

Predicting natural hyperdense regeneration after wildfires in *Pinus halepensis* (Mill.) forests using prefire site factors, forest structure and fire severity

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ABSTRACT

Postfire *Pinus halepensis* (Aleppo pine) regeneration is often hyperdense. The overstocked stands created by this hyperdense regeneration considerably increase the risk of biotic and abiotic disturbances, especially fires, by increasing the potential for widespread forest losses. Our aim was to understand the relation between prefire site factors (climate, geographical position, topography, soil), prefire forest structure variables and fire severity with regeneration density after fire. We specifically wondered: (1) what are the general drivers of natural regeneration in these forests after fire? (2) what are the necessary prefire conditions for establishing Aleppo pine hyperdense regenerations (> 4,000 plants/ha)? To answer these questions, we sampled 147 plots in 15 wildfires located in the Comunitat Valenciana, which were representative of Aleppo pine Mediterranean forests. We used full and partial redundancy analyses (RDAs) for variance partitioning, and a decision tree analysis to look for the key site factors that drive

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regeneration density after fire. We found that all the site factors measured in the study explained 34.4% of total variation in regeneration density. Prefire site factors and fire severity together explained 28.4% of total variability, while the measured postfire factors explained only 7.5%. Forest structure and climate explained 8.3% and 6.7% of variation, respectively. Five specific site factors drove regeneration density after fire: average minimum temperature, tree density before fire, resprouting shrubs coverage before fire, soil depth and bedrock type. The conclusions of this study were: (i) the average minimum temperature was the main significant variable that classified regeneration density and split data into three significant groups of Aleppo pine burned sites; (ii) the prefire forest structure (overstorey density and understorey coverage) controls regeneration density at colder burned sites, but soil depth and bedrock can be more important at warmer sites; (iii) fire severity relates positively to pine regeneration density, but negatively to resprouting vegetation coverage after fire; (iv) overstocked stands are not expected if prefire stand density is below 100 trees/ha at colder burned sites. These results may facilitate the planning of forest management and restoration actions because it may be used to identify those areas more likely to regenerate overstocked stands when faced with a changing fire regime.

Key words: Aleppo pine/ postfire/ hyperdense natural regeneration/ overstocked stand/ prefire site factors/ forest structure/ fire severity/ decision tree analysis.

1 INTRODUCTION

Aleppo pine (*Pinus halepensis* Miller) is a widely distributed tree species in the western Mediterranean Basin (Del Río et al., 2008; Gil et al., 1996), where wildfires have long since a keystone natural disturbance that impinges the regeneration of dominated and co-dominated Aleppo pine forests (hereafter referred to as Aleppo pine forests). Post fire Aleppo pine regeneration is a highly density variable that frequently reaches a density that is similar to, or higher than, prefire conditions. However, such regeneration can be extremely high, and has even been described as explosive, massive or overstocked (Broncano and Retana, 2004; Daskalidou and Thanos, 2004; Del Río et al., 2008; García-Jiménez et al., 2017; Gil et al., 1996; Hernández-Serrano et al., 2013; Moghli et al., 2021; Thanos and Doussi, 2000). Hyperdense natural regenerations could be defined as those with densities exceed 4,000 plants/ha in Mediterranean forests (but they can reach densities of >100,000 plants/ha (De las Heras et al., 2012), and pose a serious forest management problem due to economic costs (e.g. clearcutting cost) and environmental disturbances. For instance, overstocked and highly flammable stands can lead to a higher fire risk due to their homogeneous (poor) structure, fuel continuity, and high dead fine biomass density as a result of plant competition (Alfaro-Sánchez et al., 2015a). Moreover, these overstocked stands suffer from growth stagnation and delayed reproduction (Espelta et al., 2008; García-Jiménez et al., 2017; Ruano et al., 2013; Verkaik and Espelta, 2006) which make them more vulnerable to biotic disturbances (e.g. inter- and intraspecific competition; De las Heras et al. 2002). Abiotic disturbances, such as drought (Espelta et al. 2011), but specially high-intensity stand replacing fires (Palmero-Iniesta et al., 2017), also increase the potential for generalised forest losses (Rodman et al., 2020; Stevens-Rumann and Morgan, 2019) due to the immaturity risk (Ne'eman et al., 2004), i.e. the risk that a new wildfire occurs before the new canopy seed bank has developed (Espelta et al., 2008; Palmero-Iniesta et al., 2017). This potential forests loss by fire recurrence can also lead to severe ecosystem degradation through significant changes in species composition (Santana et al., 2010) and losses in soil fertility (Mayor et al., 2016).

Despite the widespread interest in understanding the ecological factors that drive postfire natural regeneration in Aleppo pine forests, identifying key prefire site conditions to predict suitable sites for hyperdense regeneration is still an important goal. Site factors may include climatic, physiographic and soil factors, as well as biotic factors, that define the habitat, and involve interactions with associated plants, animals and microorganisms

above and below ground (Barnes et al., 1998). Site factors and stand structure before fire may exert bottom-up control on fire severity conditions (García-Llamas et al., 2019), and may act as postfire filters of plant establishment (Duguy and Vallejo, 2008; Pausas and Keeley, 2014). These filters can be, for example, topographic and climatic factors (Broncano and Retana, 2004; García-Llamas et al., 2019; Mitsopoulos et al., 2019; Mitsopoulos and Xanthopoulos, 2016), prefire forest structure and development (Broncano and Retana, 2004; García-Jiménez et al., 2017), tree density and stand dominant height (Alfaro-Sánchez et al., 2015b; Mitsopoulos and Xanthopoulos, 2016), as well as mother trees' spatial structure (Ne'eman and Izhaki, 1998). Some studies have pointed out that there is no clear relation between fire severity and postfire seedling density (Pausas et al., 2003). However, fire severity appears to be a key driver of Aleppo pine regeneration, especially through changes in the soil-plant interphase (Moya et al., 2018, 2020); that is, in soil biochemical properties and microbial communities.

Doubtlessly Aleppo pine traits make this species regenerate well after fire (Ne'eman et al., 2004). For instance, many provenances present reproductive precocity at an age of 3-6 years (Climent et al., 2008; Ne'eman et al., 2004; Santos-del-Blanco et al., 2013; Tapias et al., 2001; Vega-Hidalgo, 2003; Zagas et al., 2004), which has been related to low to moderate return (20-25 years) fire intervals (Tapias et al., 2001; Vega-Hidalgo, 2003). Although seeds are already ripe by late spring, cones open gradually only in late summer and autumn (Thanos, 2000; Thanos and Doussi, 2000), when most highly destructive fires take place in Mediterranean ecosystems (Thanos and Doussi, 2000). Aleppo pine has serotinous cones (Gil et al., 1996; Ne'eman et al., 2004) with viable seeds that remain closed on trees for years until the high temperatures created by fire open them and massive seed dissemination occurs (Thanos and Doussi, 2000). Serotiny is a heritable trait in Aleppo pine (Hernández-Serrano et al., 2014; Santos-del-Blanco et al., 2010; 2013) and provenances differences in this trait could reflect divergent evolution related to different fire regimes (Climent et al., 2008; Santos-del-Blanco et al., 2013; Tapias et al., 2001). Seeds germinate best on bare soil (Gil et al., 1996; Thanos, 2000), which fire exposes by consuming understorey vegetation, litter and other surface fuels. Besides, Aleppo pine is a pioneer species (Ne'eman et al., 2004) and its growth is favoured by forest gaps created by fire (Gil et al., 1996).

Postfire Aleppo pine regeneration can be hyperdense and creates overstocked regeneration stands because of substantial cone production. The high serotiny of Aleppo

pine allows a copious canopy seed bank to accumulate in mature stands, ranging from 33,000 to 1 million seeds/ha (*sensu* Tapias et al. 2001). Aleppo pine forests are among the key components of Mediterranean Basin vegetation affected by large wildfires, and this disturbance is expected to continue to be a major disturbance in forthcoming decades (Dupuy et al., 2020). Land abandonment, joint hotter and drier conditions brought about by climate change will mean more frequent events when fire will go beyond the extinction capacity by burning extensive areas (Tedim et al., 2018). As a main vegetation component, it is very important to understand the factors controlling Aleppo pine's regeneration capacity after fire to design postfire restoration strategies and fuel management. Here we propose analysing the effects of multifactor interactions on *Pinus halepensis* regeneration density, which was evaluated in 15 wildfires located in the Comunitat Valenciana, eastern Spain. The working hypothesis was that Aleppo pine regeneration density could be predicted by the prefire forest structure, climate, topography and soil, geographical position and fire severity variables. We specifically wondered: (1) what are the general drivers of natural regeneration in these forests after fire?; (2) what are the necessary prefire conditions for establishing hyperdense regenerations (>4,000 plants/ha) and producing overstocked stands?

2 METHODOLOGY

2.1 Study sites

Our study was designed to understand the relation linking prefire site factors, forest structure and fire severity conditions, with the regeneration capacity of forests dominated by *Pinus halepensis* (Aleppo pine). We sampled 147 plots in 15 different wildfires (burned sites) located in the Comunitat Valenciana, and distributed along the Iberic and Pre-Baetic Systems (Fig. 1). Altitudes range from 110 to 823 m.a.s.l. (Table 1). The average annual precipitation at our burned sites falls within the 350-1,029 mm range, while the mean annual temperature goes from 14.7 to 18.2°C. Of the 147 sampled plots, 51.7% had arid conditions, 40.8% were semiarid, and 7.5% presented humid conditions (De Martonne, 1926), (Fig. A1). Despite this variability, the burned sites share a Mediterranean-type climate with moist, mild winters, precipitation occurring mainly in autumn and spring, and dry and hot summers, which favour large wildfires (Diaz-Delgado et al., 2002). Soils present similarities and mostly develop on dolomitic limestones and marls. The prime landscape physiognomy is a steep orography sprinkled frequently with agricultural lands (terraces), mainly olive, almond and carob trees, which are often

abandoned and colonised by forest vegetation. Shrub and herbaceous species in the understory are also similar among sites. All the sites share resprouting shrub species, such as *Quercus coccifera*, *Pistacia lentiscus* and *Rhamnus lycioides*, and obligate seeder shrubs like *Ulex parviflorus*, *Cistus salviifolius* and *Salvia rosmarinus*. The dominant resprouting species in the herbaceous stratum was *Brachypodium retusum*. Depending on the site, we found very few isolated trees of *Pinus pinaster*, *P. pinea*, *Quercus suber* or *Q. ilex*.

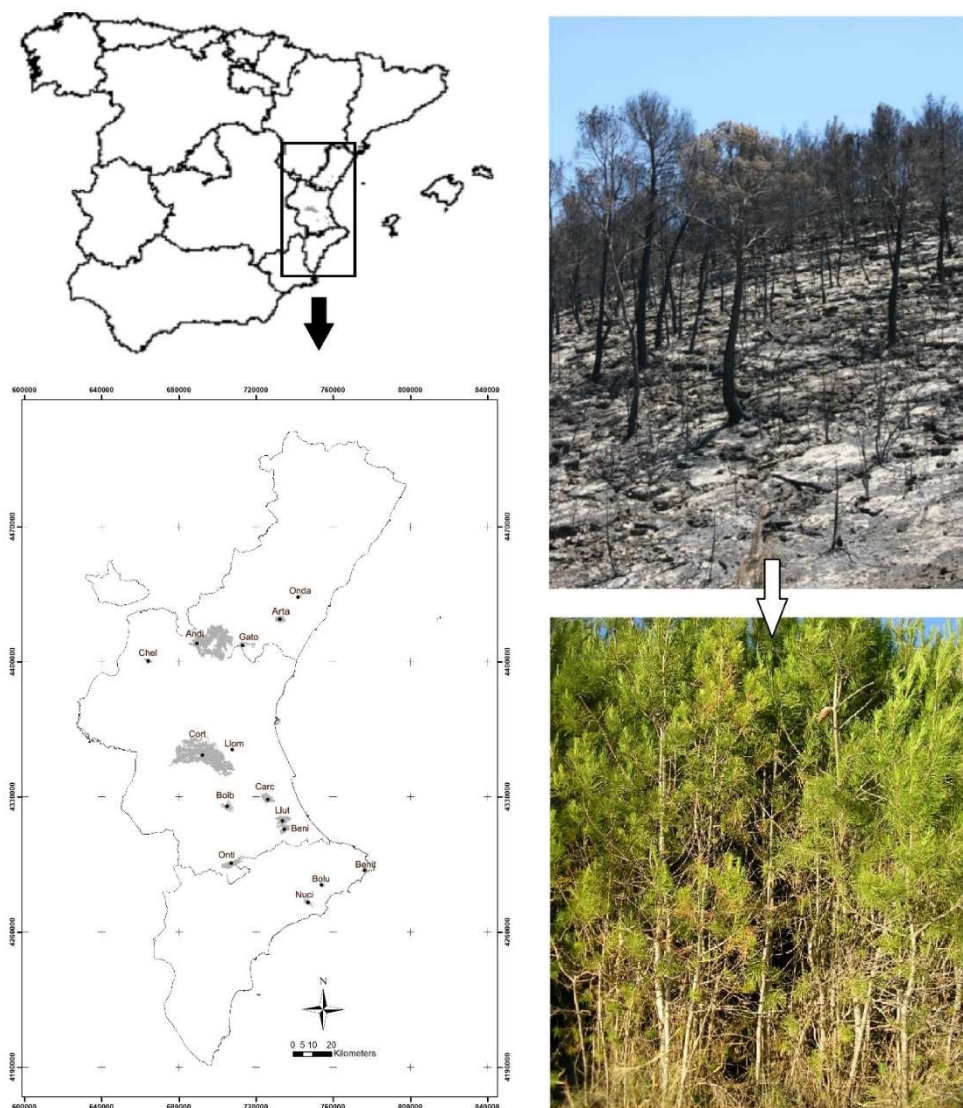


Figure 1. Maps of the study sites in the Comunitat Valenciana (Spain) showing the 15 wildfires surveyed for postfire vegetation recovery (left side), and images of an Aleppo pine burned forest (Chelva's wildfire) and an overstocked stand with hyperdense natural regeneration established after fire (right side).

Table 1. Characteristics of the 15 wildfires sampled for studying Aleppo pine (*Pinus halepensis*) regeneration in the Comunitat Valenciana (Spain). *Cortes de Pallás; Stand age: time elapsed from the fire to the evaluation sampling of Aleppo pine regeneration. Alt.: altitude; N: number of sampled plots; TM (°C): average annual temperature; TMax (°C): average maximum temperature; TMin (°C): average minimum temperature; AAP (mm): average annual precipitation.

Fire name	Fire season & year	Burned area (ha)	N	Stand age (n° years)	Alt (m.a.s.l.)	X coordinate (m)	Y coordinate (m)	TM (°C)	Tmax (°C)	Tmin (°C)	AAP (mm)
La Nucía	Winter 2009	960	5	12	670	746935	4275459	15.6	20.6	10.7	350
Onda	Summer 2009	316	6	12	143	741750	4433581	15.9	21.5	10.3	487
Ontinyent	Summer 2010	1957	6	11	611	707297	4295651	15.1	20.8	9.4	586
Benicolet	Spring 2011	1449	8	10	353	734829	4313292	17.4	23.0	11.7	832
Llombai	Summer 2011	104	6	10	192	707700	4354474	17.7	23.3	12.1	576
Chelva	Spring 2012	702	12	9	674	664149	4400478	15.5	21.8	9.2	435
Cortes*	Summer 2012	28879	14	9	460	692364	4351662	17.3	23.4	11.2	463
Andilla	Summer 2012	19985	23	9	823	689493	4409562	15.9	21.6	10.3	494
Bolbaite	Spring 2016	1536	12	2	221	705111	4325285	17.2	22.9	11.5	538
Carcaixent	Spring 2016	2211	7	2	235	726263	4328642	16.9	22.8	10.9	679
Artana	Summer 2016	1584	15	2	371	732330	4422109	16.6	21.5	11.8	566
Benitatxell	Summer 2016	698	11	2	110	776373	4292017	18.2	21.9	14.5	587
Bolulla	Summer 2016	447	7	2	339	754036	4284523	15.6	20.6	10.7	718
Gátova	Summer 2017	1181	7	3	531	713162	4408571	15.8	20.6	10.9	446
Llutxent	Summer 2018	3147	6	3	450	733667	4317673	16.9	22.7	11.2	967

2.2 Sampling plots selection and data collection

In the perimeter of each fire, a systematic grid of points was used for selecting field sampling points. Distance between points and the final number of sampled plots in each wildfire varied depending on the size of the burned area (Table 1), but an attempt was made to reach at least 6 points for fires < 500 ha, 25 for fires < 2,500 ha, and 50 points for fires > 5,000 ha (Alloza et al., 2014). As our study focused on *P. halepensis* regeneration patterns, in the analysis we only used the sampling plots where this species was present before fire (147 points extracted from a total of 423 initially sampled in different vegetation types; e.g., *Pinus pinaster* or *Quercus ilex* forests and shrublands). All data are available and can be consulted in the online platform POSTFIRE (<https://postfire.es/>). For the location of the sampling points, locations close to fire perimeter were tried to avoid. Thus, as we were working within large burned areas, distance to unburned areas did not have an effect on post-fire regeneration. Field sampling was carried out using circular plots of a 20-metre radius. No sampled plots had been burned in the previous 25 years to the studied fire. The present research work involved sampling twice, following the protocol designed by Alloza et al. (2014) for managing Mediterranean burned areas. The first postfire sampling aimed to assess prefire site conditions, such as topography, soil erosion signs, forest structure, species composition and fire impact (severity) on both soil and vegetation. Field sampling was carried out as soon as possible after fire extinction and no later than 2 or 3 weeks after fires. The second postfire sampling consisted in revisiting the sampling plots to evaluate vegetation recovery and Aleppo pine regeneration after fire. This sampling was preferentially carried out 2 years after fire. However, we had sites burned for a longer time where the impact assessment made immediately after the fire was performed but without the subsequent data from the natural regeneration. Thus, to increase sampling size, some wildfires were sampled in 2021 at older ages (up to 12 years old; Table 1), even if more than two years had passed after the fire. The germination and establishment of *P. halepensis* individuals mainly occur in the first and second year after fire, while no significant establishments take place after the second year (Daskalakou and Thanos, 2004, 1996; Thanos and Doussi, 2000). Therefore, and because in the field most of the observed regeneration was of the same height and grade of development, we initially assumed a small-time effect on regenerated pine density. Studied forests mainly came from natural regeneration without silvicultural treatments before fire (direct observation when sampling). Only 11 plots (a

7.4%) were identified as forests from old reforestations (probably from the 60's), one plot had been submitted to a previous thinning and another one to pruning.

2.3 Studied variables

2.3.1 *Geographical position, topography, soil conditions and presence of agricultural terraces*

The geographical position (longitude and latitude with Universal Transverse Mercator coordinates) of each plot was recorded in the field by GPS. Topographical variables, such as altitude (m.a.s.l.), aspect (N, E, S, W) and slope (< 15%, 15-30%, 30-45%, > 45%), were recorded. Microtopography was also checked, for example, throughout the characterization of stoniness on the forest floor (%), which was evaluated by three categories: < 30%, 30-60%, and > 60%. Soil characteristics were assumed to be represented by parent material (bedrock). The dominant bedrock type in the plot was identified (limestone, marl, clay and silt and colluvium), and soil depth (SL, < 30 cm, > 30 cm) was checked by digging. The percentage of bare soil (< 30%, 30-60%; > 60%) in the plot was estimated. The presence, abundance and state of the agricultural terraces around the plot were also recorded. Then soil erosion symptoms (sheet erosion, rills, gullies, badlands, scalding, or collapse of agricultural walls) and their intensity (none, light, moderate, severe, extreme) were evaluated.

2.3.2 *Prefire forest structure: overstorey density, age classes, canopy cover, and understorey coverage.*

The plots selection for our study was restricted to the units where the prefire plant community was a *Pinus halepensis*-dominated forest (100% of the total tree density) or co-dominated forest (60-80% of the total tree density). During the initial postfire sampling, we visually estimated (see Fig. A2) the prefire total tree canopy cover, the Aleppo pine canopy cover (%) and the coverage of other trees (in codominant Aleppo pine forests). Then the proportion was assessed in four different age natural classes (Serrada et al., 2008); (i) sapling or regeneration age class (diameter at breast height (dbh) < 7.5 cm); (ii) thicket class (dbh about 7.5-10 cm) when the crown tangency begins or a height of 130 cm is reached, and remains until natural pruning and the age of the polewood begins); (iii) polewood class (dbh about 10-20 cm), which begins when natural pruning starts and remains until the diameter reaches 20 cm; (iv) old growth class (dbh, >20 cm). The proportion of each class was visually estimated, and their coverages were

calculated in relation to the total pine canopy cover in the plot. For simplicity sake, tree coverage was finally transformed into six classes: 0%, < 20%, 20-40%, 40-60%, 60-80% and > 80%. Prefire Aleppo pine tree density (N/ha) was also calculated by counting the number of standing (or fell out) burned trees in a 10 x10 m squared subplot located in the centre of the main circular plot of a 20-metre radius. Finally, the prefire understorey coverage was also visually estimated for the whole circular plot (Fig. A2). The assessed variables were: total and resprouter shrub species coverages, and total and resprouter herbaceous species coverages. Three categories were used: < 30%, 30-60% and > 60%. We were able to identify the main shrub species by the physiognomy and characteristics of the burned stems that remained standing after fire. For herbs, we searched for remaining culm bases within the sampling plot (Fig. A2). By using wide categorical variables in the assessment of pre-fire canopy and understorey coverage, we simplified the process and reduced possible observer deviances.

2.3.3 Fire severity

Fire severity was visually evaluated during the initial postfire field sampling at three different ecosystem strata: tree canopy, understorey vegetation (shrubs and herbs) and soil (presence of white ashes and % of soil with unburned litter), following the methodology described in Alloza et al. (2014), (Table A1). Four categories were employed for evaluating fire impact on trees and shrubs: low, intermediate, high, very high severity, while fire impact on the herbaceous layer was evaluated by three categories: low, intermediate and high severity. The percentage of unaffected litter and white ash abundance were also visually estimated (Alloza et al., 2014). The white ash abundance categories were none, sporadic (only in some parts of plots) and abundant (generalised presence). With all these variables, the Composite Burn Index (CBI) was calculated with a modification of Key and Benson (2006). The CBI is an approach to derive the index values that summarise general fire effects in an area; that is, the average burn condition or fire severity, on a plot by taking into account all the ecosystem strata (Table A2). The thresholds among severity classes were no effect (0), low severity (0.1-1.24), moderate severity (1.25-2.24) and high severity (2.25-3), (Key and Benson, 2006).

2.3.4 Aleppo pine regeneration, and understorey and soil recovery after fire

These variables were assessed during the second postfire sampling, which consists in revisiting the initial sampling plots several years after fire. The number of regenerated Aleppo pine trees were counted in five squared subplots (2 x 2 m, 4 m²)

displayed in the plot of a 20-metre radius (one subplot in the centre, and one at each cardinal point, separated 10 m from the centre). Total understorey vegetation, resprouters shrubs and herbaceous species, and pine regeneration coverages were visually estimated following the same methodology used during the first sampling. Understorey vegetation recovery was estimated using three coverage classes (< 30%, 30-60%, > 60%), while pine regeneration coverage was recorded as a continuous variable (0-100%). The mean height (cm) for each vegetation stratum (trees, shrubs, herbs) was also estimated. The presence and number of surviving-to-fire Aleppo pine trees were recorded (1/0) along with signs of any management or restoration action performed after fire (e.g., salvage logging, wood removal, mulching, plantation, others). Apart from the variables related to vegetation regeneration, we sampled other ecosystem attributes related to ecosystem functions. Symptoms of soil crusting (none, light, moderate, severe) and soil erosion were evaluated following Alloza et al. (2014). In the plot of a 20-metre radius, the percentage of litter cover (< 30%, 30-60%, > 60%) and litter depth (< 1 cm, 1-3 cm, > 3 cm) were visually estimated.

2.3.5 *Climate*

The average climate variables were assigned to each plot, as well as specific pre- and post-fire seasonal climate variables (close to the fire date). The data employed for climate assignment were selected from the nearest meteorological station within a maximum 25-kilometre radius around each plot. The average annual temperature and precipitation were obtained from Pérez-Cueva (1994) (Table 1). The precipitation variables for the 3 years prior to fire and the first wet season after fire were provided by the AEMET (Agencia Estatal de Meteorología Española; the Spanish State Meteorology Service) (Table A3). Station assignment was carried out by a proximity analysis (Point Distance tool, ArcGIS Desktop). During the selection and debugging process, the stations not identified by their coordinates, invalid measurements, absent and out of rank, duplicate data and incorrect dates were identified and discarded. To be acceptable, a number of valid data from more than 95% of the days during the period in question (2000-2018) was required for each site to ensure continuity in the set of precipitation values.

Along with the average annual temperature and precipitation, which are climatic stress variables (Korb et al., 2019), we calculated the Martonne's Aridity Index for each plot (De Martonne, 1926) as the annual precipitation divided by the average temperature + 10 (>30 humid; 20-30 semiarid; 10-20 arid, 5-10 subdesert; 0-5 desert). The length of

drought periods in the year before the fire, and for the 2 and 3 years prior to the fire (Korb et al., 2019), were calculated as the sum of the days with precipitation below 5 mm. We calculated the total amount of precipitation that had fallen 2 and 3 years before fire, as well as the amount of precipitation that had fallen during the last wet season before the fire date (Tables A3 and A4). These variables were selected because they have been observed to influence pre- and postfire vegetation growth and survival, as well as fire effects. For example, positive climatic anomalies (e.g. more rainfall) can influence prior-to-fire biomass building-up and fire severity because there is more biomass available to burn (Pausas et al., 2003). Korb et al. (2019) has also pointed out a relation between postfire ponderosa pine establishment pulses and precipitation anomalies 1-3 years before fire. We checked the rainy and drought periods immediately before and after fire in each locality, and calculated the prefire last wet season and the postfire first wet season (Tables A3 and A4). For that purpose, we identified the months in which precipitation exceeded 6 mm and had fallen continuously between two dry months (rainfall below 6 mm, but below 6.9 in Llutxent). To standardise among localities, we did not use 5 mm of rainfall as a threshold because the duration of the wet season would have been much longer. The wet season comprised several seasons of the year in most localities (Table A4). We were specifically interested in prefire site conditions, however we also calculated the total amount of precipitation that had fallen during the first wet season after fire because rainfall especially plays an important role in the immediate ecosystem's response to fire (Diaz-Delgado et al., 2002).

2.4 Data analysis

2.4.1 Exploratory analyses

Firstly, we did a data exploratory analysis to describe our sample. Frequency tables and Chi-squared tests were employed with ordinal variables, while descriptive statistics were calculated for continuous variables (Table 2). The mean pine regeneration densities (N/ha) were calculated for each plot and for each burned site. Normality and homoscedasticity were checked with Shapiro-Wilk and Levene tests, respectively. We used Spearman's rank correlation coefficients to check the significant relations between site continuous factors and regeneration density. Correlation analyses were also used to assess collinearity among variables. One of our aims was to relate prefire plot factors to the probabilities of obtaining dense pine regeneration. To this end, we constructed a new categorical variable named *regeneration abundance* with two regeneration density

classes: (i) low or suitable density (< 4,000/ha); (ii) high density (> 4,000/ha). Frequently in these types of hyperdense stands, thinning is carried out to improve forest structure and functionality when postfire regenerations density is 2,000 plants/ha or higher, and by rounding density downwardly to 800-1,600 plants/ha (Alfaro-Sánchez et al., 2015b; De Las Heras et al., 2007; Moghli et al., 2021; Puértolas et al., 2012; Ruano et al., 2013). Thus, to be conservative, and to avoid considering hyperdense stands those near the management limit, we selected 4,000 plants/ha as the threshold for a stand to be considered overstocked (that value left below an accumulated percentage of 56.65% of plots after a frequency analysis of the continuous variable: regeneration density). After categorisation, we explored the significant associations between categorical site factors and density classes by Chi-squared tests. The level of significance was set as a p-value of < 0.05. Analyses were performed with the SPSS 26.0 statistical package.

Table 2. (a) Explanatory and predictors variables used in the multivariate analyses (RDAs and Decision Tree) of the postfire natural Aleppo pine regeneration density across 15 wildfires in the Comunitat Valenciana, Spain. Site factors affiliation, names and units. Q= quantitative; O= ordinal; N= nominal; D= dummy.

Prefire site factors	Variable name	Type	Units
<i>Climate</i>	Average annual temperature	Q	°C
	Average maximum temperature	Q	°C
	Average minimum temperature	Q	°C
	Average annual precipitation	Q	mm
	Martonne's aridity index	Q	-
	Total precipitation in the prefire last wet season	Q	mm
	Average annual precipitation 2 years before fire	Q	mm
	Average annual precipitation 3 years before fire	Q	mm
	Drought length 1 year before fire	Q	No. of days
	Drought length 2 years before fire	Q	No. of days
	Drought length 3 years before fire	Q	No. of days
<i>Geography</i>	Longitude	Q	°
	Latitude	Q	°
	Altitude	Q	m.a.s.l.
<i>Topography and Soil</i>	Aspect	O	-
	Slope	O	%
	Dominant bedrock	N	-
	Stoniness	O	%
	Soil layer depth	O	cm
	Presence of agricultural terraces	O	No.
	Signs of soil erosion	O	-

Table 2 (b). Continued.

Prefire vegetation and fire severity	Variable name	Type	Units
<i>Overstorey structure</i>	<i>Pinus halepensis</i> canopy cover	Q	%
	Coverage of subcanopy trees (thickets) of <i>P. halepensis</i>	Q	%
	Coverage of upper canopy trees (polewood) of <i>P. halepensis</i>	Q	%
	Coverage of upper canopy trees (old growth) of <i>P. halepensis</i>	Q	%
	Number of natural age classes of <i>P. halepensis</i>	Q	No.
	<i>P. halepensis</i> tree density	Q	N/ha
<i>Understorey structure</i>	Total shrubs coverage	O	%
	Resprouter shrubs coverage	O	%
	Total herbs cover	O	%
	Resprouter herbs coverage	O	%
	Total understorey (shrubs + herbs) coverage	O	%
	Resprouter understorey coverage	O	%
<i>Fire severity</i>	Fire severity on trees	O	%
	Fire severity on shrubs	O	%
	Fire severity on herbs	O	%
	Fire severity on litter	O	%
	Unaffected litter coverage	O	%
	Presence of white ash on the forest floor	O	%
	Composite Burn Index	Q	-

Table 2 (c). Continued.

Postfire site factors	Variable name	Type	Units
<i>Overstorey structure</i>	Presence of surviving-to-fire aleppo pine trees	D	
<i>Understorey structure</i>	Total shrubs coverage	Q	%
	Resprouter shrubs coverage	Q	%
	Total shrub's average height	Q	cm
	Total herbs coverage	Q	%
	Resprouter herbs coverage	Q	%
	Average herb height	Q	cm
<i>Soil</i>	Litter coverage on the forest floor	Q	%
	Bare soil	O	%
	Litter depth	Q	cm
	Signs of soil erosion	O	-
	Soil crusting	O	-
<i>Climate</i>	Total precipitation during the postfire first wet season	Q	mm
<i>Management</i>	Management actions after fire (wood treatment)	D	-
<i>Time elapsed since fire to pine regeneration sampling</i>	Stand age	Q	No. years

2.4.2 *Variance partitioning analyses*

An eigenvector analysis is a popular method for multivariate analysis and variation decomposition (Qinghong and Brakenhielm, 1995). We used it to investigate the general drivers of postfire natural Aleppo pine regeneration. Regeneration density (RD, N/ha) was used as a response variable throughout the procedure. Firstly, a Detrended Correspondence Analysis (DCA) showed that RD had a linear environmental response (length of axes <2 SD each). So all the analyses were based on a Redundancy Detrended Analysis (RDA), (Ter Braak and Smilauer, 2002). The RDA is a direct gradient analysis technique that can be employed to break down ecological variation (Borcard et al., 1992). Secondly, we utilised different combinations of environmental (E) or other explanatory variables (Table 2) to check their influence on RD. Full and partial RDAs were used to separate the stand age (ST, time since the fire to regeneration sampling) effects from the other site factors (E) by a variation partitioning method. A full RDA was used to ascertain the total explained variance (TEV, %) by the combined set of E and ST. Then a partial RDA was compiled from two RDA runs, where either E or ST was used as the explanatory variable, and the other as a covariable, to obtain the unique contribution of each matrix (E and ST) together with its joint effect. The joint effect represents the combined two covariances between particular combinations of single and/or paired variable matrices (Borcard et al., 1992; Qinghong and Brakenhielm, 1995). We applied the same procedure to know the unique contribution of the fire severity variables (FS), and the combined covariance between FS and the other site factors (E). Finally, we assessed the separated contribution of the different variables and datasets included in E, such as geographical position, topography and soil variables, as well as the contribution of climate, prefire forest structure, postfire site factors and postfire management. The significance of the total canonical variation in each partial RDA was tested with 499 Monte-Carlo permutations of the reduced model in the CANOCO 4.5 package. Species data (RD) were submitted to squared root transformation.

2.4.3 *Predicting regeneration from prefire factors by the decision tree analysis*

We performed a decision tree analysis to predict the chance of having hyperdense regeneration using only prefire explanatory variables. To do so, *regeneration abundance* was used as the response variable, while predictor variables were the prefire factors described in Table 2, except soil crusting (no signs in 72.9% of plots). The decision tree procedure creates a tree-based classification model that predicts future events, such as the

likelihood of a specific site for establishing more than 4,000 plants/ha after fire. We herein employed Exhaustive CHAID (based on Chi-squared Automatic Interaction Detection), which is a modification of the CHAID algorithm (Kass, 1980) and examines all the possible splits for each predictor. CHAID (and Exhaustive CHAID) is preferred to classification and regression trees (CART) when there are many categorical variables (Van Diepen and Franses, 2006). At each step, CHAID chooses the independent (predictor) variable that has the strongest interaction with the dependent variable. Categories of each predictor are merged if they are not significantly different with respect to the dependent variable. The significance value for splitting nodes and merging categories was 0.05. Category merging was calculated by the Pearson method. The maximum number of levels in the tree was established as three, and the minimum number of cases in a parent and a child node was set as 10 and 5, respectively, after evaluating the models of 15/5, 12/6, 30/15 cases in the parent/child nodes (data not shown). A Spearman correlation analysis showed that there was a very strong and significant correlation between the annual average temperature and the minimum temperature ($r_o=0.91$; $p=0.000$), a significant but low correlation between the average minimum temperature and the longitude ($r_o=0.37$; $p=0.000$), and a moderate correlation between the average minimum temperature and the altitude ($r_o= -0.58$; $p=0.000$). Thus, we carried out 15 models with different combinations of these climatic and geographical variables, along with the rest of prefire variables. An assessment of the predictive accuracy of the final tree model was made by the risk estimate and its standard error, the number of cases classified correctly and incorrectly for each category of the dependent variable, and the biological sense of the model based on the significant predictors, the number of nodes and terminal nodes and the tree depth. We used a split sample validation of 10 sampled folds to assess how well the tree structure would generalise to a larger population. The maximum number of iterations for the model estimation was 100. Analyses were performed with the SPSS 26.0 statistical package.

3 RESULTS

3.1 Topography, soil conditions, abundance of agricultural terraces and climate

Overall, 61.6% of plots were on hillsides with slopes ranging from 15% to 45%, while 14.7% of plots had slopes over 45%. North was the predominant aspect (28.3%). Over half the plots (59.3%) were located on agricultural terraces. As many as 83% plots displayed 30-60% stoniness on the forest floor. Two thirds of plots had a limestone

bedrock (68%), one third (32%) had soft substrates like marls, clays and silts, and colluvium bedrocks. The SL was deeper than 30 cm in a considerable number of plots (61.2%). An SL deeper than 30 cm is significantly associated with soft substrates, i.e., marls ($X^2=17.01$; $p=0.000$), and the presence of agricultural terraces ($X^2=21.32$; $p=0.000$). The frequency of abundant terraces on soft-marl substrates (35%) was significantly higher than in the limestone plots (24 %), ($X^2=27.95$; $p=0.000$). Stoniness and bedrock were also significantly associated ($X^2=21.28$; $p=0.000$). Frequency of plots with stoniness below 30% was higher on soft substrates (13.5%) than on limestone (4%), while stoniness > 60% was significantly more frequent (44.4%) on limestone than on soft substrates (5.4%). Intermediate stoniness values (30-60%) were significantly more frequent on marls (81.1%) than on limestone (51.5%). During the first postfire sampling, there were light soil erosion signs in 44.2% of plots, mainly sheet erosion. Severe erosion signs were observed only in 9% of plots. The degree of soil erosion was significantly associated with marl ($X^2=28.04$; $p=0.000$), but not with slope. The average climate variables and specific climate conditions before fire can be seen in Table 1 and Tables A3 and A4, respectively.

3.2 Prefire forest structure

The studied burned Aleppo pine forests were principally mature forests (Table 3) dominated by two or one age class (50.7% and 29.7%, respectively), and with pole-wood trees as the predominant class (Fig A3). The average tree density before fire was 2,173 trees/ha, which varied depending on the site (Fig A4). However, this average was biased by two plots with very high pine density (> 60,000 trees/ha) regenerated after former wildfires. When these plots were removed from calculations, the tree average in our plots was 947 trees/ha (Table 3). Tree density correlated positively with the tree canopy cover estimated in the field ($r_s=0.46$; $p=0.000$). Canopy cover was below 30% only in 14.8% of the sampled plots. The percentage of plots with a canopy cover over 80% was similar to the percentage of plots with a canopy between 60-80% (20.3% and 26.6%, respectively). In the understorey, before fire nearly half the plots (46.6%) had intermediate coverages (30-60%) of both resprouter shrubs and herbaceous species. Additionally, the coverages of prefire resprouter shrubs and herbaceous species were significantly associated ($X^2=24.44$; $p=0.000$). Thus, where there was less shrub (< 30%), there were also fewer herbaceous species, and where there was more shrub (> 60%), there were also more herbaceous species. Nevertheless, the plots with an intermediate coverage (30-60%) of resprouter shrubs were those with the lowest frequency for the resprouter

herbaceous coverage category over 60%. The resprouter herbaceous species' coverage was significantly associated with bedrock ($\chi^2=14.02$; $p=0.007$). On marls the frequency of the plots covered with > 60% of resprouter herbaceous species was significantly higher. On limestone, the frequency of the observed plots with < 30% resprouter herbaceous coverage was significantly higher. There was also a significant association between herbs' coverage of 30-60% and 30-60% stoniness ($\chi^2=11.96$; $p=0.018$). In contrast, although resprouter shrubs' coverage was greater on limestone, there was no significant association.

Table 3. Descriptive statistics of the variables of the prefire forest structure of Aleppo pine overstorey across 15 wildfires in the Comunitat Valenciana, Spain. In the understorey variables, the percentage of plots in the different vegetation coverage classes are indicated for pre- and postfire stages. RC: coverage in relation to the total canopy cover. Total prefire vegetation in the understorey, including shrubs and herbs. Total postfire vegetation including saplings of regenerated resprouter trees, shrubs and herbs.

Overstorey variables	N	Min.	Max.	Mean	SE	SD
<i>Tree density (N/ha)</i>	127	20	5000	947	97.5	1098.3
<i>Total canopy cover (%)</i>	128	3	100	54	2.4	26.9
<i>RC of saplings (%)</i>	109	0	30	1	0.4	4.1
<i>RC of thicket (%)</i>	109	0	83	12	1.9	19.6
<i>RC of polewood (%)</i>	109	0	83	26	2.2	22.4
<i>RC of old growth (%)</i>	109	0	100	15	2.2	23.3
Understorey variables	<30%		30-60%		>60%	
	Prefire	Postfire	Prefire	Postfire	Prefire	Postfire
<i>Total vegetation</i>	12%	1%	50%	31%	38%	68%
<i>Total shrub</i>	14%	16%	54%	61%	33%	23%
<i>Resprouter shrubs</i>	44%	73%	41%	25%	15%	3%
<i>Total herbs</i>	63%	52%	32%	39%	6%	9%
<i>Resprouter herbs</i>	58%	52%	29%	39%	14%	9%

3.3 Fire severity and burned area

Field observations and the calculation of the CBI showed that fire impact on vegetation was variable depending on the site. High severity was the dominant class at all the sites except La Nucía, which was moderate (Fig. A5 and Table A2). Fire severity on trees was high and very high at 32.6% and 51.1% of plots, respectively. Only 17.7% of the study plots presented some (1-3 trees) Aleppo pine surviving-to-fire trees. Fire severity on shrubs was very high at 60.7% of plots, while the herbaceous stratum had been completely consumed by fire at nearly all the plots (91.8%). At 84.7% of plots,

unaffected litter was lower than 30%. The presence of white ash on the forest floor was sporadic in over half the plots (55%) and abundant in 34.9% of them. The CBI was not significantly associated with plots' aridity, slope, aspect, bedrock or presence of agricultural terraces. However, there was a significant association between fire severity (CBI) and the season during which wildfires occurred ($X^2=22.80$; $p=0.000$). That is, frequency of the high severity CBI class was significantly higher at the sites burned in summer, but was significantly lower at the sites burned in autumn and winter. Interestingly, the burned area was inversely related to the number of days without rainfall that occurred 2 years before fire ($r_o= -0.37$; $p=0.000$), but correlated significantly with annual precipitation 1 year before fire ($r_o= 0.19$; $p=0.024$).

3.4 Aleppo pine, understory and soil recovery

The pine regeneration at the study sites showed wide variability, ranging from 0 to 181,500 pines/ha (Fig. 2), and the mean value was 9,100 pines/ha. The percentile (P) 25 was 384.50 pines/ha, the P50 was 2,500 pines/ha, and the P75 was 10,750 pines/ha. While the median was 2,500 pines/ha and the mode was 0 pines/ha. Ontinyent was the site with the lowest regenerated mean density (420/ha), while Andilla (24,100/ha), followed by La Nucía (182,000/ha), were the sites with by far the highest postfire regeneration density. As expected, a significant correlation was found between Aleppo pine tree density before fire and Aleppo pine regeneration density ($r_o=0.39$; $p=0.000$) and coverage ($r_o=0.25$; $p=0.005$) after fire. A low, but significant, correlation was observed between the CBI and regeneration density ($r_o=0.18$; $p=0.035$). Conversely, the CBI and the total resprouting vegetation coverage after fire were inversely related ($r_o= -0.23$; $p=0.041$). Natural Aleppo pine regeneration density correlated negatively with the average annual precipitation ($r_o= -0.34$; $p=0.000$), the precipitation that had fallen during the last wet season before fire ($r_o= -0.32$; $p=0.000$) and Martonne's aridity index ($r_o= -0.34$; $p=0.000$). No correlation appeared between regeneration density and the precipitation that had fallen during the first postfire wet season. A significant association was observed between the frequency of the high-density plots (>4,000 plants/ha) and a prefire coverage of resprouter herbaceous species below 30% ($X^2=7.18$; $p=0.027$). The dominant species in that stratum was *Brachypodium retusum*.

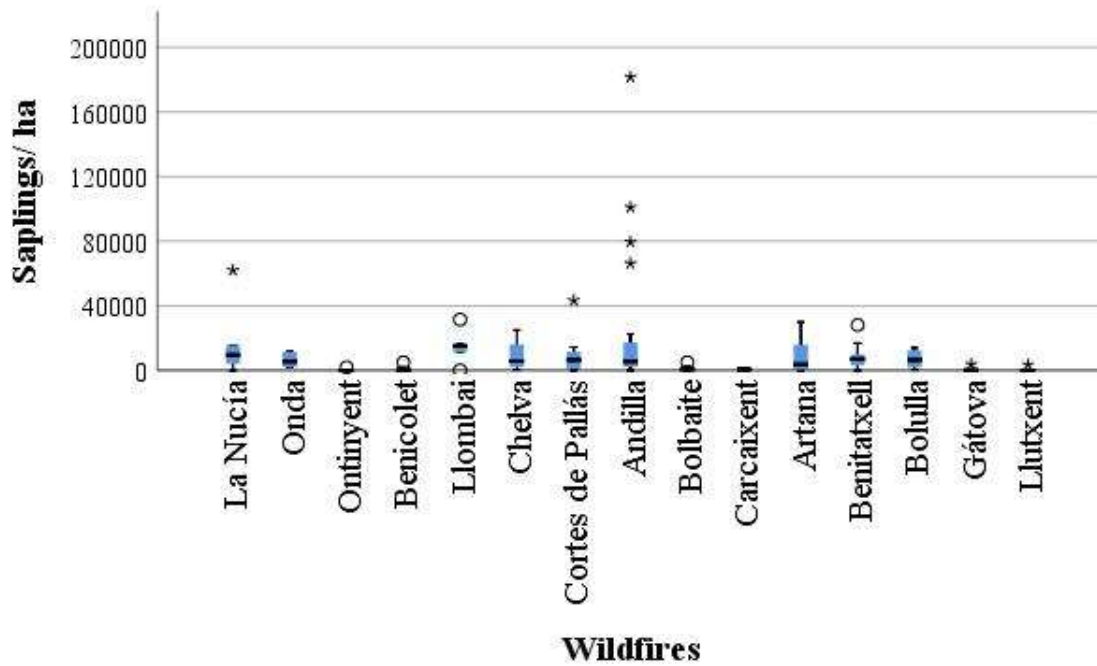


Figure 2. Postfire natural Aleppo pine regeneration density several years after fire (see Table 1) in 15 wildfires studied in the Comunitat Valenciana (Spain). White dots represent atypical cases (values distanced more than 1.5 longitudes of the box of the 75th percentile). Stars represent extreme values (values distanced more than 3 longitudes of the box of the 75th percentile).

Overall, understorey vegetation recovery was successful because 67.6% of plots had a total shrubs and herbs coverage over 60%, which differed from the estimated prefire coverage (Table 3). Litter coverage on the forest floor was intermediate for being lower than 30% in 63.3% of plots. However, litter coverage and litter depth were significantly associated ($X^2=87.64$; $p=0.000$). This all matched the fact that during the regeneration sampling (second postfire sampling), the number of plots with no soil erosion symptoms increased by about 30% in relation to the sampling for assessing the fire's impact, while the number of plots with erosion symptoms decreased in all the categories ($X^2=30.48$; $p=0.002$).

3.5 General drivers of natural regeneration in Aleppo pine burned forests

All the site factors used in this study (Table 2) explained total variance (TEV, %) in pine regeneration density of 34.4% (Fig. 3 and Table A5). As expected, variance partitioning showed that stand age (number of years since the fire to regeneration sampling) was less important for explaining density variation than other factors (Table A5). This supported our initial assumption of there being no effect of the different sampling ages after fire in our results. Fire severity variables (the CBI and the severity classes recorded in the field for each vegetation stratum) explained 2.5%. Although not statistically significant, there was a joint effect of 2.6% between the fire severity variables and the other measured site factors. That is, variation in regeneration density could be explained by the covariation between site and fire severity. There was a substantial difference in the variance explained by the prefire factors (including fire severity) and the postfire site factors (including stand age). The prefire site factors, along with fire severity, significantly explained 28.4% of total variability (Fig. 3 and Table A5), while the postfire factors explained only 7.5%. Management of the burned wood in the study plots did not explain any variability in the regeneration data (data not shown). Only 26.5% of plots showed signs of postfire burned wood management, which corresponded to timber extraction. Of the prefire site factors, when the other site factors were controlled as covariables in the RDAs analyses, forest structure explained 8.3% (the first canonical axis was not significant), while the climate and geographical position together explained 13.1% (the first canonical axis was not significant). Only the prefire climate variables explained up to 6.7% (the first canonical axis was not significant), and only the geographical variables (latitude, longitude, altitude) significantly explained 6.9% of variability in regeneration density ($p=0.018$; $F=3.68$).

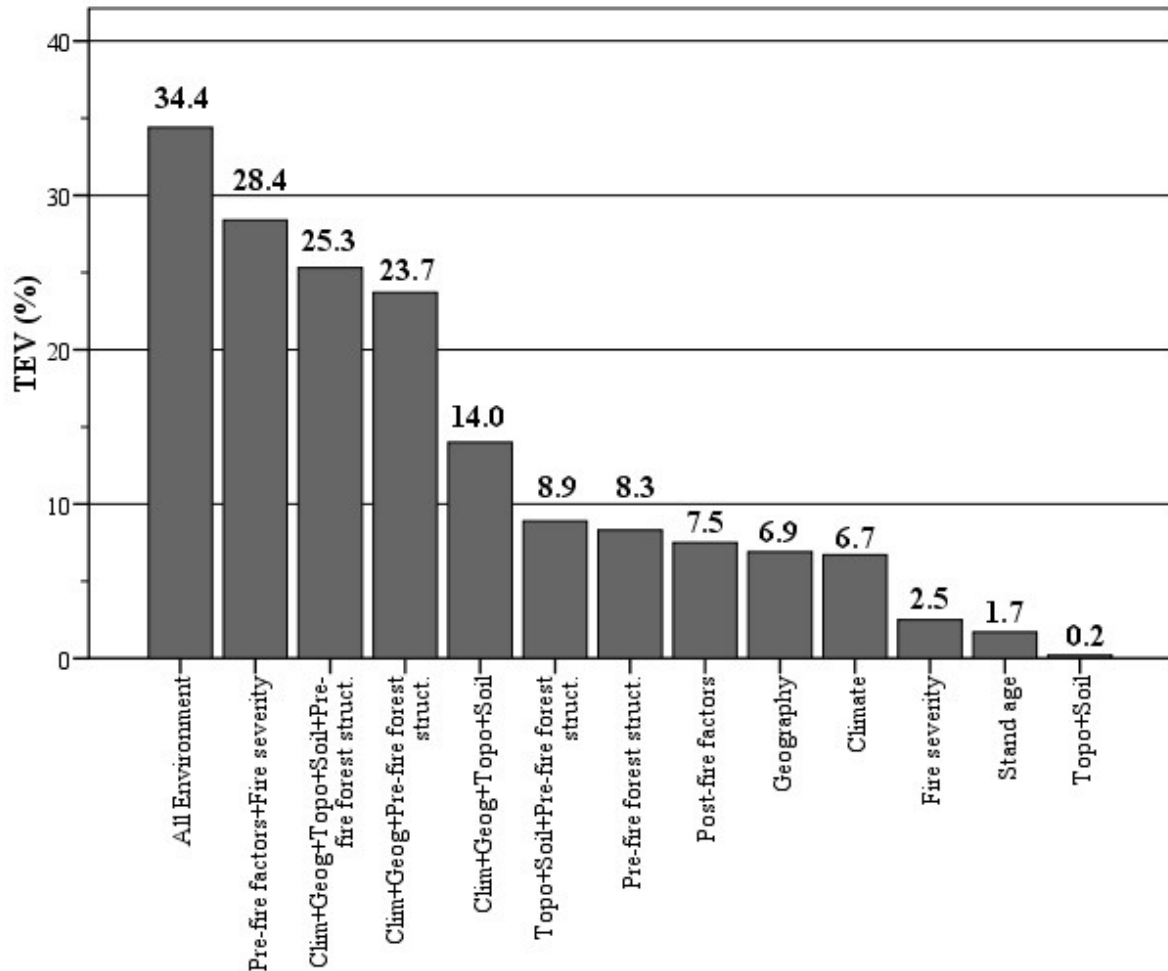


Figure 3. Total explained variation (TEV, %) of postfire natural regeneration density (N/ha) in 15 Aleppo pine forests in the Comunitat Valenciana (Spain) in relation to different environmental or site factors.

3.6 Predictors of hyperdense natural regeneration in Aleppo pine burned forests

In general, 44.1% of the 147 sampled plots regenerated in overstocked stands (>4,000 trees/ha). Five independent variables were included in the final decision tree model (M1; 9 terminal nodes; but see Table A6 and Table A7): (i) average minimum temperature (Tmin); (ii) prefire Aleppo pine tree density; (iii) prefire resprouters' shrub species coverage; (iv) SL depth; (v) bedrock type (Fig.4). Models 1, 5 and 6 (Table A7) had the same tree structure and significant variables at the same depth of the tree, but M1 has less error with the same level of prediction.

The average minimum temperature was the main significant variable that classified regeneration density and split data into three significant Tmin groups: the first or low Tmin ($\leq 10.68^{\circ}\text{C}$) formed by four sites: Andilla, Chelva, Onda and Ontinyent; a second intermediate Tmin group ($10.69\text{-}11.46^{\circ}\text{C}$) composed of six sites: Bolulla, Carcaixent, Cortes de Pallás, Gátova, La Nucía, Llutxent; and a third high Tmin group ($>11.46^{\circ}\text{C}$) made up of five sites: Artana, Benicolet, Benitatxell, Bolbaite, LLombai. The first and third groups (Node 1 and Node 3) had comparable percentages of cases with pine densities $> 4,000$ trees/ha (54-56%; Fig. 4). In the second group (Node 2), only 3.2% of cases had more than 4,000 trees/ha.

At the second tree diagram level, starting from Node 1, the next limiting variable was Aleppo pine tree density before fire with three significant groups: ≤ 100 /ha, 101-500/ha, and > 500 trees/ha. There were no cases of dense regeneration when prefire density was lower than 100 trees/ha, but 84.8% of plots had dense regeneration when prefire tree density was higher than 500 trees/ha. Only 33.3% of plots had dense regeneration in the group of 101-500 trees/ha (Node 5). However, under those conditions, the resprouter shrub species' coverage before fire negatively affected having hyperdense regeneration (Node 10). In the group of sites with an average minimum temperature over 11.46°C , hyperdense regeneration was observed preferably in deeper soils ($\text{SL}>30$ cm). In these deeper soils, overstocked stands represented 87.5% of plots on limestone and 50% on softer bedrocks. The risk estimate (0.159) and its standard error (0.03), and the classification table (Table A8), indicated that the model correctly classified 84.1% of cases, and the categories predicted by the model were wrong only for 15.9% of cases. Although the misclassifying risk was slightly higher (35.2% and Error Desv.= 0.04) with the cross-validation model, its accuracy was still good (see Tables A8-A10).

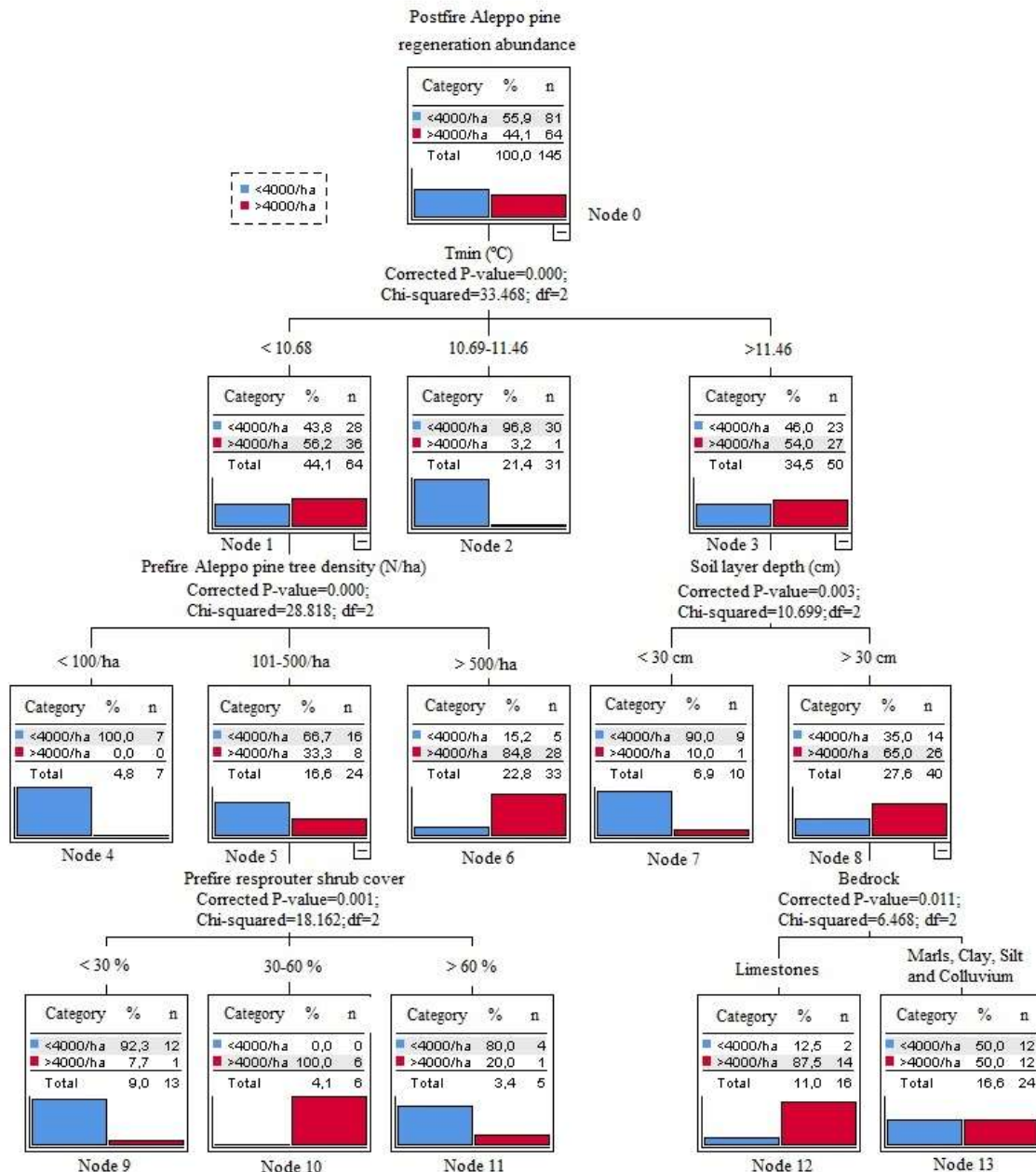


Figure 4. Decision tree diagram showing predictors of overstocked stands with hyperdense regeneration (>4,000 pines/ha) of Aleppo pine after wildfire in 15 forests of the Comunitat Valenciana (Spain). To interpret the tree, the predicted category, that with the highest count in each node, is highlighted in the classification tree. Each node contains a frequency table showing the number of cases (count and percentage) for each category of the dependent variable.

4 DISCUSSION

Many former works have documented overstocked *Pinus halepensis* stands regenerated after fire (Argiles-García, 2018; De las Heras et al., 2011; Herranz et al., 1997; Martínez-Sánchez et al., 1999). However, these studies did not focus on which specific environmental factors may explain this hyperdense regeneration. In our study, the burned sites showed similar postfire Aleppo pine regeneration density to that reported in other Mediterranean wildfires (Domenech, 2017; Pausas et al., 2004, 2003; Tsitsoni, 1997). In general, Aleppo pine did not fail to regenerate after fire, and only 12.4% of plots with previous pine presence did not show any regeneration signs. Thus, our results indicate that seed cone production was not a major limitation for Aleppo pine postfire recovery. However, postfire regeneration was density-variable across the burned sites. Pine density varied from 0 to 181,500 plants/ha, and 44.1% of plots had hyperdense regeneration (> 4,000 plants/ha). We observed that the main general drivers of natural pine regeneration were previous forest structure (8.3%), geographical factors (6.9%) and climate conditions (6.7%). Both the effect and variance explained by the prefire forest structure measured in our study was more important compared to other studies carried out in Mediterranean pine ecosystems. For example, the variables measured with LIDAR in García-Llamas et al. (2019), which included canopy density, explained only 0.04% of the total variation in postfire regeneration density. Mitsopoulus et al. (2019) found that no prefire stand structure variables (tree density and basal area) were significant predictors of postfire Aleppo-pine regeneration density. These differences could rely on the structural heterogeneity at our study sites in both overstorey and the understorey strata, as opposed to the more homogeneous conditions of the sites studied in those works. In our study, prefire overstorey density was a significant predictor. This may be related to forests' maturity and to trees' reproduction potential, but especially to the available canopy seed bank before fire (Gil et al., 1996; Rodriguez-Garcia et al., 2011; Tapias et al., 2001), which would increase with the density of mature trees (e.g., at more productive sites).

Regarding the understorey structure, the versatile and significant role of resprouter shrubs' coverage before fire, especially in intermediate tree density (100-500/ ha), and the significant and negative role of resprouter herbaceous' coverage in Aleppo pine regeneration density, demonstrate the importance of prefire understorey development in postfire Aleppo pine regeneration. This suggests that indirect interactions (e.g.

competition for different resources and/or facilitation of early plant establishment), or cross effects among trees canopy, shrubs and herbaceous coverages, could have influenced the postfire pine response (Rodríguez-García et al., 2011a, 2011c). High coverages of herbaceous or woody resprouting competitors may reduce the availability of safe germination microsites for pine. In fact it has been pointed out that postfire Aleppo pine seedling mortality increases with more perennial grass cover (Pausas et al., 2003).

As general, but important, drivers of postfire natural regeneration, we also observed geography and climate. The set of climate variables explained almost the same percentage of variation as geography, but neither of the two canonical axes of the RDA were statistically significant. Even so, climate and geography explained practically half the TEV% of regeneration density. The role of geographical position (longitude, latitude, altitude) considerably explained the variation in regeneration density in the multivariate analysis (RDAs). Therefore, the location and altitude of the burned pine forest will influence the postfire response. Geography was significantly related to local climate (significant correlation between altitude and T_{min} ($r_o = -0.58$; $p=0.000$), and between longitude and T_{min} ($r_o=0.37$; $p=0.000$)) and might be connected to the well-known differences among Aleppo pine populations, such as differences in growth, reproduction and serotiny because they are provenance-specific (De las Heras et al., 2012; Gil et al., 1996; Tapias et al., 2001). Besides, the climatic sensitivity of pines and postfire natural recruitment has been previously documented for Aleppo pine (Daskalakou and Thanos, 2004, 1996; Espelta et al., 2011; Thanos and Doussi, 2000), and other pine species, such as *Pinus pinaster* (Rodríguez-García et al., 2011b) and *P. ponderosa* (Korb et al., 2019). In contrast, natural regeneration density correlated negatively with average annual precipitation, the precipitation that had fallen during the last-wet season before fire and Martonne's aridity index (lower density at more humid sites). These apparently odd relations may be linked with local precipitation patterns, heavy rains in the first autumn after fire and high slopes that would redistribute seeds within the terrain or the altitude of each evaluated site, stand age and other site-specific factors, such as less prefire Aleppo pine overstorey tree density (e.g. in Llutxent). These results suggest new possible research steps to fully clarify the effects of distance from the coast and climate conditions on Aleppo pine regeneration patterns.

The results obtained with the decision tree model for predicting hyperdense regeneration agree with our variance partitioning analysis. The specific significant factors

were the average minimum temperature in terms of climatic variables, Aleppo pine density before fire and resprouter shrub species' coverage before fire in forest structure terms, and SL depth and limestone bedrock as micro-environmental site factors. Minimum temperature appeared as the first predictor of regeneration density by defining three groups of populations according to the proportion of plots with hyperdense regeneration. Minimum winter temperature is the most important factor to explain Aleppo pine distribution (Gil et al., 1996) and it is clearly showing an east-west gradient of annual average temperature ($r_0= 0.91$; $p<0.000$) and an altitudinal gradient ($r_0= -0.58$; $p<0.000$), with temperatures dropping as the altitude and the distance to the coast increase. The role of minimum temperature in regeneration density is indirect and, as it has been said, may be indicative of site-specific factors (e.g., geographical factors like longitude and specially altitude) but also of population-specific factors, such as the production of serotinous cones and availability of viable seeds after fire (Climent et al., 2008; Hernández-Serrano et al., 2014; Martín-Sanz et al., 2016; Santos-del-Blanco et al., 2010, 2013). This agrees with the observations made in common garden experiments (Hernández-Serrano et al., 2014; Martín-Sanz et al., 2016), where a significant negative relationship has been observed between the serotiny level of trees and summer rainfall and temperature oscillations (continentality) of their provenance sites. The population groups of each temperature range of our tree model do not fully match the already defined provenances for Aleppo pine in the Comunitat Valenciana (Fig. A6), but it is reasonable to expect a variable postfire Aleppo pine regeneration density depending on the specific population or site's temperature. In addition, temperature has a direct effect on seed germination and initial growth (Boucher et al., 2020; Gil et al., 1996; Thanos, 2000).

Nevertheless, sexual reproduction in trees is a complex and a multi-factor dependent process. Hence at the burned sites characterized by a lower minimum temperature, both overstorey and understorey structure controlled the availability of suitable microsites for hyperdense regeneration. Thus with prefire low dense canopies of ≤ 100 trees/ha, it would be difficult to obtain overstocked stands, but hyperdense regeneration after fire would be expected in forests with prefire density over 500 trees/ha; which has been related to both forests' productivity (Korb et al., 2019), and tree maturity and the availability of serotine cones and seeds before fire (Gil et al., 1996; Tapias et al., 2001). In forests with intermediate tree density (101-500 trees/ha) and with lower seed availability, a resprouter shrub coverage below 30% and over 60% limited the availability

of microsites to develop hyperdense regeneration. The early establishment phase in the life cycle of Mediterranean pines is influenced by the presence and abundance of understorey (De Las Heras et al., 2002; Fernández-García et al., 2019; Rodríguez-García et al., 2011a, 2011c). So if prefire resprout shrub coverage exceeds 60%, as shrubs resprouts quickly after fire, stem and crown interference with pine regeneration may occur in the form of competition for light and space, while root interference may take place as competition for nutrients and water (Kramer and Kozlowski 1979). This hypothesis is reinforced by the role of low temperatures in the first autumn after fire, which would delay Aleppo pine seed germination to spring (Alfaro-Sánchez et al., 2015a; Daskalidou and Thanos, 2004, 1996). Then, pine establishment would occur when shrub size grows. In the plots with resprouter shrubs coverage lower than 30%, which also presented lower herbaceous resprouter coverage than 30%, limited regeneration density can be explained by low soil availability, which would generally prevent vegetation development.

At the burned sites with warmer temperatures, having hyperdense regeneration at microsites with deep soils is more probable, which are able to retain enough seeds and soil water availability after fire to support tree recruitment. In deep limestone soils, where more hyperdense regeneration occurred, seed retention would be facilitated by the high percentage of stoniness and the abundant physical obstacles to keep seeds from runoff. Conversely on marls and other soft substrates, seed retention would be easier because they are terraced and flatter, and runoff rain would be slower. This result highlights the importance of studying microtopography conditions and their effects on natural regeneration. Besides, further research is necessary, but we cannot rule out that a significantly low resprouter herbaceous species' coverage on limestone could have contributed to higher Aleppo pine regeneration density.

Further research needs to be conducted to explain why there was no hyperdense regeneration in the group of sites with intermediate minimum temperatures. However, we cannot rule out either those factors associated with a homogeneous forest structure, or the existence of other factors or processes associated with land use and human activity, which would prevent high density regeneration. Human-driven and land-use factors control patterns of woody species establishment and cover on the Mediterranean landscape (Baeza et al., 2007). Hence different species' functional groups are more abundant in some soils/bedrock types than in others. For example, woody resprouters (e.g. *Quercus coccifera*) are typically associated with forest use (non-cultivated) and limestone soils

(Baeza et al., 2007), while seeder and herbaceous species appear more strongly associated with abandoned fields and marl-limestone soils (Baeza et al., 2007; Pausas et al., 1999). In our study, a very high proportion of plots on limestone significantly presented resprouting herbaceous species' coverages below 30%. This differentiation could result from marl soils being more easily occupied by seeder and herbaceous species with rapid colonisation and which are competitive enough to interact. In contrast in non-cultivated and limestone soils, there would be less herbaceous species' coverage because of competition with woody resprouters, which are already established there, while, almost 60% of the studied Aleppo pine plots were on abandoned terraces. This result clearly shows that the elimination of the original forests and land-use transformation to cultivation terraces have favoured the presence of these Aleppo pine forests after agricultural abandonment because of their good colonisation capacity (Richardson et al., 1994).

Fire severity was not one of the most important factors for driving the results of our study. It only explained 2.7% in co-variation with other measured site factors. We do not discard that the high serotiny (aerial seed bank) of Aleppo pine or the statistical approach selected have likely masked the potential effect of fire severity. However, we observed a significant and positive correlation between the CBI and pine regeneration density. Natural regeneration can be favoured by seeds coming into contact with bare soil exposed by fire, and by the vegetation gaps created by fire (Gil et al., 1996; Thanos, 2000). We also observed that a high burn severity in the tree canopy may not negatively affect the canopy seed bank and subsequent seedling regeneration (Pausas et al., 2003). We also noted an effect of fire severity on the understorey given a specifically significant and negative correlation between the CBI and resprouting vegetation coverage after fire. This coincides with other studies that have observed favouring seeders recovery at the expense of resprouter species (both shrubs and grasses) at high severity burned sites (Fernández-García et al., 2019; Pausas et al., 2003; Pausas and Keeley, 2014). The good relations observed in our study between the CBI and other measured variables can support the validity of our index adaptation and its usefulness for being employed in forest ecosystems in the Mediterranean Basin. This is also supported by the fact that the CBI was higher for summer fires, but lower for autumn and winter fires. This could be related to higher environmental humidity and water availability in these last-mentioned seasons.

5 CONCLUSIONS

We show the importance of environmental and site-specific conditions, and forest structure before fire for shaping the effect of wildfires on natural regeneration density in Aleppo pine forests of the Comunitat Valenciana, Spain. At cold sites (western sites located at higher altitudes), we expect dense regeneration in Aleppo pine mature populations with a prefire tree density of more than 500 trees/ha, and with a tree density of between 101-500 trees/ha, plus resprouter shrub species' coverage of 30-60% and low resprouter herbaceous species' coverage. In the populations located at warmer sites (closer to the coast and at lower altitudes), dense regeneration would be expected at the sites with a SL deeper than 30 cm, and specially on limestone bedrock. The significant site factors and the model should be explored and validated in more burned forests as our findings are promising for predicting regeneration soon after fire, carrying out the sampling of prefire conditions, and for the fire severity impact on vegetation and soil. These findings can also contribute to the planning of forest management and restoration actions because they can be used to classify those areas that are more likely to regenerate overstocked stands.

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7 AUTHORS' CONTRIBUTION

Víctor Santana: Project administration, Conceptualization, Methodology, Data collection, Supervision, Reviewing and Editing. José Antonio Alloza: Conceptualization, Funding acquisition, Methodology, Data collection, Supervision, Reviewing and Editing. V. Ramón Vallejo: Conceptualization, Funding acquisition, Data collection, Reviewing and Editing. Encarna Rodríguez-García: Data collection, Data analysis, Writing-Original draft preparation, reviewing and editing.

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9 SUPPLEMENTAL MATERIAL

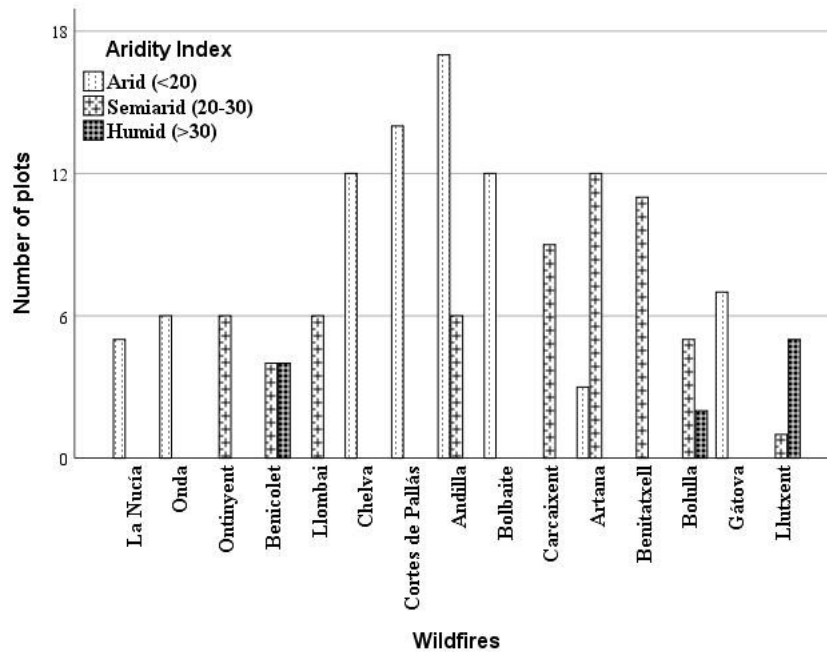


Figure A1. Aridity characterisation (De Martonne, 1926) of 147 sampled plots at the 15 studied Aleppo pine burned sites in the Comunitat Valenciana (Spain).

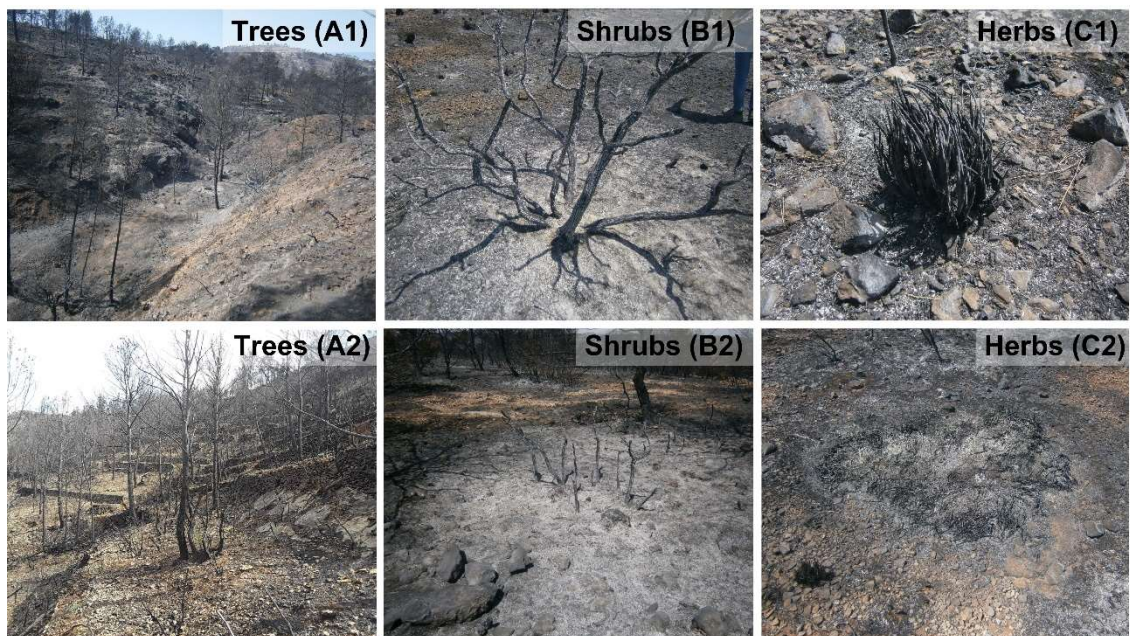


Figure A2. Aleppo pine trees (A1 and A2), shrubs (B1 and B2) and herbs (C1 and C2) affected by fire in Aleppo pine forests. Note that although the vegetation is affected by high severity fire, its prefire coverage can be estimated after fire in wide categorical ranges.

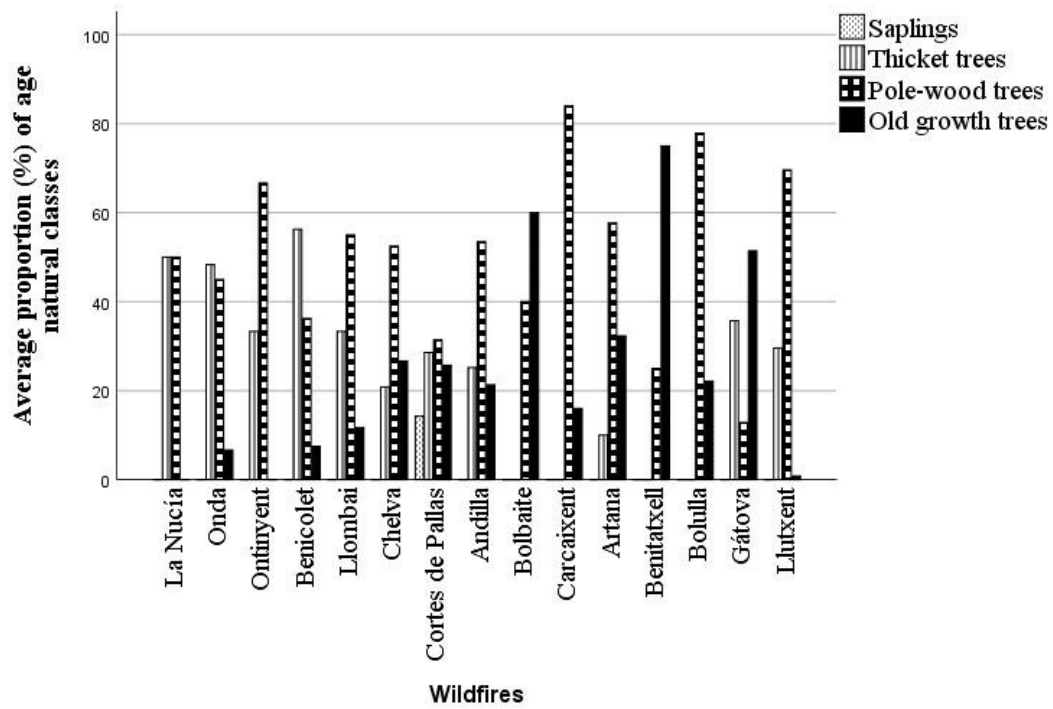


Figure A3. Prefire age natural classes in the 147 sampled plots located at the 15 studied Aleppo pine burned sites in the Comunitat Valenciana (Spain).

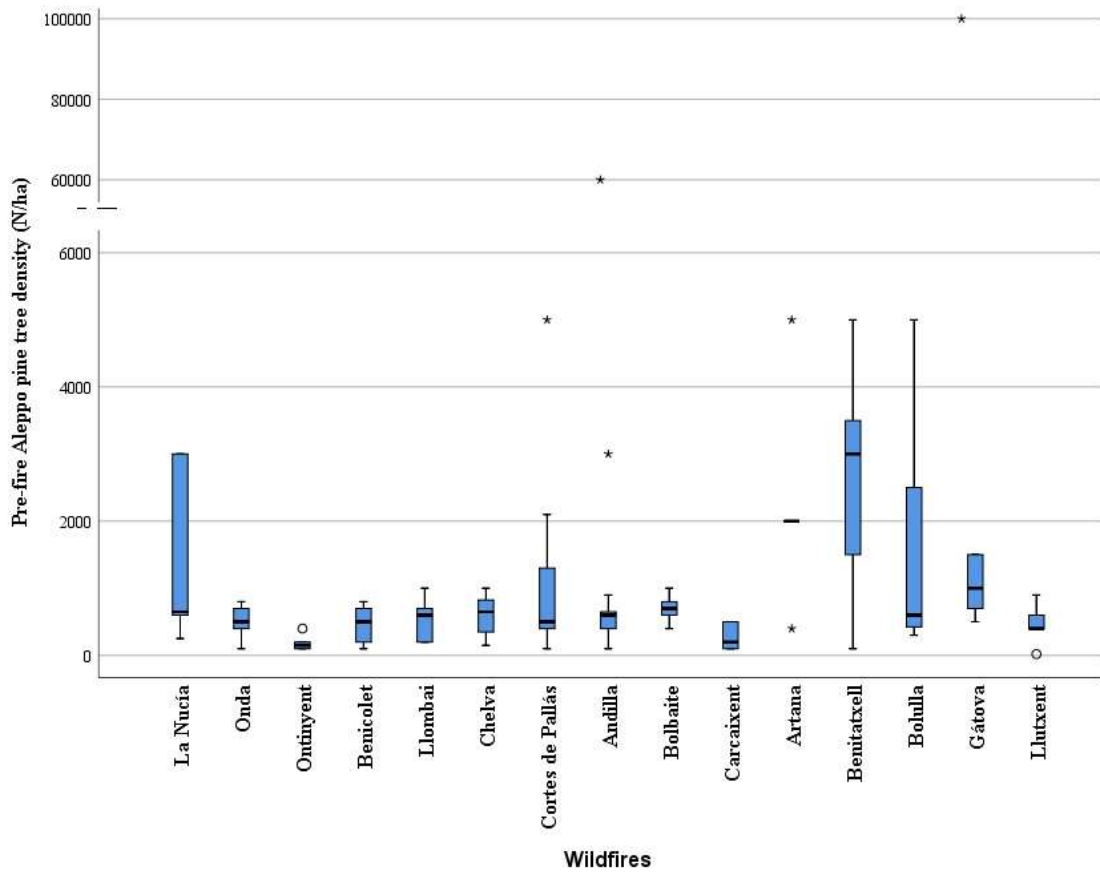


Figure A4. Prefire average tree density of Aleppo pine forests at the 15 burned sites in the Comunitat Valenciana (Spain). White dots represent atypical cases (values distanced more than 1.5 longitudes of the box of the 75th percentile). Stars represents extreme values (values distanced more than 3 longitudes of the box of the 75th percentile).

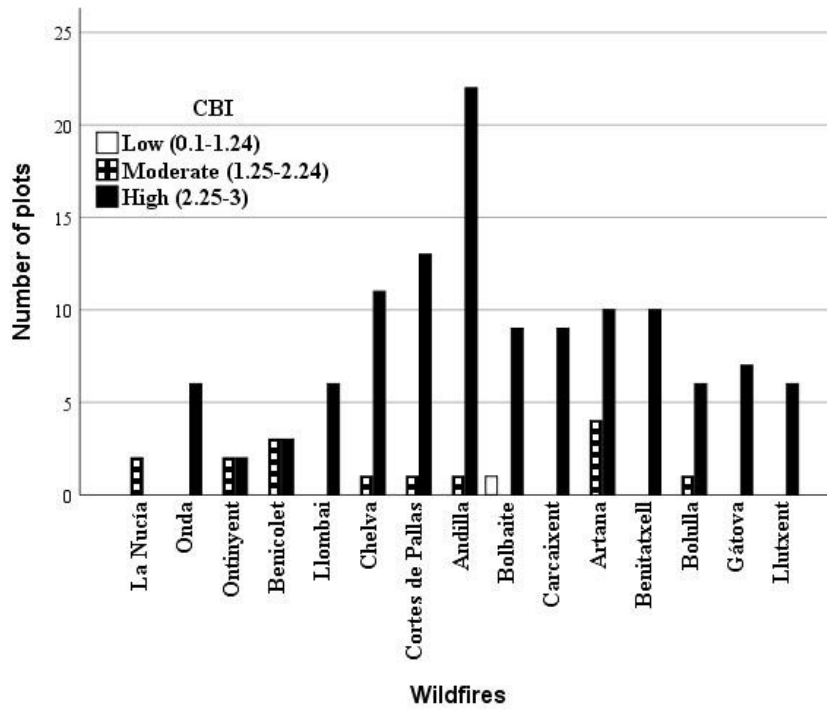


Figure A5. Fire impact on vegetation and soil summarised by the composite burn index (CBI) using a modification of Key and Benson (2006) calculated in 136 plots at 15 Aleppo pine burned sites in the Comunitat Valenciana (Spain).

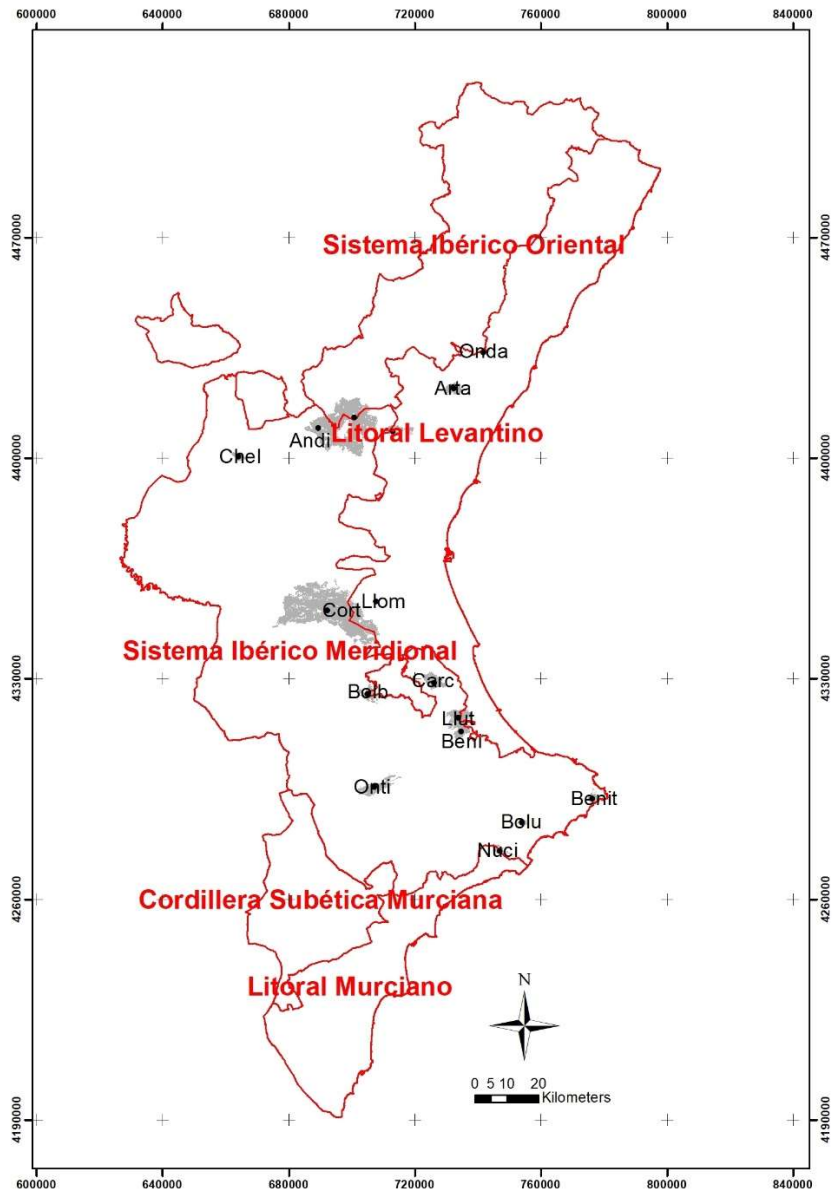


Figure A6. Sampled Aleppo pine forests in our study and Aleppo pine provenances (in red) identified in the Comunitat Valenciana, Spain (see Gil et al., 1996, and Appendix XI of the Royal Decree 289/2003 and Appendix I of the Decree 15/2006 of the Council of the Valencian Government).

Table A1. Burn severity scale and fire severity categories on soil and vegetation for field evaluations following Alloza et al. (2014).

Forest strata	No effect	Low	Moderate	High	Very high
<i>White ash</i>	None	-	Punctual	-	Abundant
<i>Unburned litter</i>	100%	>60%	30-60%	<30%	-
<i>Herbs</i>	Unburned	Significant proportions of green vegetation	Partially burned, but the structure of leaves is still recognisable	Completely burned	-
<i>Shrubs</i>	Unburned	More than 50% of its structure is unburned	More than 50% of its structure is burned	Without green leaves, but with alive terminal twigs	Completely scorched and significant branch loss (only branches standing > 6 mm)
<i>Trees</i>	Unburned	Trunk base partially burned, but all the crown is green	Trunk is partially burned, and more than 50% of the crown is green	More than 50% of dry leaves left on the crown (they can be on soil if the evaluation is done several weeks after fire)	Tree is completely burned, including leaves

Table A2. Burn severity scale after the modification of the Composite Burn Index (CBI= sum of scores/N rated.) used to obtain soil and vegetation burn severity values based on Key and Benson (2006).

Burn severity scale							
Strata rating factors	No effect	Low		Moderate		High	
	0	0.5	1	1.5	2	2.5	3
UNDERSTOREY							
1) Substrates							
<i>White ash</i>	Absent	-	-	-	Sporadic	-	Abundant
<i>% Soil with unburned litter</i>	Unchanged	-	> 60%	-	30-60%	-	< 30%
2) Herbs							
<i>% Foliage altered</i>	Unchanged	-	30%	-	80%	-	100% + branch lost
3) Shrubs							
<i>% Foliage altered</i>	Unchanged	-	20%	-	60-90%	>95%	99%
OVERSTOREY							
<i>1) % Green (unaltered)</i>	100%	-	95%	-	50%	<10%	None
<i>2) % Surviving canopy</i>	Unburned	-	> 60%	40-60%	20-40%	<20%	0%

The thresholds between severity classes were no effect (0), low severity (0.1-1.24), moderate severity (1.25-2.24) and high severity (2.25-3). Vegetation factors scored lower in specific strata when there was < 60% cover in the plot (Table A2b).

Table A2 (b). Continued. Burn severity scores for the rating factors in shrubs, herbs and overstorey according to the estimation of the total coverages in the plot before fire. * (only branches standing > 6 mm).

Prefire cover		% Foliage altered		
Rating factor	Low	Moderate	High	
Understorey	20%	60-90%	>95%	Scorched*
< 30%	0.5	1.25	2.25	2.50
30-60%	0.75	1.50	2.50	2.75
> 60%	1	2	2.75	3
		% Green unaltered		
Rating factor	Low	Moderate	High	
Overstorey	100%	80-95%	40-50%	0-10%
< 5%	-	-	-	-
5-20%	0.25	1.25	2.25	2.50
21-40%	0.5	1.5	2.50	2.75
41-60%	0.75	1.75	2.50	2.75
< 60%	1	2	2.75	3

Vegetation factors scored lower in specific strata when there was < 60% cover in the plot. Criteria may differ by stratum, but the scale applied to them all is the same. It is the full range of change between no effect and the strongest possible effect (due to fire), which forms a common denominator. Thus, the severity measure is a consistent numerical scale that gauges the extent of change. It may represent a single factor or a composite of multiple factors depending on attempts (Key and Benson, 2006). The thresholds between severity classes were no effect (0), low severity (0.1-1.24), moderate severity (1.25-2.24) and high severity (2.25-3).

Table A3. Climate variables before and after fire during each sampling at the Aleppo pine burned sites in the Comunitat Valenciana

Fire name	AP3	DP3	AP2	DP2	DP1	LWP	FWS
La Nucía	420	103	824	101	107	43	46
Onda	552	94	640	58	47	51	293
Ontinyent	873	73	741	93	78	71	37
Benicolet	1316	59	1015	100	67	52	50
Llombai	831	71	785	59	75	58	61
Chelva	381	121	653	53	55	21	59
Cortes	461	92	526	63	89	32	66
Andilla	463	151	565	68	61	28	89
Bolbaite	373	100	386	91	131	36	82
Carcaixent	600	93	286	97	152	30	104
Artana	512	94	370	88	127	30	68
Benitatxell	559	91	240	130	128	62	62
Bolulla	659	103	204	192	107	48	152
Gátova	239	104	570	133	91	62	46
Llutxent	743	125	1005	71	67	48	269

AP3 and AP2: total annual precipitation (mm) 3 and 2 years before fire, respectively; LWP and FWS: precipitation (mm) fallen continuously during the last wet season before fire, and during the first wet season after fire, respectively; DP1, DP2 and DP3: drought period length 1, 2 and 3 years before fire (see Methods for more details).

Table A4. Dates considered at each burned site for establishing the prefire last wet season and the postfire first wet season.

Fire name	Prefire last wet season (P> 6 mm)		Fire started (date)	Postfire first wet season (P> 6 mm)	
La Nucía	Sep 2008-Dec 2008	Aut 2008	24/01/2009	Win & spr 2009	Feb 2009–Mar 2009
Onda	May 2008-Apr 2009	Spr + sum 2008 + win & spr 2009	23/07/2009	Sum 2009	Sep 2009
Ontinyent	Dec 2009-Jun 2010	Win 2009 + spr 2010	06/09/2010	Aut 2010 + win 2011	Sep 2010-Jan 2011
Benicolet	Jul 2010-Mar 2011	Sum 2010 + win & spr 2011	08/04/2011	Spr & sum 2011	Apr 2011-Jul 2011
Llombai	Mar 2011-May 2011	Spr 2011	20/07/2011	Aut 2011 + Win 2012	Sep 2011-Jan 2012
Chelva	Mar 2012-May 2012	Spr 2012	01/06/2012	Aut 2012	Sep 2012–Nov 2012
Cortes	Mar 2012-Jun 2012	Spr + sum 2012	28/06/2012	Aut 2012	Sep 2012–Nov 2012
Andilla	Mar 2012-Jun 2012	Spr + sum 2012	29/06/2012	Aut 2012	Sep 2012–Nov 2012
Bolbaite	Feb 2016-May 2016	Win + spr 2016	15/06/2016	Sum & aut 2016 + win & spr 2017	Aug 2016–Jun 2017
Carcaixent	Mar 2016-May 2016	Spr 2016	16/06/2016	Sum & aut 2016 + win & spr 2017	Aug 2016–Apr 2017
Artana	Mar 2016-May 2016	Spr 2016	25/07/2016	Aut 2016 + win & spring & sum 2017	Sep 2016–Jun 2017
Benitatxell	Feb 2016-Apr 2016	Win + spr 2016	04/09/2016	Aut 2016 + win & spr 2017	Sep 2016–Apr 2017
Bolulla	Mar 2016-Apr 2016	Spr 2016	04/09/2016	Aut 2016 + win & spr 2017	Sep 2016–Apr 2017
Gátova	Sep 2015-Jun 2016	Aut 2015 + win & spr & sum 2016	28/06/2017	Sum 2017	Aug 2017
Llutxent*	Jan 2018-Jun 2018	Win + spr + sum 2018	06/08/2018	Sum + aut 2018	Aug 2018–Nov 2018*

Aut: autumn (21 September-21 December); spr: spring (21 March-21 June); sum: summer (21 June- 21 September-); win: winter (21 December-21 March); *The minimum precipitation threshold for calculating the wet season was 6.9 mm because there were no months with rainfall below 6 mm.

Table A5. The full and partial redundancy analyses (RDAs) used for partitioning the variation of aleppo pine regeneration density (N/ha) after fire. E: environmental factors (Table 2a, b, c). ST: number of years elapsed between fire and regeneration sampling; *=significant ($p < 0.05$); TEV= Total explained variance. See the Methods for more details about environmental variables. TEV= total explained variance (%).

Run	Env. Var.	Covariable	Eigenvalue (TEV, %)
1	E (prefire + postfire site factors + Fire severity) + ST	None	0.344
2	E (prefire + postfire site factors + Fire severity)	ST	0.329
3	ST	E (prefire + postfire site factors + Fire severity)	0.017
Join effect	ST \leftrightarrow E	-	-0.002
Run	Env. Var.	Covariable	Eigenvalue
1	E (prefire + postfire site factors) + Fire severity	None	0.344
2	E (prefire + postfire site factors)	Fire severity	0.293
3	Fire severity	E (prefire + postfire site factors)	0.025
Join effect	E \leftrightarrow Fire severity	-	0.026
Run	Env. Var.	Covariable	Eigenvalue
1	E (prefire + postfire site factors + Fire severity)	None	0.344
2	Prefire and severity factors	Postfire site factors	0.284*
3	Postfire site factors	Prefire and severity factors	0.075
Join effect	Prefire and severity factors \leftrightarrow Postfire site factors	-	-0.015
Run	Env. Var.	Covariable	Eigenvalue
1	Climate	Geography	0.067
2	Geography	Climate	0.069*
Join effect	Climate \leftrightarrow Geography	-	0.002

Table A5 (b). Continued

Sp. Var	Env. Var	Eigenvalue (TEV%)	
sqrt(N/ha)	Clima&Geogr (C) + Topogr&Soil (T) + Prefire forest struct. (P)	0.253	
Combination 1			
Run	Env. Var	Covariable	Eigenvalue
1	P	C + T	0.083
2	C + T	None	0.174*
3	C + T	P	0.140
4	P	None	0.113
Joint effect	$P \leftrightarrow C + T$		0.030
Combination 2			
Run	Env. Var	Covariable	Eigenvalue
1	T	C + P	0.002
2	C + P	None	0.250*
3	C + P	T	0.237
4	T	None	0.015
Joint effect	$T \leftrightarrow C + P$		0.013
Combination 3			
Run	Env. Var	Covariable	Eigenvalue
1	C	T + P	0.131
2	T + P	None	0.122
3	T + P	C	0.089
4	C	None	0.167*
Joint effect	$C \leftrightarrow T + P$	-	0.036

Table A6. Summary of prefire variables and their combination in different models in order to predict the postfire natural Aleppo pine hyperdense regeneration (>4,000 plants/ha) across 15 wildfires in the Comunitat Valenciana, Spain. ●= predictor variable included in the model (M); *= significant variable in the Model. Units of the variables can be seen in the Table 2.

Variables	M1	M2	M3	M4	M5	M6	M7	M8	M9	M10	M11	M12	M13	M14	M15
STA	●	●	●	●	●	●	●	●*		●	●*	●		●*	
MAI	●	●	●	●	●	●	●	●	●	●	●		●	●	●
TM	●	●	●*	●*					●*	●*		●*			
Tmin	●*				●*	●*			●						
Tmax	●	●	●	●	●	●	●		●						
AP	●	●	●	●	●	●	●	●*	●	●	●*	●	●		
APM3	●	●	●*	●*	●	●	●	●*	●						
APM2	●	●	●	●	●	●	●	●	●						
APM1	●	●	●	●	●	●	●	●	●*						
PLWS	●	●	●	●	●	●	●	●	●						
DL1	●	●	●	●	●	●	●	●	●*						
DL2	●	●	●	●	●	●	●	●	●						
DL3	●	●	●	●	●	●	●	●	●*						
Long	●	●*			●	●	●								
Latit	●	●	●*		●	●	●								
Altit	●	●	●	●	●		●	●	●	●	●	●	●*	●	●*
Aspect	●	●	●	●	●	●	●	●	●*	●	●	●	●	●	●
Slope	●	●	●	●	●	●	●	●	●	●	●	●	●*	●	●*
Lithol	●*	●	●	●	●*	●*	●	●	●	●	●	●	●	●	●
Stonin	●	●	●	●	●	●	●	●	●*	●	●	●	●*	●	●*
Depth-soil	●*	●	●*	●*	●*	●*	●	●	●	●*	●*	●*	●	●	●
A-terrace	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Soil-E	●	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Pre-D	●*	●*	●*	●*	●*	●*	●	●*	●*	●*	●	●*	●*	●*	●*

N-age-class	●	●	●	●	●	●	●	●	●	●	●	●*	●	●
Fcc-sp	●	●*	●	●	●	●	●	●	●	●*	●	●*	●	●*
Fcc-MB	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Fcc-L+FT	●	●	●	●	●	●	●	●*	●	●	●	●	●	●
Pre-shr	●	●	●	●	●	●	●*	●	●	●*	●	●	●	●
Pre-her	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Pre-shr-r	●*	●	●	●	●*	●*	●	●	●	●	●	●	●	●
Pre-her-r	●	●	●	●	●	●	●	●	●*	●	●	●*	●	●*
Un-li-c	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Ash-w	●	●	●	●	●	●	●	●	●	●	●	●	●*	●
Shr-sev	●	●	●*	●*	●	●	●	●	●	●	●*	●	●	●
Her-sev	●	●	●	●	●	●	●	●	●	●	●	●	●	●
Tree-sev	●	●*	●	●	●	●	●	●	●	●	●	●	●	●
CBI	●	●	●	●	●	●	●	●*	●	●	●	●*	●	●

STA: stand age or time elapsed since fire to pine regeneration sampling; MAI: Martonne's Aridity Index; TM: average annual temperature; Tmin: average minimum temperature; Tmax: average maximum temperature; AP: average annual precipitation; APM3: average annual precipitation three years before fire; APM2: average annual precipitation two years before fire; APM1: average annual precipitation in the year before fire; PLWS: total precipitation in the prefire last wet season; DL1: length of the dry period in the year before fire; DL2: length of the dry period two years before fire; DL3: length of the dry period three years before fire; Long: longitude; Latit: latitude; Altit: altitude; Aspect: orientation; Slope: inclination; Lithol: dominant bedrock's lithology; Stonin: stoniness; Depth-soil: soil layer depth; A-terrace: presence of agricultural terraces; Soil-E: signs of soil erosion; Pre-D: prefire Aleppo pine tree density; N-age-class: number of Aleppo pine age classes; Fcc-Sp: *Pinus halepensis* canopy cover; Fcc-MB: coverage of subcanopy trees (thickets) of *P. halepensis*; Fcc-L+FT: coverage of upper canopy trees (polewood + old growth) of *Pinus halepensis*; Pre-shr: prefire total shrubs coverage; Pre-her: prefire total herbs coverage; Pre-shr-r: prefire resprouter shrubs coverage; Pre-her-r:

prefire resprouter herbs coverage; Un-li-c: unaffected litter coverage; Ash-w: presence of white ash on the forest floor; Shr-sev: fire severity on shrubs; Her-sev: fire severity on herbs; Tree-sev: fire severity on trees; CBI: Composite Burn Index.

Table A7. Tree models tested for postfire Aleppo pine hyperdense regeneration analysis. FP: first predictor included in the tree model; N° T Nodes: N° of terminal nodes; Depth: depth of the Tree model; AID: Automatic Interaction Detection or variables resubstitution method; SE: Standard error of the risk estimate; G%: Global classification of the model; BS: Biological sense of the model depending on the tree depth, number of nodes and significant variables. Best model is marked in bold.

Model Summary					AID		Crossvalidation		Classification			
Model	FP	N° Nodes	N° T Nodes	Depth	Risk estimate	SE	Risk estimate	SE	< 4,000/ha	> 4,000/ha	G%	BS
1	Tmin	14	9	3	0.159	0.030	0.290	0.038	91.4%	75.0%	84.1%	High
2	Long	14	10	2	0.186	0.032	0.345	0.039	91.4%	68.8%	81.4%	Low
3	TM	20	13	2	0.166	0.031	0.393	0.041	87.7%	78.1%	83.4%	Low
4	TM	20	13	2	0.159	0.030	0.331	0.039	88.9%	78.1%	84.1%	Low
5	Tmin	14	9	3	0.159	0.030	0.352	0.040	91.4%	75.0%	84.1%	High
6	Tmin	14	9	3	0.159	0.030	0.324	0.039	91.4%	75.0%	84.1%	High
7	Long	14	10	2	0.186	0.032	0.324	0.039	91.4%	68.8%	81.4%	Low
8	D	15	10	3	0.172	0.031	0.366	0.040	76.5%	90.6%	82.8%	Low
9	D	29	20	3	0.186	0.032	0.386	0.040	82.7%	79.7%	81.4%	Low
10	TM	20	14	2	0.159	0.030	0.297	0.038	90.1%	76.6%	84.1%	Low
11	D	19	13	3	0.214	0.034	0.400	0.041	85.2%	70.3%	78.6%	Low
12	TM	18	12	2	0.159	0.030	0.036	0.040	88.9%	78.1%	84.1%	Low
13	D	22	14	3	0.200	0.033	0.441	0.041	88.9%	68.8%	80.0%	Low
14	STA	15	10	3	0.172	0.031	0.345	0.039	85.2%	79.7%	82.8%	Low
15	D	23	15	3	0.200	0.033	0.359	0.040	87.7%	70.3%	80.0%	Low

Table A8. Classification table for the categorical dependent variable: *postfire Aleppo pine regeneration abundance* (<4,000/ha and >4,000/ha) with the number of cases classified correctly and incorrectly for each category of the dependent variable in the model M1.

Observed	Predicted		Correct percentage
	<4,000	>4,000	
<4,000	74	7	91.4%
>4,000	16	48	75.0%
Global percentage	62.1%	37.9%	84.1%

Table A9. Nodes performance for the category <4,000 plants/ha of the dependent variable *postfire Aleppo pine regeneration abundance* in the model M1. Percentage gain, the response percentage and the index percentage per node. Gain is the percentage of the total cases in the target category in each node, computed as (node target n / total target n) x 100. Index is the ratio of the node response percentage for the target category compared to the overall target category response percentage for the entire sample.

Node	Node		Gain		Response	Index
	N	Percentage	N	Percentage		
4	7	4.8 %	7	8.6 %	100.0	179.0 %
2	31	21.4 %	30	37.0 %	96.8	173.2 %
9	13	9.0 %	12	14.8 %	92.3	165.2 %
7	10	6.9 %	9	11.1 %	90.0	161.1 %
11	5	3.4 %	4	4.9 %	80.0	143.2 %
13	24	16.6 %	12	14.8 %	50.0	89.5 %
6	33	22.8 %	5	6.2 %	15.2	27.1 %
12	16	11.0 %	2	2.5 %	12.5	22.4 %
10	6	4.1 %	0	0.0 %	0.0	0.0 %

Table A10. Node performance for the category >4,000 plants/ha of the dependent variable *postfire Aleppo pine regeneration abundance* in the model M1. Percentage gain, the response percentage and the index percentage per node. Gain is the percentage of the total cases in the target category in each node computed as: (node target n / total target n) x 100. Index is the ratio of the node response percentage for the target category compared to the overall target category response percentage for the entire sample.

Node	Node		Gain		Response	Index
	N	Percentage	N	Percentage		
10	6	4.1%	6	9.4%	100.0	226.6
12	16	11.0%	14	21.9%	87.5	198.2
6	33	22.8%	28	43.8%	84.8	192.2
13	24	16.6%	12	18.8%	50.0	113.3
11	5	3.4%	1	1.6%	20.0	45.3
7	10	6.9%	1	1.6%	10.0	22.7
9	13	9.0%	1	1.6%	7.7	17.4
2	31	21.4%	1	1.6%	3.2	7.3
4	7	4.8%	0	0.0%	0.0	0.0