Post-print of the article published in *Journal of Vegetation Science* as open access under a Creative Commons Attribution (CC BY) license. DOI of the published article:https://doi.org/10.1111/jvs.70062

Key factors influencing post-fire vegetation recovery in *Pinus halepensis* forests: divergent effects for canopy and shrub species

Mara Paneghel[1,2] Judith Solé[3,4] Gil Torné[1] Teresa Valor[5] Aitor Ameztegui[1,2] Josu G. Alday[1,6] Lluís Coll[1,2]

[1]Department of Agricultural and Forest Sciences and Engineering (DCEFA), Lleida, Spain

[2]Joint Research Unit CTFC—Agrotecnio—CERCA, Solsona, Spain

[3]Universitat Autònoma de Barcelona, Barcelona, Spain

[4]CREAF, Cerdanyola del Vallès, Barcelona, Spain

[5]Department of Agri-Food Engineering and Biotechnology, Polytechnic University of Catalonia-BarcelonaTech, Castelldefels, Spain | 6Joint Research Unit CTFC – Agrotecnio – CERCA, Lleida, Spain

Abstract

Aims. Rapid revegetation of burnt forest is essential for recovering ecosystem functioning, especially in the context of climate-change driven shifts in fire regime. This study aims to provide a comprehensive understanding of how abiotic factors (topography, fire behaviour) and biotic factors (pre-fire forest characteristics, plant reproductive strategies, land-use trajectories) influence the recovery of *Pinus halepensis* forests, identifying regeneration vulnerabilities that could inform management practices.

Location. A *P. halepensis* forest burnt in 2019 (4000 ha) in NE Iberian Peninsula.

Methods. We established 72 sampling sites within the burnt forest, covering gradients of pre-fire canopy cover, topography, fire severity and land-use history. At each site, we recorded the abundance of *P. halepensis* seedlings within a 100 m^2 plot. We also conducted a floristic inventory of all associated woody species along two parallel 20 m transects to assess woody species cover, richness and distribution. Woody species were classified based on their post-fire reproductive strategies (obligate seeding, facultative resprouting and resprouting) to explore the relationship between functional characteristics and plant distribution along the studied gradients.

Results. Northern exposures enhanced the abundance of *P. halepensis*, whereas coexisting woody species cover was higher on southern ones, probably due to the contribution of obligate seeders, as fire-responsive reproductive traits vary along the north-south gradient. Pre-fire canopy cover boosted pine regeneration and species richness, while high fire severity reduced both cover and richness of woody species, likely due to damage of reproductive structures.

Conclusions. We show that the drivers of post-fire regeneration influence in different and even divergent ways the vegetation components considered (canopy and shrub layer), as in the case of aspect. From a management perspective, post-fire forest interventions should be tailored to restoration objectives and to the post-fire vegetation communities that better respond to them.

Keywords: forest fires, regeneration, fire severity, woody vegetation cover, fire-responsive reproductive traits, land-use history, Mediterranean

Introduction

Wildfires are major disturbances that significantly impact the distribution, functioning and dynamics of Mediterranean forest ecosystems (Scott, 2000; Blondel, 2006). In the Mediterranean basin, the wildfire regime results from the interaction between weather conditions, fuel availability and anthropogenic activity, which often drives ignition (Fréjaville & Curt, 2017) while influencing also fuel availability through modification of landscape vegetation patterns (Moreira et al., 2011). While Mediterranean forests have the capacity to recover after stand-replacing fires due to their adaptive reproductive strategies and a tolerance to adverse conditions (Vallejo, Arianoutsou and Moreira, 2012), in the last decades both climate and land cover change have intensified the fire regime by increasing the number, frequency, intensity and extent of wildfires (San-Miguel-Ayanz et al., 2012; Turco et al., 2018; Ruffault et al., 2020). In this context, rapid vegetation recovery is crucial for the long-term stability and functionality of forest ecosystems after a fire (Moya et al., 2018).

Post-fire vegetation recovery is modulated by a complex interplay of abiotic and biotic factors. Among abiotic factors, post-fire climatic conditions and topography (aspect and slope) contribute to spatio-temporal variation of vegetation by controlling water availability for plants (Keeley & Keeley, 1981; Martín-Alcón & Coll, 2016). Moisture rich north-facing slopes tend to exhibit higher post-fire vegetation recovery compared to drier south-facing ones (Pausas et al., 1999; Buhk et al., 2006; Ireland & Petropoulos, 2015), as water scarcity and drought-duration have been identified as key factors inhibiting post-fire recovery across a wide range of Mediterranean burnt forests (Blanco-Rodríguez et al., 2023). Simultaneously, flat slopes and valley bottoms often show higher post-fire vegetation recovery due to deeper soils and greater accumulation of seeds and nutrients from the hillsides (Tsitsoni, 1997).

Fire severity also influences the recovery of Mediterranean post-fire plant communities, although its effects on forest structure and competition are variable (DeRose & Long, 2014). Some studies report a lower and/or slower recovery of vegetation after high severity fires (Ireland & Petropoulos, 2015; Viana-Soto, Aguado and Martínez, 2017; Fernández-García et al., 2019). This is in part attributed to the fact that high-severity burning, which is related to high fire intensity and/or prolonged residence time (Certini, 2005), can lead to the destruction of seeds (both in soil and aerial seedbanks) or resprouting stumps, thereby inhibiting regeneration dynamics by reducing the availability of reproductive structures (Keeley et al., 2011; Fernández-García et al., 2019). In addition, fire severity significantly affects the physical, chemical and biological properties of soils, directly impacting plant regeneration (Certini, 2005; Romeo et al., 2020). For instance, high fire severity can result in the loss of most superficial organic matter, nutrient leaching, reduced soil structural complexity and can cause substantial changes in soil microbiota and invertebrate communities. Although ash deposition can cause a transient increase in nutrient availability (Caon et al., 2014), it also forms an impermeable layer that reduces water infiltration, thus increasing erosion risk (Certini, 2005). In contrast, other works have found positive effects of fire severity on post-fire revegetation, by reducing competition for resources (light, nutrients, and water), creating a “window of opportunity” for plant species colonization (Lavorel et al., 1994; Romeo et al., 2020). Additionally, low to intermediate fire severity can stimulate seed release and germination in some species or enhance sprouting vigour in others (Bond & van Wilgen, 1996; Naveh, 2007), while also promoting nutrient increase in soil that can facilitate plant regeneration (Romeo et al., 2020).

Vegetation recovery is also mediated by fire-responsive reproductive traits in Mediterranean plants, such as resprouting from fire-resistant structures (López-Soria & Castell, 1992), or fire-

induced seed release and germination from soil and canopy seed banks (Noble & Slatyer, 1980; Pausas et al., 2004a; Santana, Alday and Baeza, 2014). In this regard, morphological and physiological differences exist between obligate seeders and resprouters, with seeders generally being more drought-tolerant (Arnan, Rodrigo and Retana, 2007). As a result, plant reproductive strategies can reflect species distribution along environmental gradients and influence regeneration patterns therein. Besides, a well-developed forest structure positively influences plant regeneration, as the presence of adult plants prior to the fire determines the variety and availability of post-fire reproductive structures (Broncano & Retana, 2004; Martín-Alcón & Coll, 2016; Guz, Gill and Kulakowski 2021).

Finally, past land-uses determine the structure and composition of forest vegetation (Lloret & Vilá, 2003; Vilà-Cabrera et al., 2023). Thus, land-use legacies can play important roles in plant regeneration after fires. Long-established forest areas generally promote greater plant recovery compared to more recent ones (Walck et al., 2011; Puerta-Piñero et al., 2012), but the role of land-use legacies in post-fire dynamics has yet to be fully explored. In fact, higher species richness could be found in abandoned crops due to the presence of early and intermediate successional species, as well as persistent species from old fields (Kouba et al., 2015), which could contribute to a faster post-fire vegetation recovery. Land-use trajectories are especially important in the Mediterranean basin, as socio-economical changes lead to wide-spread abandonment of agricultural fields since the 19th century (Lasanta et al., 2017).

Covering more than 2 million hectares (Quézel, 2000; Girard et al., 2012), the Aleppo pine (*Pinus halepensis* Mill.) is a dominant tree species of thermo- and meso-Mediterranean forests (Aranbarri et al., 2020). It is typically associated with xero-thermophilous shrubs, often forming dense, fire-prone forests that are recurrently studied by fire and plant ecologists, as

114 they present fire-responsive traits at both the species and community level. The Aleppo pine
115 exhibits a set of fire-embracing traits at the vegetative and reproductive level (*sensu* Keeley,
116 2012). On the vegetative side, it does not self-prune dead branches, thereby promoting the
117 spread of fire to the canopy. Additionally, its thin bark exposes the cambium to high
118 temperatures during fire (Keeley, 2012). In terms of reproductive traits, the Aleppo pine is a
119 partially serotinous obligate seeders, producing both regular and serotinous cones. While
120 regular cones release seeds at maturity promoting the colonisation of open areas, serotinous
121 cones remain sealed in the canopy, creating an aerial seedbank until heat triggers their
122 opening (Daskalakou & Thanos, 1996). Serotinous cones protect the seeds from burning and
123 ensure abundant seed release after fire, fostering post-fire autosuccessional dynamics (Moya
124 et al., 2008). The shrubs associated with Aleppo pine form a dense layer beneath the canopy,
125 creating fuel continuity between the dry lower branches and the canopies, increasing the
126 likelihood of stand-replacing fires (Keeley, 2012). Considering their circum-Mediterranean
127 extension and their fire-responsive characteristics, Aleppo pine forests are an excellent study
128 system for evaluating post-fire regeneration dynamics. Despite substantial research over the
129 past decades on post-fire dynamics of these Mediterranean forests (Daskalakou & Thanos,
130 1996; Retana et al., 2002; Marzano, Lingua and Garbarino, 2012; Martín-Alcón & Coll, 2016;
131 Nolan et al., 2021; among others), there is still a lack of integrative field-based studies of plant
132 recovery, particularly at the community level, limiting our understanding of regeneration
133 vulnerabilities. This study aims to disentangle the effects of abiotic and biotic factors,
134 including land-use legacies, on the post-fire vegetation recovery of forests dominated by the
135 Aleppo pine.

136 Specifically, we assess the role of local topography, pre-fire canopy cover, fire severity and
137 land-use history (i) on the abundance of pine seedlings; and (ii) on the cover and richness of

coexisting woody vegetation. Moreover, (iii) we analyse how these factors influence the distribution of woody species according to their preferred post-fire reproductive strategy, to disentangle their distinct roles in post-fire community assembly.

We hypothesize that the post-fire regeneration of both Aleppo pine (in terms of seedlings abundance) and woody vegetation (species cover and richness) would be enhanced in northern exposures (subjected to less evaporative demand), flatter slopes (with deeper soils), in areas with a higher canopy cover prior to fire and in long-established forests (with a more developed species composition and a higher variety and abundance of reproductive structures). Additionally, we also expect higher fire severities to reduce pine seedlings abundance and species cover and richness, regardless of the effect of other conditions, due to their disruptive effect on reproductive organs. Overall, our study may contribute to a better understanding of the short-term drivers of post-fire plant recovery, which could contribute to the identification of sites where regeneration might be constrained, and restoration efforts might be needed.

Methods

Study area and fire characteristics

The study comprised a large area affected by a wildfire in the Ribera d'Ebre region (North-east Iberian Peninsula in the western Mediterranean basin, Fig. 1) that took place by the end of June 2019 and burned about 4,000 ha of forests and 1,000 ha of agricultural lands. Before the fire, the area was mainly covered by Aleppo pine woodlands, interspersed with olive and almond cultures, and rainfed crops (mainly wheat). The area represented a typical Mediterranean agro-forest mosaic (Marull et al., 2015), although rural abandonment led to forest encroachment processes in terraces and former fields (Lloret et al., 2002). Most of the forested area is privately owned and had not been managed prior to fire, probably due to the low economic value of the Aleppo pine.

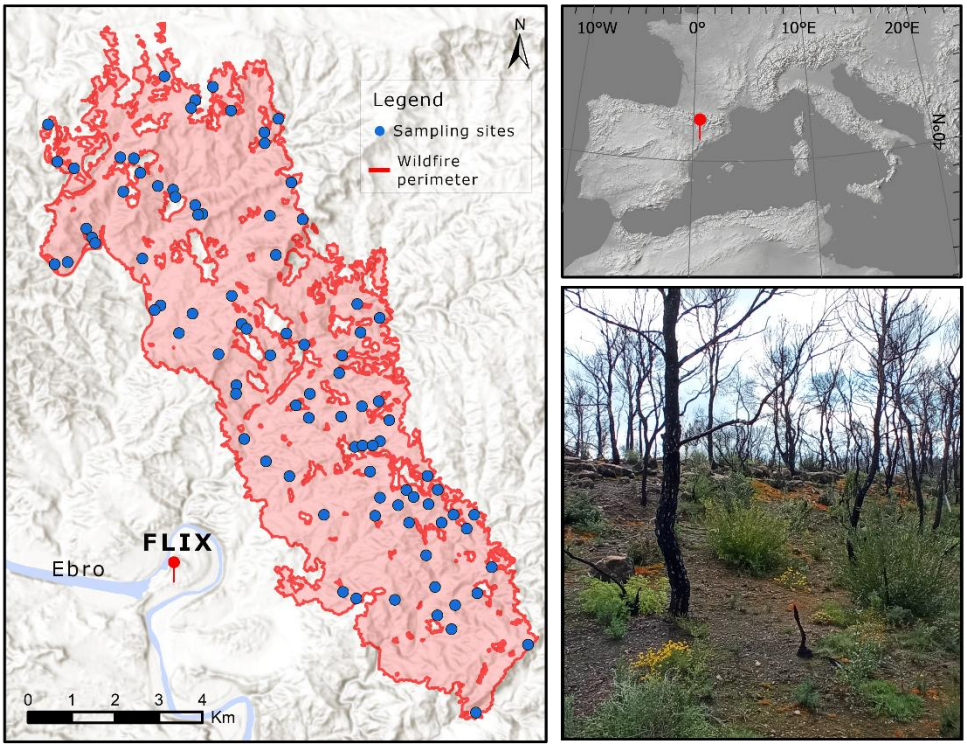


Fig. 1. Burnt area and position of sampling site within the wildfire perimeter (left). Localisation of the wildfire in central-western Mediterranean basin (top right). Picture of the regenerating forest during fieldwork (bottom right). The base maps were built using the Shaded Relief (left) and Gray Earth (right) rasters, available freely at naturalearthdata.com.

The study area belongs to the cold semi-arid climate ("Bsk"), in the upper meso-Mediterranean bioclimatic belt (Kottek et al., 2006). The annual mean temperature is 16.5 ºC, and the average yearly precipitation is 379 mm, most of which occurs during the spring and autumn (March, April, October, and November), as calculated from a 15-year time series (data from Vinebre weather station of the Meteorological Service of Catalonia). The months of July and August have the lowest annual rainfall. Soil types are mainly calcaric leptic cambisols and calcaric regosols from conglomerates weathered in glacis and in the soft slopes of the Ebre river Basin (ICGC, 2022). The forest was dominated by *P. halepensis* prior to fire, with *Quercus coccifera* L. (Kermes oak), *Pistacia lentiscus* L. (Mastic tree), *Rhamnus lycioides* L. (Black hawthorn), *Salvia rosmarinus* Spenn. (Rosemary), *Genista scorpius* (L.) DC., *Erica multiflora* L., *Cistus clusii* Dunal, and *Brachypodium retusum* (Pers.) P.Beauv. in the understory, and with the presence of *Cytisus fontanesii* Spach ex Ball and *Diplotaxis erucoides* (L.) DC. (GeoVeg, 2014).

Sampling sites selection

Prior to fieldwork, we used a remote-sensing-based random sampling to select sites based on fire severity, pre-fire canopy cover and terrain aspect. Within the wildfire perimeter, we first selected the burnt area dominated by Aleppo pine before the fire, according to the information provided by the Spanish Forestry Map 1:50.000 (MITECO, 2006). Within this area, three fire severity classes were derived from the analysis of Sentinel-2 imagery (resolution 20 m), using delta Normalized Burnt Ratio (dNBR), a widely used fire severity index (Miller & Thode, 2007; Fernández-García et al., 2019; Sivrikaya & Demirel, 2025), calculated following Key & Benson (2006). After creating a dNBR-based fire severity map (image processing details in Appendix 1), we classified each pixel according to 3 categories of dNBR: low severity (dNBR

values from 100 to 269), medium-low severity (270 to 439), and medium-high severity (440 to 659) (Key & Benson, 2006). We then defined pre-fire canopy cover classes (PCC) of the study area at a resolution of 20 m, based on data provided in the Map of Biophysical Variables of Wooded Forest Areas of Catalonia (ICGC, 2017): low (PCC<30 %), medium (30% ≤ PCC ≤ 60%), and high (PCC > 60%). Finally, we classified the study area into two aspect categories from a 2-m resolution digital elevation model (DEM): northern (from 225º to 45º) and non-northern exposures (from 45º to 225º). Sampling sites for performing fieldwork were defined by randomly locating 4 points within each combination of factors (three fire severities x three PCC x two aspect classes) using GIS tools (ArcMap® software by Esri, version 10.4.1), totalling 72 sites within the wildfire perimeter.

Post-fire regeneration measurements and variable calculations

Field surveys were conducted between April and May 2021, less than two years after the fire. At each sampling site we established a 10 m x 10 m square plot and two linear transects of 20 m, set up along the two edges of the plot, one following the slope of the area. Transect were extended beyond the plot edges to fully capture site-level species richness and diversity in the context of sparse post-fire regeneration, and to provide a more accurate measurement of plant coverage, allowing comparison between small seeding species and resprouting species with an extensive cover. Within the square plots, we counted all living Aleppo pine seedlings regenerating after the fire (hereafter, pine abundance), while a plant species floristic inventory was carried out along the transects. We refer to regenerating individuals of Aleppo pine as seedlings based on an age (< 2 years old individuals, see Gómez-Aparicio, 2008) and a height criterion (< 100 cm). The maximum plant height recorded for *P. halepensis* in the area during fieldwork was of 58 cm (unpublished data), that stays within one of the suggested

thresholds for a general seedling definition (Martini, 2024). For the floristic inventory, we identified and measured the width of all woody plant species and the overall herbaceous layer intercepting the transects. Here, the basal cover percentage of woody and overall herbaceous species cover was calculated following the "*Line Intercept method"* (Canfield, 1941; Bonham, 2013). Species richness of each site was calculated as the number of woody species surveyed. Plant nomenclature was standardised following World Flora Online (WFO, 2024).

The woody species recorded in the floristic inventories were classified according to their fire-adaptive reproductive traits (i.e. post-fire resprouting ability and/or post-fire seedling emergence) into three different groups based on information provided in the BROT 2.0 database (Tavşanoğlu & Pausas, 2018): obligate seeders, resprouters, and facultative resprouters. We considered as facultative resprouters those species theoretically capable of regenerating by both sexual and vegetative reproduction, although most facultative resprouters in the study area (mainly *Fabaceae*, *Cistaceae* and *Lamiaceae*) act like seeders after a fire (Verdú, 2000).

To quantify physiographic variables, we recorded in the field the slope (%) and aspect (º) for each plot, using a vertex (VERTEX 5, Haglöf, Sweden) and a compass (Suunto KB-14/360, SUUNTO, Finland) respectively. Aspect measurements were converted into a Northness Index (NI) using the cosine transformation. The NI varies from -1 (southern exposures) to 1 (northern exposures), while eastern and western exposures were assigned a value of 0. Fire severity at the plot level was also estimated in the field and classified into four categories (1, 2, 3 and 4) from low (1) to high (4) fire severity based on detailed clues (Appendix S2). Finally, each sampling site was also characterized by past land-use (PLU). We used direct photo interpretation of 1956 aerial orthophotographs (taken in the American Flight of 1956) to

classify burnt areas into “recent forest” (i.e. forested areas that were croplands in 1956) or “long-established forest” (i.e. forested areas that were already forests in 1956).

Data analysis

All statistical analyses were run using R version 4.4.1 (R Core Team, 2024). Pine abundance was modelled using a generalized linear model with a negative binomial distribution of the errors, as these data showed overdispersion (i.e. the variance was larger than the mean) (MASS package; Venables & Ripley, 2002). Linear models were applied to analyse woody vegetation cover and species richness. Each target variables (i.e. pine abundance, woody vegetation cover, and species richness) was modelled as a function of NI, slope, PCC, PLU and fire severity as explanatory variables. We started the analyses by including both main effects and all interactions. The saturated model was then reduced by progressively removing non-significant interactions starting from the high level ones, and comparing their respective table of deviance for assessing models fit. We then evaluated the AIC of subsequent models to select the one with the lowest AIC. We finally retained the models with all the main effects. Model fit and assumptions were checked through visual inspection of graphs performed with the check_model function from the performance package (Lüdecke et al., 2021). For pairwise comparisons of discrete variables (i.e., PCC, fire severity and PLU), a Kruskall-Wallis and a Dunn’s test were applied for pine abundance, while Tukey post-hoc tests were used for vegetation cover and species richness.

To explore the relationship between plot characteristics and post-fire woody species distribution, we performed a canonical correspondence analysis (CCA) using the cca function in the vegan package (Oksanen et al., 2022). We included some of the studied explanatory variables (i.e., NI, slope, PCC, and fire severity), while the species cover matrix

255 was composed by the measurements of the 33 most frequent woody species in each site
256 (i.e. those species recorded in 7 or more sites). Prior to the CCA, this matrix was log-
257 transformed to reduce the influence of dominant species (Borcard, Gillet and Legendre, 2018)
258 and categorical variables (PCC and fire severity) were transformed to ordinal ones. In the
259 biplot, species were represented according to their fire-adaptive reproduction traits, to
260 identify potential drivers of the distribution of species with certain strategies along
261 environmental gradients (CCA1 and CCA2). The significance of the canonical model,
262 canonical axes and the environmental variables contributions were assessed using
263 permutation tests (999 permutations).

Results

During our field survey, we counted a total of 2,596 Aleppo pine seedlings with a mean density of 0.36 ± 0.06 (mean ± SE) seedlings/m^2. We found three plots with no pine regeneration, and the maximum pine density was 2.38 seedlings/m^2. We identified 45 woody species, including shrubs, dwarfs, lianas and trees (the complete list of species surveyed is available in Appendix S3). Woody species cover ranged between 5% and 125% (with percentages superior to 100% due to vertical overlapping of species).

Drivers of post-fire Aleppo pine regeneration

Among the variables studied, only NI and PCC had a significant effect on post-fire pine abundance (Appendix S4). Northness positively influenced the amount of pine seedlings (β =

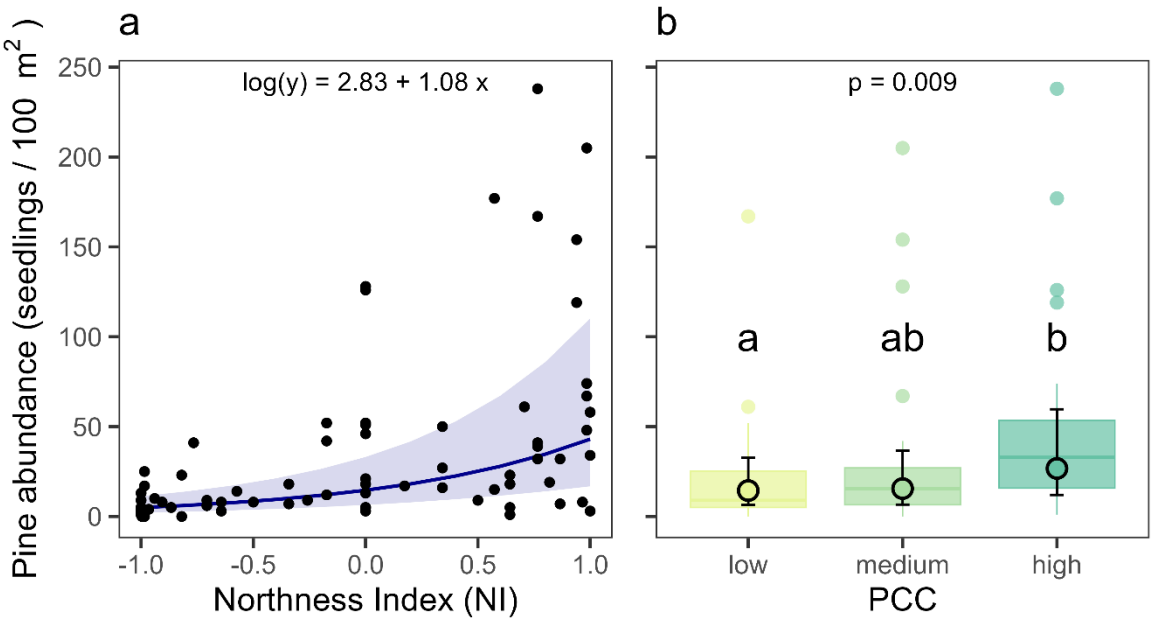


Fig. 2. *Pinus halepensis* abundance (number of seedlings per 100 m^2) as a function of northness index (NI) (a) and pre-fire canopy cover (PCC) (b). The negative binomial generalised linear model predictions are plotted on top of observed data with 95% confidence interval. In (a) the negative binomial model equation for NI is reported. In (b), point-ranges reports predicted values for PCC, keeping the rest of model predictors to their average (for NI and slope) or to their reference level (for fire severity and past land use). Different letters show differences among groups obtained with Kruskall-Wallis and Dunn's post-hoc tests for significance (α = 0.05).

274 1.081 ± 0.17, z = 6.28, p < 0.001; Fig. 2a). Sites with high PCC showed a greater pine seedling
275 abundance than sites with low PCC, which in turn had similar levels of pine abundance (Fig.
276 2b). We found no significant effects of slope, PLU, fire severity and the tested interactions on
277 pine abundance (Appendix S4).

278 *Drivers of post-fire vegetation cover*

279 Vegetation cover was significantly influenced by NI, fire severity and PLU ($F_{[63, 8]}$ = 2.92,
280 Adjusted R^2 = 0.178, p = 0.007) (Appendix S5). Northness negatively influenced vegetation
281 cover, with sites at northern exposures showing lower shrub cover (β = -9.92, t = -2.69, p =
282 0.009) (Fig. 3a). Sites burned at high severity (severity class 4) had lower shrub cover than

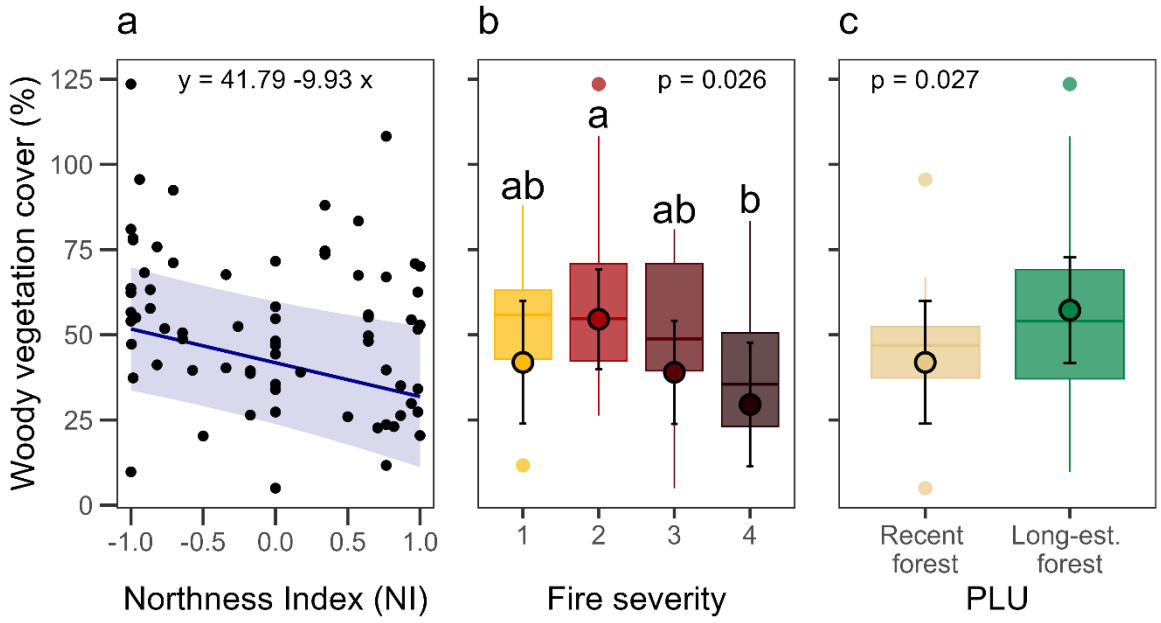


Fig. 3. Vegetation cover (% of woody plants covering the soil) as a function of northness index (NI) (a), fire severity (b) and past land-use (PLU, recent forest and long-established forest) (c). Linear model predictions are plotted on top of observed data with 95% confidence interval. In (a), the linear model predictions and model equation are reported, with the model intercept adjusted to represent the effect of NI. In (b) and (c), point-ranges reports predicted values for fire severity and PLU respectively, keeping the rest of model predictors to their average (for NI and slope) or to their reference level (for discrete ones). The different letters show differences among groups obtained with Tukey post-hoc test for significance (α = 0.05). Percentages go above 100 since the vertical coverage of shrubs is considered.

283 those burned at lower classes, but significantly different only to severity class 2 (Fig. 3b). In
284 terms of PLU, long-established forests had higher vegetation cover than recent forests (Fig.
285 3c). Neither slope nor PCC nor the tested interactions significantly influenced shrubs
286 vegetation cover.

287 *Post-fire diversity trends*

288 *Drivers of post-fire species richness*

289 The number of woody species recorded per site ranged from 7 to 22. The linear model ($F_{[63,}$
290 $_{8]} = 3.55$, Adjusted $R^2 = 0.22$, p-value = 0.002) highlighted a significant contribution of PCC to
291 species richness, while slope (p = 0.054) , PLU (p = 0.095) and fire severity (p = 0.073) had
292 only marginal effects (Appendix S6). Species richness was higher at sites with high PCC, than
293 at sites with low and medium PCC, which had similar values (Fig. 4a). In terms of fire severity,
294 species richness was lower at sites with high fire severity (i.e. category 4) than at category 2

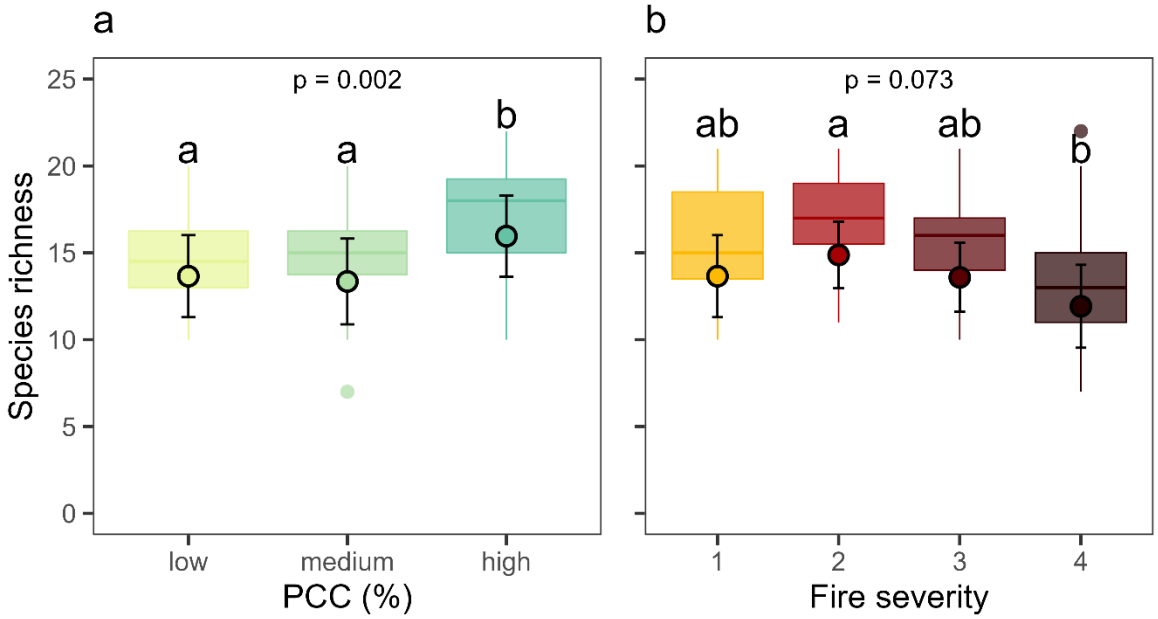


Fig. 4. Species richness (nº of woody species) as a function of: (a) pre-fire canopy cover (PCC) and (b) fire severity. Linear model predictions are plotted on top of observed data with 95% confidence interval. Point-ranges reports predicted values for PCC and fire severity respectively, keeping the rest of model predictors to their average (for NI and slope) or to their reference level (for discrete ones). The different letters show differences among groups obtained with Tukey post-hoc test for significance ($\alpha = 0.05$).

295 sites (i.e. low to moderate fire severity), but similar to the other fire severity classes (i.e.
296 categories 1 and 3) (Fig. 4c). Even though category 2 sites had the highest species richness,
297 no significant differences were observed compared to categories 1 and 3 (low and
298 moderate-high fire severity, respectively) (Fig. 4b). Burnt long-established forests had
299 slightly higher species richness than recent ones, but the difference was only marginally
300 significant (Appendix S6).

301 *Woody species ordination along NI, slope, PCC, and fire severity*

302 The CCA model highlighted that a 15.98% of the total variance in species distribution could
303 be explained by the environmental variables, while 84.02% remained unexplained. The

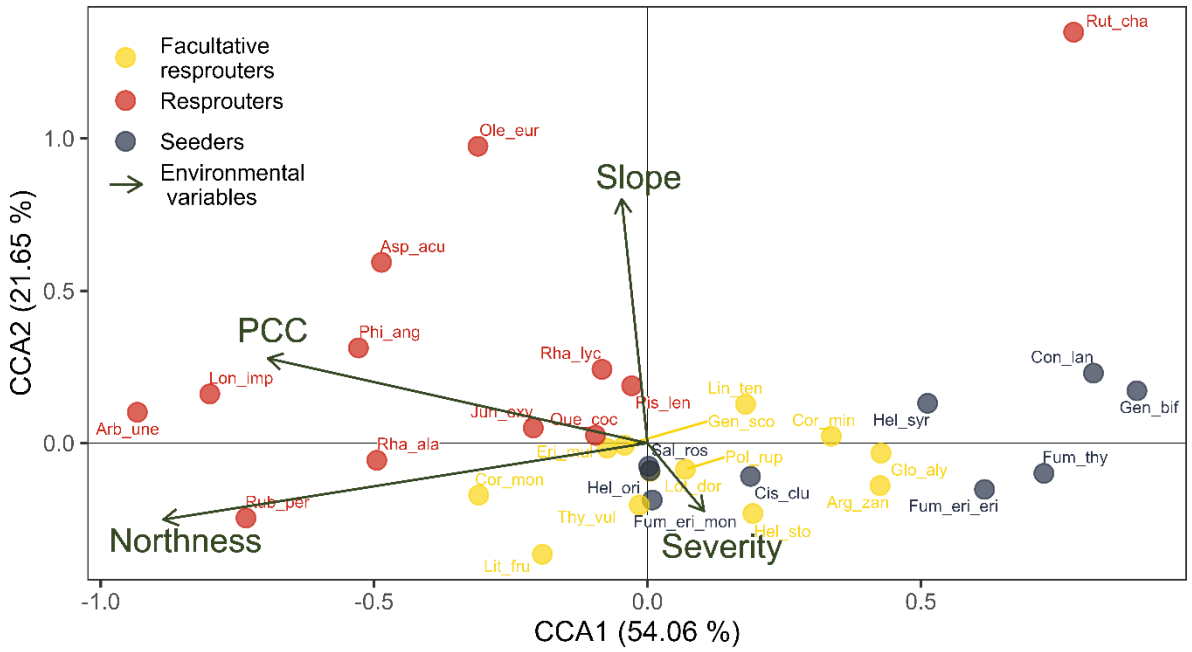


Fig. 5. Canonical Correspondence Analysis (CCA) biplot. CCA was run on four of the studied variables: northness index (Northness, continuous values from -1 for southern, to 1 for northern), slope (%), pre-fire canopy cover (PCC, categorical variable), and fire severity (Severity, categorical variable from low (1) to high (4) severity), and the 33 most frequent surveyed woody species. Categorical variables (PCC and severity) were included as ordinal variables and are pictured as vectors. Fire-adaptive strategies are obligate seeders (Seeders), resprouters and facultative resprouters. Canonical axis 1 and 2 are represented, collecting a 75.71 % of the explained variance. Species are labelled with a shortened name composed by the first three letters of the Genus and specific epithet. Complete species names can be checked in Appendix S3.

304 model was significant ($F_{[4, 67]} = 3.186$, $p = 0.001$), although the permutation test showed that
305 only CCA1 and CCA2 were significant and together described 75.71% of the explained
306 variation (Appendix S7). The CCA biplot highlighted a strong correlation between CCA1 and
307 Northness and PPC, while CCA2 was correlated to slope and, to a lower extent, to fire
308 severity (Fig. 5). The four environmental variables included in the model were significantly
309 affecting species distribution (Appendix S7). A clear gradient of species distribution was
310 visible along CCA1, with species being clustered according to their preferred post-fire
311 reproductive strategy. Specifically, we could observe that resprouters were mostly arranged
312 to the left side of the panel, corresponding to north-facing areas and a high PPC, in
313 opposition to obligate seeders and facultative resprouters.

Discussion

In this study, we provide a field-based integrative assessment of the factors driving post-fire vegetation recovery in a Mediterranean Aleppo pine forest in Catalonia, focusing on the abundance of the dominant canopy species (the Aleppo pine), woody plant cover, species richness and composition two years after the fire. While a tendency towards autosuccessional dynamics is suggested by the fire-responsive traits of the studied vegetation community, our results highlight that the abiotic and biotic drivers of post-fire regeneration dynamics affect the two vegetation components – the dominant canopy species (*P. halepensis*) and the coexisting woody understory – in distinct and even divergent ways. Even if these differences could be driven by species-specific characteristics, they could highlight the need for a tailor-made approach in potential post-fire restoration practices depending on their underlying objectives.

Drivers of post-fire regeneration of Aleppo pine

In the sampled plots, the density of pine seedlings two years after the fire ranged from 0 to 2.38 plants m^{-2}, with a mean of 0.36 individuals m^{-2}. These values are comparable to those found in other studies on early post-fire Aleppo pine regeneration (Thanos, Daskalakou and Nikolaidou, 1996; Retana et al., 2002; Pausas et al., 2002), evidencing a successful regeneration potential of the Aleppo pine in our study area. Our results confirmed the hypothesis that exposure and pre-fire vegetation conditions drive Aleppo pine post-fire regeneration, while slope and fire severity have negligible effects. These results evidence the importance of factors related to water availability for post-fire regeneration of Aleppo pine in Mediterranean areas. In fact, the more successful regeneration of Aleppo pine on northern aspects might be explained by the cooler and moister microclimate, which reduces

337 the evaporative demand in these areas as previously observed by Pausas, Ribeiro and Vallejo
338 (2004) and Buhk et al. (2006), and more recently with remote sensing data (Blanco-
339 Rodríguez et al., 2023).). Similarly, we expected flatter slopes, associated to deeper soils
340 with higher water retention capacity (Gómez-Plaza et al., 2001), to also present a higher
341 pine regeneration (Tsitsoni, 1997). Nevertheless, the contribution of slope was not
342 significant, suggesting that other topographical factors may play a more important role in
343 determining the regeneration of this pine (Broncano & Retana, 2004).

344 In agreement with our hypotheses, the presence of a dense pre-fire canopy positively
345 influenced pine regeneration, likely due to the pre-fire abundance of adult pines enriching
346 the seedbank (Broncano & Retana, 2004; Pausas, Ribeiro and Vallejo, 2004). However, we
347 did not find land-use legacy effects on post-fire pine regeneration, likely due to the fast-
348 growing early-successional nature of Aleppo pine. On one hand, its partially serotinous
349 cones and long dispersal distances give it the ability to easily colonise post-disturbance
350 environments, regardless of land use history (Puerta-Piñero et al., 2012). On the other hand,
351 Aleppo pine reaches sexual maturity early (3-9 years for first cone production), ensuring
352 seed availability within short-time frames (Climent et al., 2008). Altogether, these facts
353 suggest that land-use trajectories have a negligible effect on fast-growing pine regeneration,
354 especially considering that our “recent forest” class was at least 65 years old.

355 We found no significant effect of fire severity on pine seedlings abundance. Previous studies
356 reported greater pine regeneration after both high (Moya et al., 2020) and moderate
357 severity fires (González-De Vega, De las Heras and Moya 2018; Romeo et al., 2020),
358 highlighting the disturbance-tolerant character of Aleppo pine (Nathan & Ne’eman, 2000).
359 Differences between our results and literature could be explained by the different

methodologies used to estimate fire severity. In our study, this variable was estimated qualitatively using visual clues (Appendix S2). Despite the reliability of our method, the minimum heat exposure required to open the serotinous cones and release the seeds might have already been reached in plots characterized as “low severity”. In addition, other factors such as post-fire germlings and seedlings mortality (Broncano & Retana, 2004; Paneghel et al., 2024), or seed predation (Broncano, Rodrigo and Retana, 2008) could act as greater filters for pine recruitment than fire severity. Plus, other studies highlight that fire frequency is more detrimental to Aleppo pine post-fire regeneration by reducing the time for the formation of an abundant canopy seedbank, thus leading to structural and compositional shifts in vegetation communities (Baeza et al., 2007; Rodrigo, Retana and Picó, 2004).

If matched in time and space with the favourable climatic conditions (Baeza et al., 2007), the Aleppo pine shows an effective autosuccessional dynamic or “direct regeneration” (*sensu* Rodrigo, Retana and Picó, 2004) thanks to heat-induced self-seeding from its serotinous cones. In this context, pre-fire characteristics such as canopy cover, that mediates seed availability, and northern exposure, which ensures higher water availability (through lower evaporative demand), positively influence seedling abundance after fire. In contrast, fire severity and land use legacy do not appear to play a significant role. Other dominant mediterranean trees of fire-prone areas, including certain pines (such as *P. sylvestris* L., *P. nigra* J.F. Arnolf and *P. pinea* L.) do not exhibit direct regeneration. In these cases, post-fire seedlings abundance is strongly dependent on the presence of unburned patches that provide regeneration material (Martín-Alcón & Coll, 2016; Mendez-Cartin et al., 2025).

Such a regeneration dynamic can lead to the replacement of the dominant canopy species

or to structural simplification, especially in large burnt areas (Rodrigo, Retana and Picó, 2004). It may also drive substantial compositional changes, as the recovery of the dominant tree species has been suggested to facilitate the recovery of the overall pre-fire vegetation (Arnan, Rodrigo and Retana, 2007). Therefore, direct regeneration is strongly contingent to the presence of species-specific regenerative traits in response to fire, such as serotiny or resprouting (Rodrigo, Retana and Picó, 2004) and results as critical as environmental conditions in determining the timing and success of post-fire plant recovery.

Drivers of post-fire woody vegetation cover, species richness and distribution

Although we initially expected that vegetation cover and richness would be enhanced in northern sites, we found higher woody vegetation cover on southern exposures. This result contrasts with previous findings in sub-Mediterranean mountainous areas (Puerta-Piñero et al., 2012), but may reflect the contrasting distribution of reproductive strategies across aspects, as observed in the CCA biplot (Fig. 5). There, southern exposures were characterised by a higher abundance of obligate seeders in contrast to resprouters, which were mainly found on northern slopes. Thus, the higher vegetation cover found on southern slopes could be attributed to a higher abundance of obligate seeders, which tend to be more drought tolerant and dominate in more water-limited environments (Verdú, 2000; Arnan, Rodrigo and Retana, 2007).

Contrary to our expectations, we found no effects of aspect on species richness, which contradicts previous studies that reported lower floristic richness on southern slopes 2-4 years after the fire (Kutiel, 1997; Buhk et al., 2006). However, we did find that a high fire severity negatively impacted both woody species cover and richness, which resulted higher at a mid-low fire severity level (category 2). There are contrasting results in literature

406 regarding the effect of fire severity on species richness and composition. Moya et al. (2020)
407 found that high burnt severity influenced a shift in community composition and increased
408 diversity, but not on species number (richness) nor cover. Contrastingly, Marzano, Lingua and
409 Garbarino (2012) describes a fire-severity induced reduction in floristic richness shortly after
410 fire. Differences in the effect of fire severity on species richness and composition could be
411 driven by how fire affects soil properties and the soil seedbank (Robichaud & Waldrop, 1994;
412 González-De Vega, De las Heras and Moya, 2018), resprouting vigour (Pausas et al., 2002;
413 Marzano, Lingua and Garbarino, 2012), and fire induced seedling emergence (Moya et al.,
414 2020). In fact, beside directly affecting seed availability, viability and germination, a high fire
415 severity has overall negative effects on soil properties, including the loss of organic matter,
416 nutrient depletion through volatilisation or leaching, and the disaggregation of soil structure
417 that enhance soil erosion and runoff, combined with the waterproof effect of the ash layer
418 (Certini, 2005). On the other hand, an intermediate fire severity can boost species richness
419 and cover by creating a competition-free environment (Lavorel et al., 1994), while not
420 significantly reducing propagule availability, and even favouring heat-induced seed
421 dissemination. The highest levels of species richness during post-fire recovery are typically
422 observed in the first few years after the fire, when autosuccessional dynamics favour the
423 presence of pre-fire species reproducing either by seeding or resprouting and of transient
424 herbaceous species (Capitanio & Carcaillet, 2008). Although not strongly significant, our
425 results appear to support the intermediate disturbance hypothesis (Grime, 1973), as an
426 intermediate fire severity causes a sufficient disturbance to reduce competition, while
427 preserving enough seeds and resprouting structures to facilitate diverse plant community
428 with a transient increase in species richness. Finally, the methodological choices in assessing
429 fire severity may contribute to the lack of clear statistical significance in the observed effects

of fire severity on species richness and cover. Specifically, the visual criteria used for determining fire severity (Appendix S2) may not always accurately reflect the actual fire severity experienced or its impact on soils and reproductive structures.

Species richness was favoured in areas with high pre-fire canopy cover, even though this did not affect vegetation cover. A higher post-fire richness in previously denser forest could be related to the development of the understory. In fact, dense Aleppo pine forests are characterised by a species richer understory, often composed by resprouting species, which are more abundant in northern slopes (Fig. 5). Finally, long-established forests appeared to support higher vegetation cover than those established more recently, without influencing species richness. On one hand, higher vegetation cover in long-established forests and on southern slopes could be also related to land abandonment patterns. Southern sites, less productive in the hot and dry continental Mediterranean climate, may have been abandoned earlier or never cultivated, as land abandonment patterns are often linked to unfavourable environmental conditions, among others socio-ecological factors (Kosmas et al., 2015). On the other hand, long-established forests also tend to have more structured vegetation communities and thus a richer abundance of reproductive structures, aiding the post-fire ecosystem recovery. For example, previous studies have reported a higher presence of resprouting species in long-established forests (Baeza et al., 2007). These results build on previous findings, suggesting that land-use trajectories may influence plant composition and post-fire vegetation recovery regardless of other environmental factors shaping species assembly. This influence persists even though we observed a clear distribution of species by reproductive strategies along the north-south exposure gradient, with seeders more common on southern exposures. Further research is needed to fully understand how land-use changes

453 modulate post-fire recovery of plant communities in the Mediterranean and how these
454 interact with other variables influencing species distribution and ecology (but see Baeza et al.,
455 2007).

456 *Conclusions and management implications*

457 Our results showed that sites with low pre-fire canopy cover, with southern aspects and
458 affected by a high severity fire, may be those where vegetation may experience challenges
459 to re-establishing quickly after fire, at least in the short term. These areas might be
460 prioritized when defining restoration strategies to protect soil from erosion and further
461 degradation. In unburnt areas, management actions aimed at enhancing forest resilience
462 should focus on promoting species diversity, with particular attention to species functional
463 responses to disturbances, as well as species-specific environmental requirements. We can
464 highlight that the main drivers of post-fire regeneration diverge depending on the
465 vegetation strata considered. While pre-fire canopy cover positively influences *P. halepensis*
466 regeneration, fire severity plays a more critical role in determining overall woody vegetation
467 cover. Furthermore, aspect had opposite effects on the recovery of different vegetation
468 components, with north-facing slope favouring pine establishment, and southern aspects
469 supporting a greater woody vegetation cover, mainly due to the presence of obligate
470 seeders. Our results also highlight the importance of the presence of fire-responsive
471 regenerative plant life-traits, which *per se* foster the autosuccessional dynamic of the plant
472 community.

473 It is worth mentioning that our study provides short-term information on post-fire
474 vegetation recovery, offering a partial assessment of these processes. While longer-term
475 studies or broader spatial scales might be necessary to fully understand the evolution of

post-fire plant communities in water-limited Mediterranean environments, this study offers valuable information on the key factors driving plant regeneration after wildfires, which could guide future management actions. In post-fire conditions, restoration goals could span from ensuring the regeneration of the dominant canopy species (as *P. halepensis* in our case study), to rapid soil coverage to avoid soil erosion and degradation and enhancing diversity. Thus, our work can help in the identification of areas that might require targeted restoration efforts to optimise post-fire vegetation recovery according to the specific goals and objectives of each forest community.

Appendices

Appendix S1. Image processing for dNBR calculation for the study area.

Appendix S2. Fire damage clues for fire assessment in the field based on visual estimation of damage.

Appendix S3. Complete list of woody species recorded in the floristic inventories.

Appendix S4. Results tables of the generalized linear model for pine abundance.

Appendix S5. Results tables of the linear model for woody species cover.

Appendix S6. Results tables of the linear model for woody species richness.

Appendix S7. Summary table of the Canonical Correspondence Analysis.

References

Aranbarri, J., Alcolea, M., Badal, E., Vila, S., Allué, E., Iriarte-Chiapusso et al. (2020). Holocene history of Aleppo pine (*Pinus halepensis* Mill.) woodlands in the Ebro Basin (NE Spain): Climate-biased or human-induced? *Review of Palaeobotany and Palynology*, *279*, 104240. https://doi.org/10.1016/j.revpalbo.2020.104240

Arnan, X., Rodrigo, A., & Retana, J. (2007). Post-fire regeneration of Mediterranean plant communities at a regional scale is dependent on vegetation type and dryness. *Journal of Vegetation Science*, *18*(1), 111–122. https://doi.org/10.1111/j.1654-1103.2007.tb02521.x

Baeza, M. j., Valdecantos, A., Alloza, J. a., & Vallejo, V. r. (2007). Human disturbance and environmental factors as drivers of long-term post-fire regeneration patterns in Mediterranean forests. *Journal of Vegetation Science*, *18*(2), 243–252. https://doi.org/10.1111/j.1654-1103.2007.tb02535.x

Blanco-Rodríguez, M. Á., Ameztegui, A., Gelabert, P., Rodrigues, M., & Coll, L. (2023). Short-term recovery of post-fire vegetation is primarily limited by drought in Mediterranean forest ecosystems. *Fire Ecology*, *19*(1), 68. https://doi.org/10.1186/s42408-023-00228-w

Blondel, J. (2006). The 'Design' of Mediterranean Landscapes: A Millennial Story of Humans and Ecological Systems during the Historic Period. *Human Ecology*, *34*(5), 713–729. https://doi.org/10.1007/s10745-006-9030-4

Bond, W. J., & van Wilgen, B. W. (1996). Surviving fires—Vegetative and reproductive responses. In W. J. Bond & B. W. van Wilgen (Eds.), *Fire and Plants* (pp. 34–51). Springer Netherlands. https://doi.org/10.1007/978-94-009-1499-5_3

Bonham, C. D. (2013). Spatial Sampling Designs for Measurements. In *Measurements for terrestrial vegetation.* (pp. 75–97). John Wiley & Sons, Ltd.

Borcard, D., Gillet, F., & Legendre, P. (2018). *Numerical Ecology with R*. Springer International Publishing. https://doi.org/10.1007/978-3-319-71404-2

Broncano, M. J., & Retana, J. (2004). Topography and forest composition affecting the variability in fire severity and post-fire regeneration occurring after a large fire in the Mediterranean basin. *International Journal of Wildland Fire*, *13*(2), 209. https://doi.org/10.1071/WF03036

Broncano, M. J., Rodrigo, A., & Retana, J. (2008). Post-dispersal seed predation in Pinus halepensis and consequences on seedling establishment after fire. *International Journal of Wildland Fire*, *17*(3), 407–414. https://doi.org/10.1071/WF07095

Buhk, C., Götzenberger, L., Wesche, K., Gómez, P. S., & Hensen, I. (2006). Post-fire regeneration in a Mediterranean pine forest with historically low fire frequency. *Acta Oecologica*, *30*(3), 288–298. https://doi.org/10.1016/j.actao.2006.05.010

Canfield, R. H. (1941). Application of the Line Interception Method in Sampling Range Vegetation. *Journal of Forestry*, *39*(4), 388–394. https://doi.org/10.1093/jof/39.4.388

Caon, L., Vallejo, V. R., Ritsema, C. J., & Geissen, V. (2014). Effects of wildfire on soil nutrients in Mediterranean ecosystems. Earth-Science Reviews, 139, 47–58. https://doi.org/10.1016/j.earscirev.2014.09.001

Capitanio, R., & Carcaillet, C. (2008). Post-fire Mediterranean vegetation dynamics and diversity: A discussion of succession models. Forest Ecology and Management, 255(3), 431–439. https://doi.org/10.1016/j.foreco.2007.09.010

Certini, G. (2005). Effects of fire on properties of forest soils: A review. *Oecologia*, *143*(1), 1–10. https://doi.org/10.1007/s00442-004-1788-8

Climent, J., Prada, M. A., Calama, R., Chambel, M. R., Sànchez de Ron, D., & Alía, R. (2008). To grow or to seed: Ecotypic variation in reproductive allocation and cone production by young female Aleppo pine (Pinus halepensis, Pinaceae). *American Journal of Botany*, *95*(7), 833–842. https://doi.org/10.3732/ajb.2007354

Daskalakou, E. N., & Thanos, C. A. (1996). Aleppo Pine (Pinus Halepensis) Postfire Regeneration: The Role of Canopy and Soil Seed Banks. *International Journal of Wildland Fire*, *6*(2), 59–66. https://doi.org/10.1071/wf9960059

DeRose, R. J., & Long, J. N. (2014). Resistance and Resilience: A Conceptual Framework for Silviculture. *Forest Science*, *60*(6), 1205–1212. https://doi.org/10.5849/forsci.13-507

Fernández-García, V., Fulé, P. Z., Marcos, E., & Calvo, L. (2019). The role of fire frequency and severity on the regeneration of Mediterranean serotinous pines under different environmental conditions. *Forest Ecology and Management*, *444*, 59–68. https://doi.org/10.1016/j.foreco.2019.04.040

Fréjaville, T., & Curt, T. (2017). Seasonal changes in the human alteration of fire regimes beyond the climate forcing. *Environmental Research Letters*, *12*(3), 035006. https://doi.org/10.1088/1748-9326/aa5d23

GeoVeg. (2014). *Vegetation Map of Catalonia [Catalan].* [Map]. Grup de recerca de Geobotànica i Cartografia de la Vegetació. http://www.ub.edu/geoveg/cast/mapes.php#veg

Girard, F., Vennetier, M., Guibal, F., Corona, C., Ouarmim, S., & Herrero, A. (2012). Pinus halepensis Mill. Crown development and fruiting declined with repeated drought in Mediterranean France. *European Journal of Forest Research*, *131*(4), 919–931. https://doi.org/10.1007/s10342-011-0565-6

Gómez-Aparicio, L. (2008). Spatial patterns of recruitment in Mediterranean plant species: Linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of Ecology*, 96(6), 1128–1140. https://doi.org/10.1111/j.1365-2745.2008.01431.x

Gómez-Plaza, A., Martínez-Mena, M., Albaladejo, J., & Castillo, V. M. (2001). Factors regulating spatial distribution of soil water content in small semiarid catchments. *Journal of Hydrology*, *253*(1), 211–226. https://doi.org/10.1016/S0022-1694(01)00483-8

González-De Vega, S., De las Heras, J., & Moya, D. (2018). Post-Fire Regeneration and Diversity Response to Burn Severity in Pinus halepensis Mill. Forests. *Forests*, *9*(6), Article 6. https://doi.org/10.3390/f9060299

568 Grime, J. P. (1973). Competitive Exclusion in Herbaceous Vegetation. Nature, 242(5396), 344–347.
569 https://doi.org/10.1038/242344a0
570 Guz, J., Gill, N. S., & Kulakowski, D. (2021). Long-term empirical evidence shows post-disturbance
571 climate controls post-fire regeneration. *Journal of Ecology*, *109*(12), 4007–4024.
572 https://doi.org/10.1111/1365-2745.13771
573 ICGC. Institut Cartogràfic i Geològic de Catalunya. (2017). *Map of bio-physical variables of Catalan*
574 *forested areas [Catalan]* [Map]. Generalitat de Catalunya. https://www.icgc.cat/ca
575 ICGC. Institut Cartogràfic i Geològic de Catalunya. (2022). *Map of Soils of Catalonia 1:25.000, Soil*
576 *Taxonomy [Catalan]* [Map]. Generalitat de Catalunya. https://www.icgc.cat/ca/
577 Ireland, G., & Petropoulos, G. P. (2015). Exploring the relationships between post-fire vegetation
578 regeneration dynamics, topography and burn severity: A case study from the Montane
579 Cordillera Ecozones of Western Canada. *Applied Geography*, *56*, 232–248.
580 https://doi.org/10.1016/j.apgeog.2014.11.016
581 Keeley, J. E. (2012). Ecology and evolution of pine life histories. *Annals of Forest Science*, *69*(4),
582 Article 4. https://doi.org/10.1007/s13595-012-0201-8
583 Keeley, J. E., Bond, W. J., Bradstock, R. A., Pausas, J. G., & Rundel, P. W. (2011). *Fire in Mediterranean*
584 *Ecosystems: Ecology, Evolution and Management*. Cambridge University Press.
585 Keeley, J. E., & Keeley, S. C. (1981). Post-Fire Regeneration of Southern California Chaparral.
586 *American Journal of Botany*, *68*(4), 524–530. https://doi.org/10.2307/2443028
587 Key, C. H., & Benson, N. C. (2006). Landscape Assessment (LA). *In: Lutes, Duncan C.; Keane, Robert E.;*
588 *Caratti, John F.; Key, Carl H.; Benson, Nathan C.; Sutherland, Steve; Gangi, Larry J. 2006.*
589 *FIREMON: Fire Effects Monitoring and Inventory System. Gen. Tech. Rep. RMRS-GTR-164-CD.*
590 *Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research*
591 *Station. p. LA-1-55*, *164*. https://research.fs.usda.gov/treesearch/24066
592 Kosmas, C., Kairis, O., Karavitis, C., Acikalin, S., Alcalá, M., Alfama, P., et al. (2015). An exploratory
593 analysis of land abandonment drivers in areas prone to desertification. *CATENA*, *128*, 252–
594 261. https://doi.org/10.1016/j.catena.2014.02.006
595 Kottek, M., Grieser, J., Beck, C., Rudolf, B., & Rubel, F. (2006). World Map of the Köppen-Geiger
596 climate classification updated. *Meteorologische Zeitschrift*, *15*(3), 259–263.
597 https://doi.org/10.1127/0941-2948/2006/0130
598 Kouba, Y., Martínez-García, F., Frutos, Á. de, & Alados, C. L. (2015). Effects of Previous Land-Use on
599 Plant Species Composition and Diversity in Mediterranean Forests. *PLOS ONE*, *10*(9),
600 e0139031. https://doi.org/10.1371/journal.pone.0139031

601 Kutiel, P. (1997). Spatial and Temporal Heterogeneity of Species Diversity in a Mediterranean
602 Ecosystem Following Fire. *International Journal of Wildland Fire*, *7*(4), 307–315.
603 https://doi.org/10.1071/wf9970307
604 Lasanta, T., Arnáez, J., Pascual, N., Ruiz-Flaño, P., Errea, M. P., & Lana-Renault, N. (2017). Space–time
605 process and drivers of land abandonment in Europe. *CATENA*, *149*, 810–823.
606 https://doi.org/10.1016/j.catena.2016.02.024
607 Lavorel, S., Lepart, J., Debussche, M., Lebreton, J.-D., & Beffy, J.-L. (1994). Small Scale Disturbances
608 and the Maintenance of Species Diversity in Mediterranean Old Fields. *Oikos*, *70*(3), 455–
609 473. https://doi.org/10.2307/3545786
610 Lloret, F., Calvo, E., Pons, X., & Díaz-Delgado, R. (2002). Wildfires and landscape patterns in the
611 Eastern Iberian Peninsula. *Landscape Ecology*, *17*(8), 745–759.
612 https://doi.org/10.1023/A:1022966930861
613 Lloret, F., & Vilá, M. (2003). Diversity patterns of plant functional types in relation to fire regime and
614 previous land use in Mediterranean woodlands. *Journal of Vegetation Science*, *14*(3), 387–
615 398. https://doi.org/10.1111/j.1654-1103.2003.tb02164.x
616 López-Soria, L., & Castell, C. (1992). Comparative genet survival after fire in woody Mediterranean
617 species. *Oecologia*, *91*(4), 493–499. https://doi.org/10.1007/BF00650321
618 Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P., & Makowski, D. (2021). performance: An R
619 Package for Assessment, Comparison and Testing of Statistical Models. *Journal of Open*
620 *Source Software*, *6*(60), 3139. https://doi.org/10.21105/joss.03139
621 Martín-Alcón, S., & Coll, L. (2016). Unraveling the relative importance of factors driving post-fire
622 regeneration trajectories in non-serotinous *Pinus nigra* forests. *Forest Ecology and*
623 *Management*, *361*, 13–22. https://doi.org/10.1016/j.foreco.2015.11.006
624 Martini, F. (2024). On the definition of tree seedlings. Plant Ecology, 225(1), 75–79.
625 https://doi.org/10.1007/s11258-023-01378-2
626 Marull, J., Otero, I., Stefanescu, C., Tello, E., Miralles, M., Coll, F., et al. (2015). Exploring the links
627 between forest transition and landscape changes in the Mediterranean. Does forest
628 recovery really lead to better landscape quality? *Agroforestry Systems*, *89*(4), 705–719.
629 https://doi.org/10.1007/s10457-015-9808-8
630 Marzano, R., Lingua, E., & Garbarino, M. (2012). Post-fire effects and short-term regeneration
631 dynamics following high-severity crown fires in a Mediterranean forest. *iForest -*
632 *Biogeosciences and Forestry*, *5*(1), 93–100. https://doi.org/10.3832/ifor0612-005

633 Mendez-Cartin, A. L., Coll, L., Krawchuk, M. A., Gelabert, P. J., Fontova-Musté, A., & Ameztegui, A.
634 (2025). Biophysical drivers of Pinus nigra subsp. salzmannii post-fire regeneration: Role of
635 fire refugia. Landscape Ecology, 40(4), 79. https://doi.org/10.1007/s10980-025-02093-1
636 Miller, J. D., & Thode, A. E. (2007). Quantifying burn severity in a heterogeneous landscape with a
637 relative version of the delta Normalized Burn Ratio (dNBR). *Remote Sensing of Environment*,
638 *109*(1), 66–80. https://doi.org/10.1016/j.rse.2006.12.006
639 MITECO. (2006). *Map of Forests of Spain (MFE50) [Spanish]* [Map]. Ministerio para la Transición
640 Ecológica y el Reto Demográfico.
641 https://www.miteco.gob.es/es/biodiversidad/servicios/banco-datos-
642 naturaleza/informacion-disponible/mfe50.html
643 Moreira, F., Viedma, O., Arianoutsou, M., Curt, T., Koutsias, N., Rigolot, E., et al. (2011). Landscape –
644 wildfire interactions in southern Europe: Implications for landscape management. *Journal of*
645 *Environmental Management*, *92*(10), 2389–2402.
646 https://doi.org/10.1016/j.jenvman.2011.06.028
647 Moya, D., González-De Vega, S., García-Orenes, F., Morugán-Coronado, A., Arcenegui, V., Mataix-
648 Solera, J., et al. (2018). Temporal characterisation of soil-plant natural recovery related to
649 fire severity in burned *Pinus halepensis* Mill. Forests. *Science of The Total Environment*, *640–*
650 *641*, 42–51. https://doi.org/10.1016/j.scitotenv.2018.05.212
651 Moya, D., Sagra, J., Lucas-Borja, M. E., Plaza-Álvarez, P. A., González-Romero, J., De Las Heras, J., et
652 al. (2020). Post-Fire Recovery of Vegetation and Diversity Patterns in Semiarid Pinus
653 halepensis Mill. Habitats after Salvage Logging. *Forests*, *11*(12), Article 12.
654 https://doi.org/10.3390/f11121345
655 Moya, D., Saracino, A., Salvatore, R., Lovreglio, R., de Las Heras, J., & Leone, V. (2008). Anatomic
656 basis and insulation of serotinous cones in Pinus halepensis Mill. *Trees*, *22*(4), 511–519.
657 https://doi.org/10.1007/s00468-008-0211-1
658 Nathan, R., & Ne'eman, G. (2000). Serotiny, seed dispersal and seed predation in Pinus halepensis. In
659 *Ecology, biogeography and management of Pinus halepensis and Pinus brutia forest*
660 *ecosystems in the Mediterranean Basin* (pp. 105–118). Bachuys publisher.
661 Naveh, Z. (2007). Fire in the Mediterranean – A Landscape Ecological Perspective In: Goldammer,
662 J.F., Jenkins M.J. (Eds.) Fire in Ecosystems Dynamics. Proceedings of the Third International
663 Symposium in Freiburg, FRG, May 1989. SPB Academic Publishing by, the Hague, the
664 Netherlands, pp. 1–20. In Z. Naveh (Ed.), *Transdisciplinary Challenges in Landscape Ecology*
665 *and Restoration Ecology: An Anthology with Forewords by E. Laszlo and M. Antrop and*

Epilogue by E. Allen (pp. 95–115). Springer Netherlands. https://doi.org/10.1007/1-4020-4422-4_3

Noble, I. R., & Slatyer, R. O. (1980). The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. *Vegetatio*, *43*(1), 5–21. https://doi.org/10.1007/BF00121013

Nolan, R. H., Collins, L., Leigh, A., Ooi, M. K. J., Curran, T. J., Fairman, T. A., et al. (2021). Limits to post-fire vegetation recovery under climate change. *Plant, Cell & Environment*, *44*(11), 3471–3489. https://doi.org/10.1111/pce.14176

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., et al. (2022). *_vegan: Community Ecology Package_* (Version R package version 2.6-4) [Computer software]. <https://CRAN.R-project.org/package=vegan>

Paneghel, M., Torné, G., Morin, X., Alday, J. G., & Coll, L. (2024). Increasing temperature threatens post-fire auto-successional dynamics of a Mediterranean obligate seeder. *Journal of Ecology*. https://doi.org/10.1111/1365-2745.14433

Pausas, J. G., Bradstock, R. A., Keith, D. A., & Keeley, J. E. (2004a). Plant Functional Traits in Relation to Fire in Crown-Fire Ecosystems. *Ecology*, *85*(4), 1085–1100. https://doi.org/10.1890/02-4094

Pausas, J. G., Carbó, E., Neus Caturla, R., Gil, J. M., & Vallejo, R. (1999). Post-fire regeneration patterns in the eastern Iberian Peninsula. *Acta Oecologica*, *20*(5), 499–508. https://doi.org/10.1016/S1146-609X(00)86617-5

Pausas, J. G., Ouadah, N., Ferran, A., Gimeno, T., & Vallejo, R. (2002). Fire severity and seedling establishment in Pinus halepensis woodlands, eastern Iberian Peninsula. *Plant Ecology*, *169*(2), 205–213. https://doi.org/10.1023/A:1026019528443

Pausas, J. G., Ribeiro, E., & Vallejo, R. (2004). Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. *Forest Ecology and Management*, *203*(1), 251–259. https://doi.org/10.1016/j.foreco.2004.07.061

Puerta-Piñero, C., Espelta, J. M., Sánchez-Humanes, B., Rodrigo, A., Coll, L., & Brotons, L. (2012). History matters: Previous land use changes determine post-fire vegetation recovery in forested Mediterranean landscapes. *Forest Ecology and Management*, *279*, 121–127. https://doi.org/10.1016/j.foreco.2012.05.020

Quézel, P. (2000). Taxonomy and biogeography of Mediterranean pines (Pinus halepensis and P. brutia). In *Ecology, biogeography and management of Pinus halepensis and P. brutia forest ecosystem in the Mediterranean Basin* (pp. 1–12). Bachuys publisher.

R Core Team. (2024). *R: a language and environment for statistical computing* [Computer software]. R Foundation for Statistical Computing. https://www.R-project.org/

Retana, J., Maria Espelta, J., Habrouk, A., Luis OrdoÑEz, J., & de Solà-Morales, F. (2002). Regeneration patterns of three Mediterranean pines and forest changes after a large wildfire in northeastern Spain. *Écoscience*, *9*(1), 89–97. https://doi.org/10.1080/11956860.2002.11682694

Robichaud, P. R., & Waldrop, T. A. (1994). A Comparison of Surface Runoff and Sediment Yields from Low- and High-Severity Site Preparation Burns. *JAWRA Journal of the American Water Resources Association*, *30*(1), 27–34. https://doi.org/10.1111/j.1752-1688.1994.tb03270.x

Rodrigo, A., Retana, J., & Picó, F. X. (2004). Direct Regeneration Is Not the Only Response of Mediterranean Forests to Large Fires. *Ecology*, *85*(3), 716–729. https://doi.org/10.1890/02-0492

Romeo, F., Marziliano, P. A., Turrión, M. B., & Muscolo, A. (2020). Short-term effects of different fire severities on soil properties and Pinus halepensis regeneration. *Journal of Forestry Research*, *31*(4), 1271–1282. https://doi.org/10.1007/s11676-019-00884-2

Ruffault, J., Curt, T., Moron, V., Trigo, R. M., Mouillot, F., Koutsias, N., et al. (2020). Increased likelihood of heat-induced large wildfires in the Mediterranean Basin. *Scientific Reports*, *10*(1), Article 1. https://doi.org/10.1038/s41598-020-70069-z

San-Miguel-Ayanz, J., Rodrigues, M., de Oliveira, S. S., Pacheco, C. K., Moreira, F., Duguy, B., et al. (2012). Land Cover Change and Fire Regime in the European Mediterranean Region. In F. Moreira, M. Arianoutsou, P. Corona, & J. De las Heras (Eds.), *Post-Fire Management and Restoration of Southern European Forests* (pp. 21–43). Springer Netherlands. https://doi.org/10.1007/978-94-007-2208-8_2

Santana, V. M., Alday, J. G., & Baeza, M. J. (2014). Effects of fire regime shift in Mediterranean Basin ecosystems: Changes in soil seed bank composition among functional types. *Plant Ecology*, *215*(5), 555–566. https://doi.org/10.1007/s11258-014-0323-1

Scott, A. C. (2000). The Pre-Quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, *164*(1), 281–329. https://doi.org/10.1016/S0031-0182(00)00192-9

Sivrikaya, F., & Demirel, D. (2025). Fire risk mapping using machine learning method and remote sensing in the Mediterranean region. *Advances in Space Research*. https://doi.org/10.1016/j.asr.2025.01.050

Tavşanoğlu, Ç., & Pausas, J. G. (2018). A functional trait database for Mediterranean Basin plants. *Scientific Data*, *5*(1), 180135. https://doi.org/10.1038/sdata.2018.135

Thanos, C. A., Daskalakou, E. N., & Nikolaidou, S. (1996). Early post-fire regeneration of a Pinus halepensis forest on Mount Párnis, Greece. *Journal of Vegetation Science*, *7*(2), 273–280. https://doi.org/10.2307/3236328

Tsitsoni, T. (1997). Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests of Kassandra Peninsula (North Greece). *Forest Ecology and Management*, *92*(1), 199–208. https://doi.org/10.1016/S0378-1127(96)03909-6

Turco, M., Rosa-Cánovas, J. J., Bedia, J., Jerez, S., Montávez, J. P., Llasat, M. C., et al. (2018). Exacerbated fires in Mediterranean Europe due to anthropogenic warming projected with non-stationary climate-fire models. *Nature Communications*, *9*(1), Article 1. https://doi.org/10.1038/s41467-018-06358-z

Vallejo, V. R., Arianoutsou, M., & Moreira, F. (2012). Fire Ecology and Post-Fire Restoration Approaches in Southern European Forest Types. In F. Moreira, M. Arianoutsou, P. Corona, & J. De las Heras (Eds.), *Post-Fire Management and Restoration of Southern European Forests* (pp. 93–119). Springer Netherlands. https://doi.org/10.1007/978-94-007-2208-8_5

Venables, W. N., & Ripley, B. D. (2002). *Modern Applied Statistics with S. Fourth Edition* [S]. Springer.

Verdú, M. (2000). Ecological and evolutionary differences between Mediterranean seeders and resprouters. *Journal of Vegetation Science*, *11*(2), 265–268. https://doi.org/10.2307/3236806

Viana-Soto, A., Aguado, I., & Martínez, S. (2017). Assessment of Post-Fire Vegetation Recovery Using Fire Severity and Geographical Data in the Mediterranean Region (Spain). *Environments*, *4*(4), Article 4. https://doi.org/10.3390/environments4040090

Vilà-Cabrera, A., Astigarraga, J., Jump, A. S., Zavala, M. A., Seijo, F., Sperlich, D., et al. (2023). Anthropogenic land-use legacies underpin climate change-related risks to forest ecosystems. *Trends in Plant Science*, *28*(10), 1132–1143. https://doi.org/10.1016/j.tplants.2023.04.014

Walck, J. L., Hidayati, S. N., Dixon, K. W., Thompson, K., & Poschlod, P. (2011). Climate change and plant regeneration from seed. *Global Change Biology*, *17*(6), 2145–2161. https://doi.org/10.1111/j.1365-2486.2010.02368.x

WFO. (2024). *WFO. The World Flora Online.* https://www.worldfloraonline.org/