and species occurrence data

To characterize the climatic niche of the 34 woody species present in the understory of the *P. halepensis* and *Q. ilex* burned plots (including the two dominant species), we used their European geographic distribution and the inter-annual climatic variability extracted from their spatial locations. We restricted species occurrences to Europe, the native distribution region of both species, thus ensure environmental and genetic consistency with Spanish populations, and matching the spatial extent of the European climatic data used, as described below. Species occurrence data were collected from GBIF (Global Biodiversity Information Facility, 2025; Supplementary Material 2. GBIF occurrence download references), using exclusively human observation records located in Europe, with valid geographic coordinates and no reported geospatial errors. To reduce sampling bias associated with spatial clustering and uneven sampling effort, we retained only one occurrence per 1 km² grid cell. GBIF records were downloaded with R using the *rgbif* package (Chamberlain et al., 2024).

Climatic data were obtained from *Easyclimate: Easy access to high-resolution daily, monthly and annual climate data for Europe* (Cruz-Alonso et al., 2023; Moreno and Hasenauer, 2016; Pucher, 2023). Using precipitation, minimum temperature, and maximum temperature data at 1 km² spatial resolution for the period 1980–2022, we derived the following bioclimatic variables: bio1 (mean annual air temperature), bio4 (temperature seasonality), bio5 (mean daily maximum air temperature of the warmest month), bio6 (mean daily minimum air temperature of the coldest month), bio10 (mean daily mean air temperatures of the warmest quarter), bio11 (mean daily mean air temperatures of the coldest quarter), bio12 (annual precipitation amount), bio13 (precipitation amount of the wettest month), bio14 (precipitation amount of the driest month), bio15 (precipitation seasonality), bio16 (mean monthly precipitation amount of the wettest quarter) and bio17 (mean monthly precipitation amount of the driest quarter). We selected these 12 bioclimatic variables, rather than the full set of 19 commonly used, to avoid those that include implicit relationships between temperature and precipitation (Pérez-Navarro et al., 2024b).

For each location of the species' occurrence datasets, we extracted yearly climate values from 1980 to 2022, rather than using average values for the entire period, to incorporate the inter-annual variability in the environmental conditions experienced by the species (Pérez-Navarro et al., 2021).

2.4.2. Climatic niche characterization

We performed Principal Component Analysis (PCA), using the yearly climate data for each geographic occurrence of the 34 species considered here, to transform the environmental data encompassing the 12 bioclimatic variables into a standardized two-dimensional climatic space, defined by the first and second principal components (PCA1 and PCA2, respectively) covering the environmental range of all species. The PCA was performed using the *ade4* R package (Dray and Dufour, 2007). Together, the first and second principal components explained 74.7% of the variability of the original variables, with the first axis (49.4%) mostly representing temperature-aridity related variables and the second axis (25.3%) representing precipitation-thermal seasonality related variables (Figure S1, Table S5).

To characterize the climatic niche of each species included in our analyses, we calculated the density of their occurrences within the PCA climatic space using kernel density functions (Broennimann et al., 2012; Chacón and Duong, 2018), with optimal bandwidth selected by cross-validation (Duong and Hazelton, 2005). Kernel density analyses were performed using the *ks* R package (Duong, 2007). Then, we estimated the position of the niche core or optimum, defined as the center of gravity of the species niche (assuming that it is the point with the highest density of occurrences), and of the climatic niche edge or limit, set at the 0.05 lowest percentile of occurrences density (Perez-Navarro et al., 2022).

2.4.3. Climatic disequilibrium

Using the computed climatic niches, we quantified the climatic disequilibrium (CD) of the understory communities, defined as the difference between the climate inferred from the community composition (CIC) and the observed climate (OC). The CIC was calculated as the average of the coordinates (in PCA space) of all the species' climatic optimum present in each plot, weighted by species' relative abundance within the plot in terms of plant cover. CIC values were computed separately for pre-fire and post-fire understory communities.

Observed climate (OC) was calculated as the mean PCA values computed on the basis of the 12 bioclimatic values recorded at each study plot for the reference study period. Specifically, we estimated the OC for two different time windows: 1) over the 10 years preceding the fire (pre-fire OC) and 2) the years between the fire event and the SNFI4 resampling in each site (post-fire OC). Community climatic disequilibrium (CD) was then quantified as the Euclidean distance between the pre- and post-fire OC of each plot and the corresponding species centroid or community-inferred climate (CIC), following Blonder et al. (Blonder et al., 2015).

CD was calculated based on OC mean conditions considering climate both before and after fire, as historical climatic conditions during a given period are likely to determine the composition of plant communities shown to be more related to historical climatic conditions during mid-term periods rather than single years (Díaz-Borrego et al., 2025; Pérez-Navarro et al., 2024b). Community-level CD can therefore be interpreted as an indicator of climatic suitability at the plot level (Díaz-Borrego et al., 2025), with higher CD values indicating a stronger mismatch between the climate inferred from understory species composition and the actual climatic conditions of the plot. Nonetheless, to assess the influence of potential extreme conditions (Batllori et al., 2019), we also calculated disequilibrium peaks (maximum CD values) in the three years immediately before and after the fire event. In this case, OC was calculated using annual bioclimatic values, and CD was computed for each individual year. The disequilibrium peak was then defined as the maximum CD value observed during the three years preceding the fire and during the three years following the fire in each plot.

2.5. Statistical analysis

To assess changes in woody species composition of the understory,

we analyzed differences in community composition based on species relative abundances between pre-fire and post-fire periods. These analyses were performed using PERMANOVA with Bray–Curtis dissimilarity, implemented with the *vegan* R package (Oksanen et al., 2024), applying plot-restricted permutations to account for the paired design (i.e. the same plot sampled at two time points). To aid interpretation of understory compositional changes, a similarity percentage analysis (Clarke, 1993) was used to identify species contributing most to the observed dissimilarity between periods. In addition, for each species, differences in relative abundance between pre-fire and post-fire conditions across plots were tested using non-parametric Wilcoxon tests. We applied the same procedure to assess differences in understory composition in those plots where climatic disequilibrium increased or decreased after fire.

To evaluate differences in the climatic disequilibrium (CD) of the understory communities before and after fire, and among forest types, we used non-parametric Wilcoxon tests. Parametric alternatives were not used because the normality assumption was not met in all groups (Shapiro–Wilk tests, $p < 0.05$ for at least one group), indicating deviations from normality in CD distributions. These analyses were conducted for all plots combined and separately for *P. halepensis* and *Q. ilex* forests.

To identify the main factors explaining post-fire changes in the climatic disequilibrium of the woody understory community, we used as response variable CDdiff, defined as the difference in climatic disequilibrium between post-fire and pre-fire understory communities ($\text{CDdiff} = \text{CD}_{\text{post}} - \text{CD}_{\text{pre}}$). Therefore, positive CDdiff values indicated an increase in climatic disequilibrium after fire, whereas negative values indicated a decrease. Values equal or close to zero indicated little or no net change in CD. Because no ecologically validated threshold was available to distinguish marginal from substantial changes in CD, we used the lower and upper tertiles (33th and 67th percentile, respectively) of the CDdiff distribution, calculated separately within each forest type, to identify plots showing the largest decreases and increases in CD, respectively.

We explored linear mixed-effects models (LMMs) to assess relationships between CDdiff (response variable) and a set of candidate variables based on our hypotheses: fire severity (RdNBR), time since fire, climatic disequilibrium peaks before and after fire, resprouting ability (RespFire), seedling establishment ability (Seedl), and tree cover before and after fire. Because some plots could be associated with the same fire event, models included fire ID as a random intercept. Models were explored separately for each forest type and were evaluated both with and without interaction terms. Final model selection for each forest type was refined through a stepwise selection procedure using Akaike's Information Criterion (AIC) and marginal and conditional R^2 values (Table S6–7).

All statistical analyses were performed using R version 4.2.2 (R Core Team, 2022).

3. Results

Overall, species richness and total understory cover remained relatively stable between the assessed pre- and post-fire periods regardless of forest type. In *P. halepensis* forests, total species richness slightly decreased after fire (from 31 to 29 species), while total cover (scaled to 1) remained similar (1.06–1.07) (Table S1). In *Q. ilex* forests, total species richness increased after fire (from 23 to 28 species), whereas total cover showed only minor changes (0.97–1.00) (Table S2). Similar patterns were observed when eastern and western *Q. ilex* forests were analyzed separately, with modest increases in species richness after fire and relatively stable understory cover (Table S3–S4). The relative contribution of resprouter and seeder species also showed limited variation between pre- and post-fire communities. However, resprouter species tended to dominate the understory cover in *Q. ilex* forests, while both regeneration groups contributed similarly in *P. halepensis* forests

(Table S8).

Clear differences were detected in CD values between forest types both before (Wilcoxon rank-sum test: $W = 637$, $p < 0.001$) and after fire ($W = 881$, $p < 0.01$), with understory communities in *Q. ilex* forests showing consistently and significantly higher CD values (mean CD ranging from 1.63 ± 0.73 SD to 1.33 ± 0.56 SD, before and after fire, respectively) than those in forests dominated by *P. halepensis* (mean CD ranging from 0.94 ± 0.61 SD to 0.96 ± 0.46 SD before and after fire, respectively) (Table S8). Overall, wildfires did not significantly alter the climatic disequilibrium of woody understory communities in either forest type (Fig. 2; Fig. 3, Figure S3), as CD values did not differ significantly between pre- and post-fire conditions in *P. halepensis* forests (paired Wilcoxon signed-rank test: $V = 1735$, $p = 0.583$) or in *Q. ilex* forests ($V = 208$, $p = 0.081$) – though in *Q. ilex*, there was a marginal trend toward decreasing CD after fire.

Despite the overall stability in CD after fire, significant compositional changes in the understory community were detected in *P. halepensis* forests using PERMANOVA, based on Bray–Curtis dissimilarity with permutations restricted by plot ($R^2 = 0.04$, pseudo- $F_{1,170} = 6.9$, $p < 0.001$), both at the community level and in the relative abundance of individual species (Fig. 4). Additionally, compositional shifts occurred both in plots where CD decreased, characterized by significant increases in *G. scorpius*, as well as in plots where CD increased, characterized by significant increases in *U. parviflorus* and decreases in *J. oxycedrus*, *J. phoenicea*, and *P. lentiscus* (Fig. 4, Figure S4).

In contrast, the woody understory communities in *Q. ilex* forests did

not show significant compositional changes (Fig. 4). Likewise, no significant changes were detected when eastern and western holm oak forests were analyzed separately (Figures S4, S8).

Explanatory models indicated that post-fire changes in the climatic disequilibrium (CD_diff) of the woody understory communities were driven by different sets of variables in *P. halepensis* and *Q. ilex* forests (Fig. 5). In *P. halepensis* forests, understory CD_diff was mainly explained by climatic conditions before fire, specifically pre-fire climatic disequilibrium peaks (CD_pre_peak) and the number of years since fire (Fig. 5A). Pre-fire climatic disequilibrium peaks and year since fire showed a significant and negative relationship with CD_diff ($p = 0.0001$ and $p = 0.0048$, respectively) (Table S6). Other explanatory variables showed significant effects in univariate models (Table S9), including post-fire climatic disequilibrium peaks ($p = 0.0251$) and *Q. ilex* tree cover before fire ($p = 0.0159$), but these effects were not retained in the final multivariate models (Fig. 5A). In the understory communities of *Q. ilex* forests, CD_diff was primarily explained by post-fire *Q. ilex* tree cover (Fig. 5B), showing a significant positive relationship with CD_diff ($p = 0.0284$) (Table S7). In these forests, no significant effects were detected for any variable in the univariate models (Table S10).

4. Discussion

Despite the disruptive nature of fire on vegetation structure and composition (Broncano et al., 2005; Gelabert et al., 2020; Ortega et al., 2025), fires did not significantly change the degree of climatic

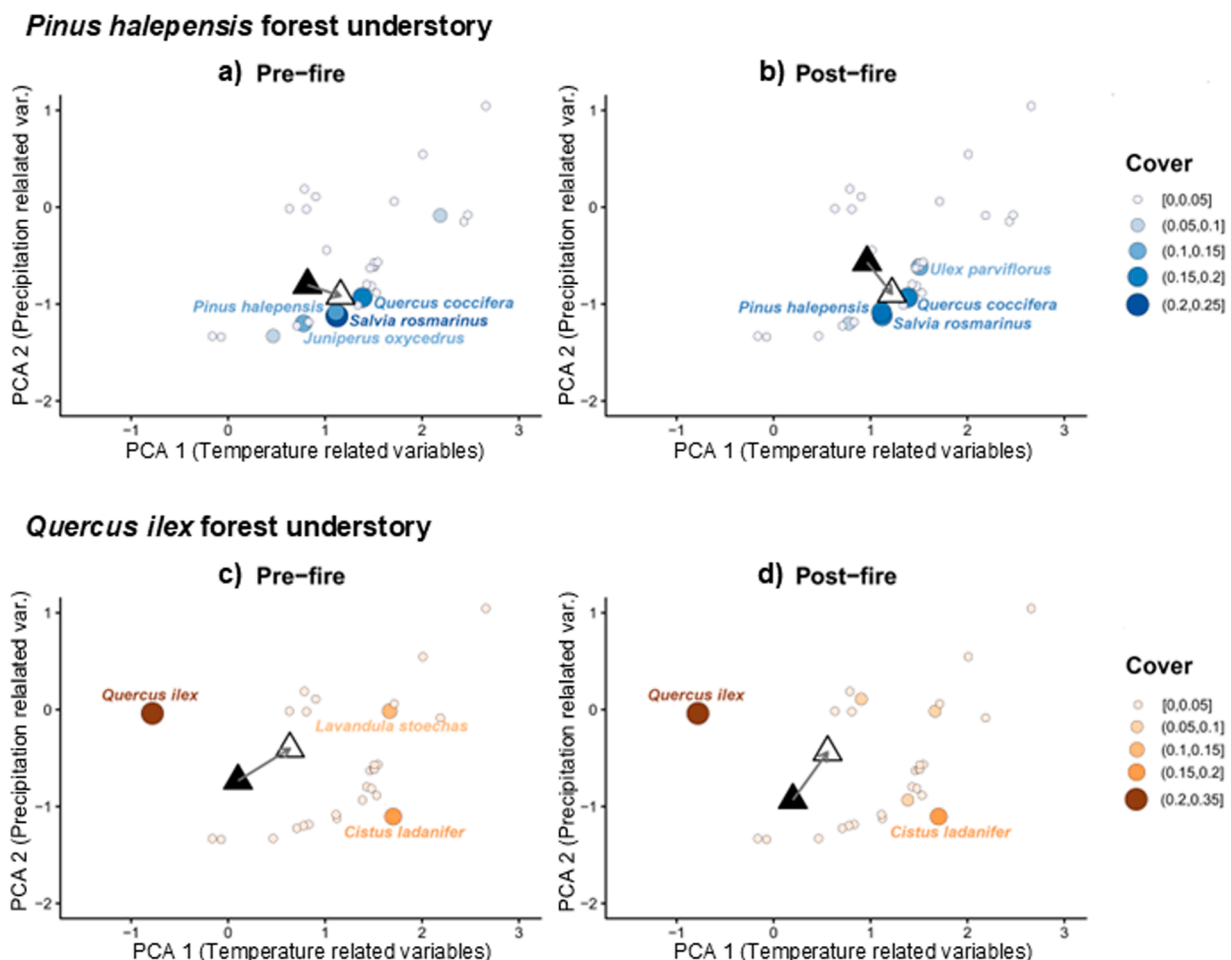


Fig. 2. Climatic space of understory communities in forests dominated by *Pinus halepensis* before (a) and after fire (b), and *Quercus ilex* before (c) and after fire (d). White triangle represents the mean community inferred climate (CIC) and black triangle represents the mean observed climate (OC) across study plots. The connecting segment represents the mean climatic disequilibrium (CD), calculated as the Euclidean distance between OC and CIC. Species centroids are represented by dots, with symbol size and color weighted according to mean cover across the study plots. The species names shown are those with abundances exceeding 10%.

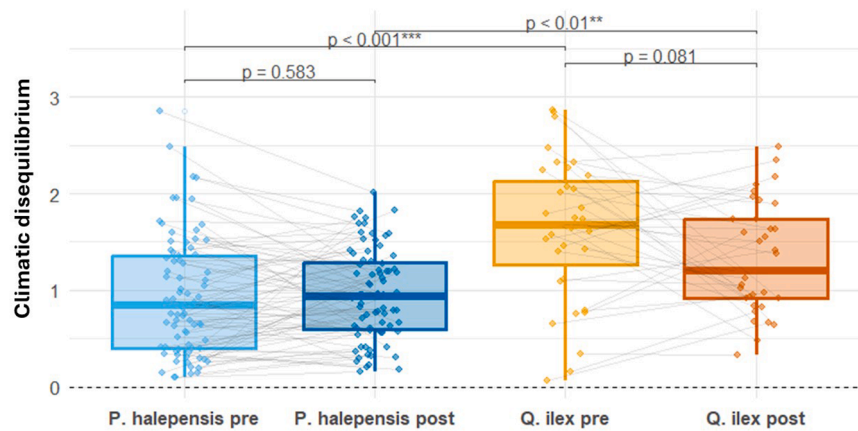


Fig. 3. Community climatic disequilibrium (CD) values in forests dominated by *Pinus halepensis* (blue boxes) and *Quercus ilex* (orange boxes) before (pre) and after (post) fires. Boxplots show the distribution of CD values across plots for each forest type and period; points represent individual plots. The horizontal dashed line indicates CD = 0. Differences between pre- and post-fire periods within each forest type, as well as differences between forest types, were tested using non-parametric Wilcoxon tests; corresponding p-values are shown above the boxplots.

disequilibrium (CD) of the woody understory communities in Mediterranean forests dominated by *Pinus halepensis* and *Quercus ilex* (Fig. 3). This stability resulted either from small compositional changes in the post-fire understory community or, when composition changed, through replacement by climatically similar species (i.e., with similar climatic optimum; Fig. 2). In both cases, this is an example of climatic resilience, meaning that the community maintains or recovers its climatic characteristics after a disturbance, regardless of the taxonomic identity of the species (Díaz-Borrego et al., 2025).

In forests dominated by *P. halepensis*, there were changes in the composition of the woody understory community after fire (Fig. 2A; Fig. 4; Table S1), as reported elsewhere (González-De Vega et al., 2018; Moya et al., 2020; Ricci et al., 2024). As such, fire acts as a species filter and resets forests to early successional stages or implies changes to other plant communities (Baudena et al., 2020; Capitano and Carcaillet, 2008; Codina et al., 2026; Lloret and Zedler, 2009). Compositional changes within the study plots were mainly due to an increase in *Ulex parviflorus* (Figs. 2, 4, Table S1), which is a very successful post-fire seeder (De Luis et al., 2005; Santana et al., 2012) and a decrease in *Juniperus oxycedrus* (Figs. 2, 4, Table S1), which is considered a post-fire resprouter (Arianoutsou et al., 2012; López-Soria and Castell, 1992; Pausas et al., 2008) but that exhibited poor post-fire recovery in our study locations (Fig. 4). However, species' compositional changes did not translate into a variation in CD (Fig. 3). This situation suggests that, although fire causes floristic changes, these changes can be compensated in climatic terms if the species that increase after fire have a climatic optimum similar to that of the species that decrease. This phenomenon is understood even better if we observe the variation of Observed Climate (OC) and Community Inferred Climate (CIC) in the climatic space before and after fire. After fire, changes in composition and variation in OC occur, but CIC practically does not shift since the climatic optimum (centroid) of the new species that becomes incorporated in the understory is very close to that of the species that were present before the fire (Fig. 2). This turn-over of climatically redundant understory species can be comparable to the behavior of functional redundancy (Pillar et al., 2013; Rosenfeld, 2002) and to response diversity (Elmqvist et al., 2003; Mori et al., 2013), as species replacement can maintain community-level properties despite changes in species composition following disturbance. In summary, the climatic resilience observed in the understory of forests dominated by *P. halepensis* (i.e., stable CD) appears to result from the fact that, although fire alters the abundance and species composition of the woody plant community, these species occupy similar climatic spaces, with equivalent climatic niches and optima (Fig. 2A).

In forests dominated by *Q. ilex*, the understory dynamics are different: the composition of the woody understory community

practically does not change after fire, in agreement with the resilient behaviour of this vegetation type after fire (Lloret and Zedler, 2009). Therefore, CD did not significantly change, in spite a trend to diminish (Fig. 2B, Fig. 4, Table S2). This pattern is consistent with the strong resprouting capacity and persistence of *Q. ilex*, whose post-fire recovery is largely based on survival of the root system, resprouting, and gradual recovery of the canopy cover (Clarke et al., 2013; Parra and Hinojosa, 2023; Pausas et al., 2016; Pausas and Keeley, 2014). Specifically, this recovery operates through two complementary mechanisms driven by *Q. ilex* (the dominant species): a direct vegetative response through vigorous resprouting, and an indirect structural effect as the recovering canopy re-establishes a shaded understory microclimate (i.e., conditioning the growing environment), thereby favoring its own persistence and preventing the establishment and turnover of shade-intolerant or open-habitat species. Similar conditioning effects by dominant post-fire canopy formers on both the growing environment and species composition have been described in other fire-prone forest ecosystems (Harvey and Holzman, 2014; Romme et al., 2016). As a result, the understory dominated by *Q. ilex* returned more easily to the pre-fire compositional state (Broncano et al., 2005; Rodrigo et al., 2004). Although the dominant species, *Q. ilex*, plays a clear role in climatic resilience through its post-fire resprouting capacity, it is not the only driver of this stability, as coexisting thermophilous understory species, particularly pioneer seeders as *Cistus ladanifer*, also recover well after fire (Figs. 2–3) (Ulm et al., 2026). Similarly to *P. halepensis* forests, the CD of the woody understory in *Q. ilex* forests remained stable by maintaining CIC practically static despite variation in OC (Fig. 2B). In fact, the trend to diminishing CD could be explained by a slight change in OC during the post-fire period.

To understand the dynamics of forests dominated by *Q. ilex*, it is important to consider that the forests burned during the study period correspond to sites where *Q. ilex* experiences the driest and warmest conditions of its climatic niche (Fig. 1). Despite its current persistence and vigorous post-fire recovery, these marginal *Q. ilex* forests may increasingly lag its adjustment to ongoing climate change, accumulating climatic debt and potentially compromising future ecosystem functioning (Bertrand et al., 2016; Stemkovski et al., 2026). These climatic conditions likely have an influence on the composition of the understory of the studied forests (Moreno-Fernández et al., 2021; Salazar Zarzosa et al., 2024), which are mainly dominated by thermophilous shrub species. In eastern areas, these forests resemble typical dry mesomediterranean holm oak forests, with understories dominated by species such as *Q. coccifera*, *S. rosmarinus*, and *G. scorpius* (Table S3; Figure S4) (Castro Díez, 1996; Rodà et al., 2009), whereas in more western areas they correspond to continental holm oak forest 'carrascal' with a

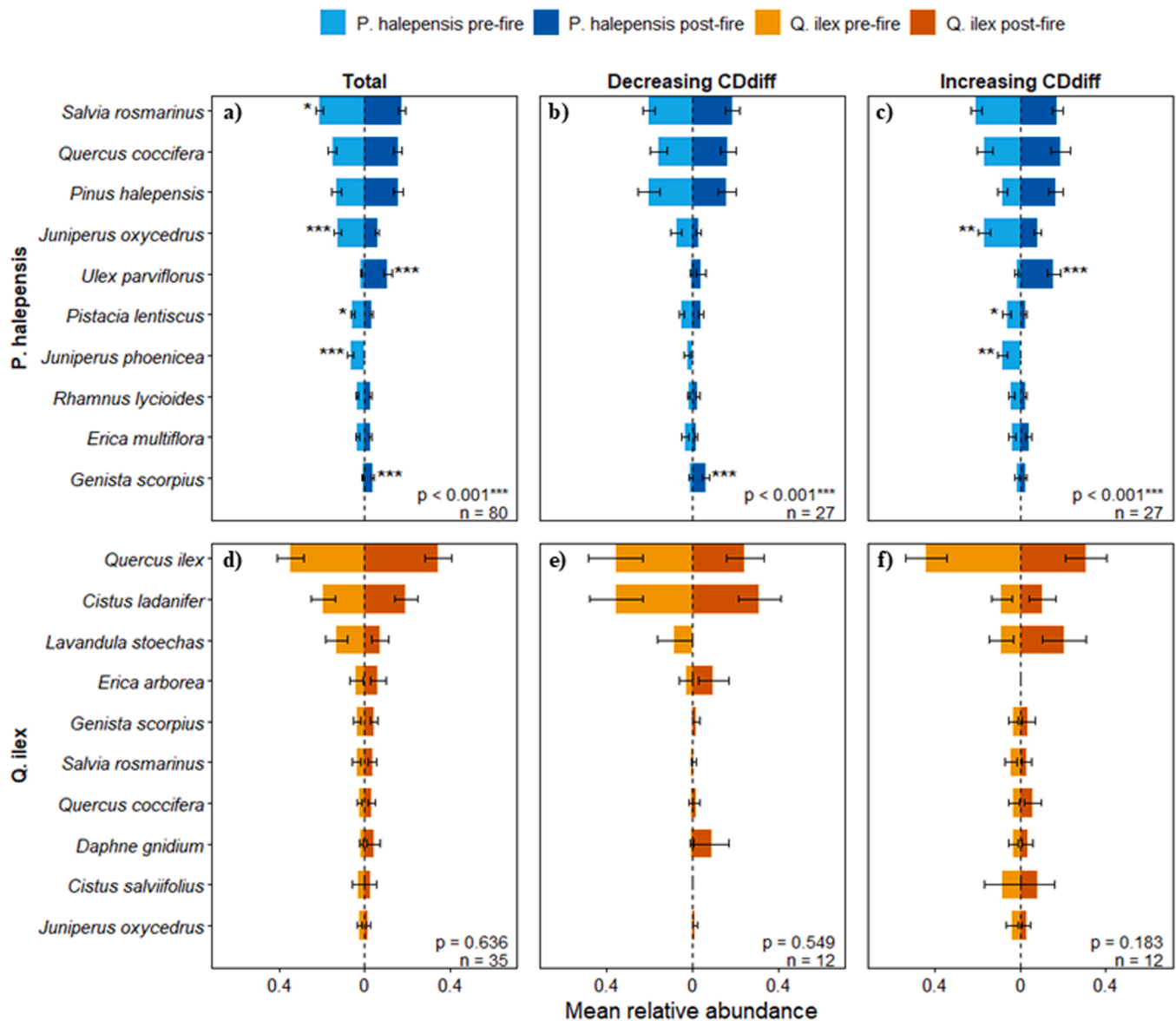


Fig. 4. Mean relative abundance of the species that contribute most to the understory community in forests dominated by *Pinus halepensis* (upper panels) and *Quercus ilex* (lower panels), before (left; pre-fire) and after (right; post-fire) fire. Across all plots, the species displayed accounted for 78.9–87.6% of the total understory cover, depending on forest type and fire period. Results are shown across all plots (Total) (a-d) and for plots classified as Decreasing CDdiff (lower tertile of the CDdiff) (b-e) and Increasing CDdiff (upper tertile of the CDdiff) (c-f). Changes in community composition between pre- and post-fire periods were assessed using PERMANOVA (Bray–Curtis dissimilarity) with permutations restricted by plot; the global p-value is shown in the lower right corner of each panel. For each species, pre- versus post-fire differences were tested using a non-parametric Wilcoxon test; asterisks next to species indicate the level of statistical significance, when present.

predominance of *C. ladanifer* and *L. stoechas* (Table S4; Figure S8) (Quinto Canas et al., 2021; Rodà et al., 2009; Salazar Zarzosa et al., 2024). These forests greatly differ from *Q. ilex* forests growing under more optimal (cooler and more humid) climatic conditions, which typically develop into denser stands with understories dominated by late successional species such as *Viburnum tinus* and *Arbutus unedo*, with little or no presence of thermophilous shrubs (Barbero et al., 1992; Terradas, 1999).

Although CD did not overall vary after fire in either forest type, some plots showed increases in CD whereas others showed decreases (Fig. 3). In *P. halepensis* understory forest community, post-fire changes in CD (CDdiff) were strongly influenced by pre-fire climatic conditions. Specifically, pre-fire peaks in climatic disequilibrium were negatively related to CDdiff and were the primary factor explaining changes in CD after fire (Fig. 5A). Because pre-fire community composition was characterized using data from SNFI3 and held constant over this period,

variations in pre-fire CD peaks reflect short-term climatic adversity for the established community rather than compositional turnover. This suggests that pre-fire adverse climatic conditions, in combination with fire, influence understory compositional change (Codina et al., 2026; Elvira et al., 2026, 2021), reducing post-fire climatic disequilibrium by favoring understory communities more aligned with the post-fire observed climate (Batllori et al., 2019; Díaz-Borrego et al., 2025; Pérez-Navarro et al., 2021).

In contrast, in forests dominated by *Q. ilex*, variation in CD, was mainly associated with forest structure, particularly post-fire *Q. ilex* tree cover (Fig. 5B). This relationship may be ecologically meaningful only in those locations where CD is primarily driven by *Q. ilex* regeneration, given its ability to resprout and persist under milder microclimatic conditions provided by the canopy (Zellweger et al., 2020). In contrast, in locations where thermophilous and heliophilous understory species (e.g., *Cistus* spp., *Lavandula* spp.) are more abundant, the effect of *Q. ilex*

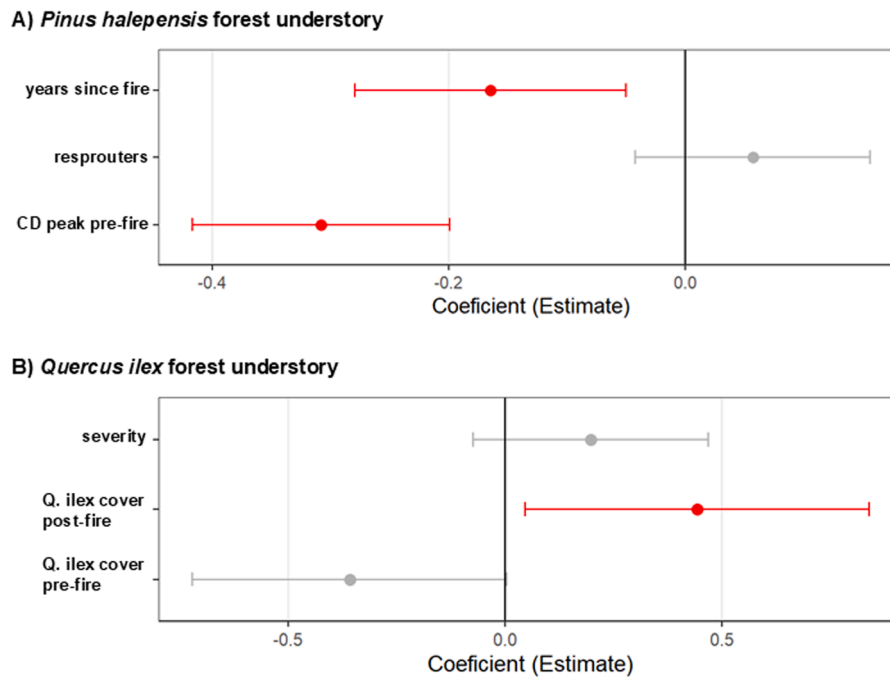


Fig. 5. Estimated coefficients ($\pm$ 95% CI) of the linear model relating climatic disequilibrium (CD_diff) to climatic variables (pre-fire disequilibrium peak = CD_pre_peak, post-fire disequilibrium peak = CD_post_peak, and their interactions), fire-related variables (years since fire, fire severity), forest tree cover (*Q. ilex* tree cover), and relative abundance of species with post-fire resprouting ability (resprouters), for the two understory types studied: those in forests dominated by *P. halepensis* (A) and those in forests dominated by *Q. ilex* (B). Coefficients shown in red correspond to significant effects ($p < 0.05$).

canopy on CD should be weaker, as these species tend to regenerate more successfully under open post-fire conditions (Aguayo-Villalba et al., 2021; Ghaderi-Far et al., 2021). Note, however, that our climate characterisation was based on mesoclimate data and, therefore, may not fully represent the small-scale temperature and humidity conditions experienced by understorey plants (De Frenne et al., 2021; Lembrechts et al., 2019). Future studies incorporating microclimatic measurements at plot level could determine whether the microclimatic buffering effect driven by the canopy moderates the changes in CD and understorey composition caused by fire.

The understory of forests dominated by *P. halepensis* presented lower CD (closer to climatic equilibrium) than the understory of forests dominated by *Q. ilex*, which shows considerably higher CD (Fig. 3, Figure S3), in both pre- and post-fire situations. The lower CD of *P. halepensis* understories likely reflects the dominance of opportunistic post-fire seeders and early-successional species that establish rapidly after disturbance (Table S8; Fig. 2A) (Buhk and Hensen, 2006), making community composition more closely aligned with present-day climatic conditions (Parra and Moreno, 2018, 2017). In contrast, the mechanisms underlying the higher CD observed in *Q. ilex* forests are more complex and seem largely determined by the fact that the burned forests are located in the driest and warmest portion of *Q. ilex* climatic niche (Fig. 1B). Under these conditions, the understory of these forests is mainly composed of *Q. ilex* regeneration and thermophilous shrub species – which live under relatively cooler or moister conditions than their optimum –, and, thus, both the dominant tree and the woody understory exhibit climatic optima (climatic niche centroids) far from the observed climate (OC) (Fig. 2B; Fig. 3). Within the post-fire period covered by our study, these contrasting responses can also be interpreted as different pathways of forest reorganization, including structural and compositional changes following fire (Seidl and Turner, 2022). The recovery of the dominant tree species in both forest types was consistent with self-replacement. However, at the understory level, the structural change but limited shrub species compositional change in *Q. ilex* forests was analogous to self-replacement, whereas the compositional change observed in *P. halepensis* forests represented a form of reassembly that

nevertheless preserved the community-level climatic properties (Lecina-Diaz et al., 2026). The observed responses are particularly relevant because the early, post-disturbance reorganization phase constitutes a critical regenerating window that can shape forest structure and composition for long time periods (Seidl et al., 2024; Seidl and Turner, 2022).

Overall, this study reveals the stability of Mediterranean woody understory communities in terms of climatic disequilibrium, and a limited effect of fire (Fig. 3) as a filter favoring more climatically adapted species. In fact, post-fire dynamics in the understory community largely reproduce the pre-existing climatic disequilibrium, either through the persistence of resprouting species or through the replacement by pioneer species with climatic characteristics similar to those of the species present before the disturbance. These two contrasting dynamics explain the climatic resilience of both understory communities. Still, clear differences emerge in the drivers of such stability between forests dominated by a tree seeder (*P. halepensis*) and a tree resprouter (*Q. ilex*) (Figs. 3–5). Such interpretations are more robust for *P. halepensis* understories, where post-fire dynamics and understories compositions are more homogenous across the study range, than for *Q. ilex* forests, with fewer occurrences and distinct understory species associated with different geographic regions (Figure S2). These compositional differences across the range likely imply divergent ecological responses despite the general patterns observed (Table S8; Figure S3). Future studies with larger sample sizes and considering regional variations on understory composition will be necessary to fully understand post-fire climatic disequilibrium dynamics in Mediterranean forest understories.

CRedit authorship contribution statement

Enric Batllori: Writing – review & editing, Validation, Supervision, Project administration, Methodology, Funding acquisition, Conceptualization. **Jordi Margalef-Marrase:** Writing – review & editing, Validation, Data curation. **Maria Angeles Perez-Navarro:** Writing – review & editing, Validation, Methodology. **Francisco Lloret:** Writing – review

& editing, Validation, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Gerard Codina:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Adriana Tovar-Rodríguez:** Writing – review & editing, Validation, Software, Data curation.

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.2026.124153](https://doi.org/10.1016/j.foreco.2026.124153).

Data availability

Data will be made available on request.

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