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Spatial and temporal variations of overstory and understory fuels in Mediterranean landscapes

Martina Sánchez-Pinillos [a,b,c,*], Miquel De Cáceres [a,d], Pere Casals [a], Albert Alvarez [d], Mario Beltrán [e], Juli G. Pausas [f], Jordi Vayreda [d,g], Lluís Coll [a,h]

[a] Joint Research Unit CTFC – AGROTECNIO – CERCA, Ctra. St. Llorenç de Morunys km 2, 25280 Solsona, Spain
[b] Centre for Forest Research (CEF), Université du Québec à Montréal (UQAM), Montreal H3C 3P8 Quebec, Canada
[c] Faculty of Forestry and Environmental Management, University of New Brunswick, Fredericton, E3B 5A3 New Brunswick, Canada
[d] CREAF, E08193 Bellaterra (Cerdanyola del Vallès), Catalonia, Spain
[e] Forest Science and Technology Centre of Catalonia (CTFC), Ctra. St. Llorenç de Morunys km 2, 25280 Solsona, Spain
[f] Centro de Investigaciones sobre Desertificación (CIDE-CSIC), 46113 Montcada, Valencia, Spain
[g] InForest Jru (CTFC-CREAF), Ctra. St. Llorenç de Morunys km 2, 25280 Solsona, Spain
[h] Department of Agriculture and Forest Engineering (EAGROF), University of Lleida, Av. Alcalde Rovira Roure 191, 25198 Lleida, Spain

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ABSTRACT

Mediterranean forests are prone to fire and highly diverse in environmental conditions, species composition, and forest structure. While much is known about fire hazard and forest responses to fire in Mediterranean climate regions, our understanding of the spatial distribution of fuel characteristics and their dynamics remains incomplete. We hypothesized that fire hazard in heterogeneous Mediterranean regions is primarily explained by the variation in fuel loading and flammability characteristics of the understory layer across the landscape and over time. We used the Spanish National Forest Inventory data to estimate overstory and understory fuel characteristics, compare their spatial and temporal variations across Catalonia (NE Spain) over the last 25 years, and assess the role of climate conditions in explaining spatial distribution and dynamics of fuel characteristics. Our results showed that fuel characteristics strongly depend on the species composition of the overstory and understory layers. Fuel characteristics of both vegetation layers were significantly different and poorly correlated with each other. Although both strata showed significantly different rates of change in most fuel characteristics, the average changes were, in general, very small for the time window considered. Forests in the warmest and driest environments showed the highest flammability characteristics in both overstory and understory layers in contrast to mountain communities. We did not find, however, a remarkable effect of climatic conditions on the rates of change of fuel characteristics during the study period. Altogether, these findings confirm the importance of considering the spatial variation of fuel characteristics of different vegetation strata separately and provide critical information on forest vulnerability to develop appropriate fire mitigation policies in Mediterranean ecosystems.

1. Introduction

In recent decades, the intensification of drought periods and the changes at the landscape scale are promoting fire-regime changes, leading to a generalized increase of the frequency, severity, and burned area in many forest ecosystems (Pausas and Keeley, 2014; Pausas and Paula, 2012; San-Miguel-Ayanz et al., 2018; Westerling et al., 2011). Under this context, unraveling the determinants that make forests more vulnerable to high-intensity crown fires has emerged as a research and technical issue of utmost importance (Alvarez et al., 2013; Sande Silva et al., 2010). Among factors influencing fire behavior – weather, topography, and vegetation – a major effort must be done to understand the role of spatial and temporal variations of fuel characteristics (Keane, 2016; Simeoni et al., 2011). Indeed, the distribution and characteristics of plant biomass are the factors that mostly govern the combustion processes (Weise and Wright, 2014) and fire hazard (i.e. “a fuel complex, defined by volume, type, condition, arrangement, and location, that determines the degree of ease of ignition and of fire suppression

* Corresponding author at: Joint Research Unit CTFC – AGROTECNIO – CERCA, Ctra. St. Llorenç de Morunys km 2, 25280 Solsona, Spain.
E-mail address: martina.sanchezpinillos@gmail.com (M. Sánchez-Pinillos).

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difficulty", (FAO, 2005)). Besides, vegetation is the only factor that can be modified through adequate management strategies to anticipate potential catastrophic shifts driven by extreme wildfires (Stephens et al., 2009).

In Mediterranean forests, many plant species have morphological and physiological traits that make them highly flammable (Keeley et al., 2011; Saura-Mas et al., 2010). Species-specific characteristics such as live fuel moisture, the distribution, and size of live and dead organs, or the presence of volatile chemical compounds are all known to contribute to plant flammability (Pausas et al., 2017). In addition to species composition, the stand structure plays an essential role in fire behavior, determining the arrangement of fuels in the stand, and therefore, governing the spreading and crowning potential of fire (Alvarez et al., 2012; Nunes et al., 2019). Once a fire starts in a surface fuel, its intensity and the distance to the overstory will determine the probability that fire spreads to tree crowns (Agee and Skinner, 2005; Cruz et al., 2004; Van Wagner, 1987). Then, sustained crown-to-crown fire spread will depend on the existence of continuous cover of canopy fuels and wind conditions but requires additional energy from the understory (Scott and Reinhardt, 2001; Van Wagner, 1977; Werth et al., 2011). Although many Mediterranean forests are prone to crown fires, they are highly diverse in terms of fuel loading, condition, and structure (Alvarez et al., 2012; Fernandes, 2009). In this sense, the combined effects of species composition and structure in all forest strata and their variations over time and space determine important differences in fire hazard across forest communities (Dimitrakopoulos, 2002; Nunes et al., 2019).

At the landscape scale, the spatial distribution of fuel characteristics across heterogeneous Mediterranean regions responds to the variability of overstory-understory species assemblages and structures. On the one hand, species composition is constrained by climate and other environmental factors, and the understory layer may be influenced by the structure and composition of the overstory, which regulates microenvironmental conditions and light availability (Ameztegui and Coll, 2013; Majasalmi and Rautiainen, 2020; Messier et al., 1998). On the other hand, Mediterranean forests have been modulated by natural disturbances and long and intense human activity since historical times (Keeley et al., 2012; Nocentini and Coll, 2013). Consequently, multiple overstory-understory combinations of heterogeneous landscapes may result in even greater variability of forest fuel characteristics and fire behavior at the stand level (Baeza et al., 2002; Curt et al., 2011; Fernandes et al., 2008; Santana et al., 2011). Besides, the effects of forest dynamics together with climate and land-use changes may influence the rate of variation of fuel characteristics in vegetation strata depending on species composition or environmental conditions (Keane, 2016; Sánchez-Pinillos et al., 2019).

At the stand scale, the effects of forest composition and structure on fire hazard have been addressed for different shrublands (Baeza et al., 2002; Castagneri et al., 2013; De Luis et al., 2004) and forest types (Alvarez et al., 2012; Fernandes et al., 2004; Molina et al., 2011). However, few studies have evaluated in detail the factors involved in the geographic or temporal variation of fuel characteristics across large Mediterranean regions and over relatively long periods (Fernandes, 2009; Keane, 2013; Sánchez-Pinillos et al., 2019). Moreover, the degree of correlation between fuel characteristics of the overstory and understory layers is often ignored, overlooking the influence that different combinations of vegetation strata may have on fire hazard (Coll et al., 2011; Keane, 2016) and their potential use to generate fuel cartography from the overstory species (Keane, 2013).

In this study, we assess the spatial and temporal variation of wildland fuels in the understory (i.e. woody vegetation stratum up to 2 m height, excluding floor fuels) and overstory (i.e. woody vegetation stratum above 2 m height) layers for common Mediterranean forests. In particular, we aimed to answer the following questions: (1) Are fuel characteristics in the understory and overstory layers correlated? (2) Does the temporal and spatial variation of fuel characteristics differ between the understory and overstory layers? (3) To what extent the differences in climate conditions explain the observed variation of fuel characteristics (hence fire hazard) and their change over time? We considered forests without recent evidence of natural and anthropic disturbances in Catalonia (NE of Spain) as a case study to answer these questions. We hypothesized that the variation in fire hazard was primarily explained by differences in loading and flammability properties of the understory layer. Besides, we expected that these differences were mainly driven by climate conditions determining differences in species composition.

2. Methods

2.1. Study area

Our study area covers the forested area of Catalonia (NE of Spain), which occupies about 13,080 km^2 (42% of the region). This region is characterized by a long human history and encompasses great environmental variability due to its contrasting topography, varied edaphic conditions, and strong climatic gradients resulting from the complex relief and its variable distance to the coast (Fig. 1, Appendices C.2). The climate is predominantly Mediterranean; rainfall peaks in autumn and spring and it is relatively low during summer and winter. Mean annual temperature ranges between 2 and 17 °C (average 11.6 °C) and annual rainfall varies between 350 and 1600 mm (average 680 mm) (Ninyerola et al., 2005). Spatial heterogeneity in environmental conditions results in a range of forest ecosystems representative of the western Mediterranean Basin. According to the Third Spanish National Forest Inventory (Ministerio de Medio Ambiente, 2007), the most abundant tree species in lowland forests of Catalonia are Aleppo pine (*Pinus halepensis* Mill.) and holm oak (*Quercus ilex* L.) forming forests of different stand structures and degree of mixture. Cork oak (*Quercus suber* L.) forests are restricted to siliceous areas of the northeastern coast. At mid altitudes, forests are often dominated or co-dominated by holm oak, downy oak (*Q. pubescens* Willd.), Portuguese oak (*Q. faginea* Lam.), black pine (*P. nigra* ssp. *salzmannii* (Dunal) Franco), and Scots pine (*P. sylvestris* L.), whereas European beech (*Fagus sylvatica* L.) is restricted to the most humid sites and mountain pine (*P. uncinata* Mill.) to the highest altitudes. Common Mediterranean understory woody species in lowlands include evergreen species such as mastic tree (*Pistacia lentiscus* L.), kermes oak (*Q. coccifera* L.), laurustinus (*Viburnum tinus* L.), heathers (*Erica* sp. pl.), and a wide range of shrubs, many of them from the *Lamiaceae* and *Cistaceae* families. Junipers (*Juniperus communis* L.), box (*Buxus sempervirens* L.), and deciduous species such as snowy mespilus (*Amelanchier ovalis* Medik.), common dogwood (*Cornus sanguinea* L.), or wayfaring tree (*V. lantana* L.) are common at mid-elevations. Woody understory in Pyrenean high mountains is dominated by alpenrose (*Rhododendron ferrugineum* L.) in the north-facing forests and *Cytisus oromediterraneus* Rivas Mart. et al. in the southern slopes.

2.2. Forest inventory data

We used the Spanish National Forest Inventory (SNFI; Ministerio de Agricultura Alimentación y Medio Ambiente, 2019; Ministerio de Medio Ambiente, 2007, 1996) as the data source to assess the variation in forest fuel characteristics across space and over time. The SNFI in Catalonia comprises three repeated surveys (SNFI2 1990, SNFI3 2001, and SNFI4 2014) carried out in permanent circular plots located at the intersections of a 1 × 1 km^2 UTM grid covering all forested areas. Each circular plot includes four nested subplots of 5–25 m radii in which different trees were inventoried depending on the species and size. Species identity, height, and diameter at breast height (dbh) were recorded for each living tree with a dbh larger than 7.5 cm. For trees with dbh lower than 7.5 cm, the SNFI provides the number of saplings (dbh between 2.5 and 7.5 cm) per species and average height, and the abundance of seedlings (dbh < 2.5 cm) per species in ranges of density and height. For each shrub species, percent cover and average height are recorded in the 10-m-radius subplot.

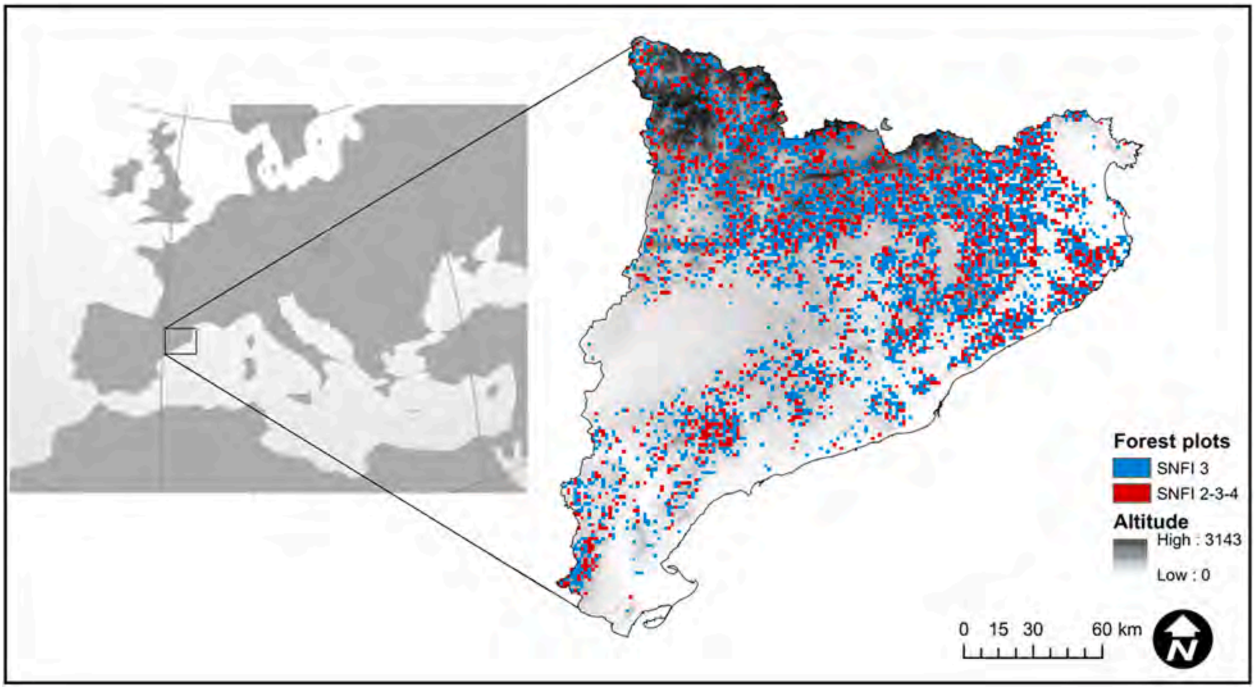

Fig. 1. Distribution of permanent plots of the Spanish National Forest Inventories (SNFI) in Catalonia (NE Spain) used to assess the variation of fuel characteristics across space (6,633 plots; SNFI3) and over the last 25 years (2,859 plots; SNFI 2–3-4).

We selected a total number of 6,633 plots sampled in the SNFI3 (Fig. 1) to assess spatial patterns. We discarded the plots burned in forest fires during the period covered by the SNFI (1990–2014) and those with evidence of intense forest management or disturbances (percentage of stumps or dead trees higher than 50%) to avoid abrupt changes in fuel characteristics and focus on the effects of forest succession and development after the abandonment of past intensive management. Besides, we only considered the plots with a measurable understory-overstory gap (see definition below). Further, standing dead trees were also excluded and fine fuels were assumed to fall soon after tree death. We considered 278 woody plant taxa, mostly at the species level. To assess the temporal variation of fuel characteristics, we only considered the common subset of plots among the three surveys (n = 2,856, Fig. 1).

2.3. Understory and canopy fuel characteristics

We defined understory and overstory as the vegetation layers below and above 2 m height, respectively (Rothermel, 1972; Sandberg et al., 2001). For each plot and stratum, we estimated the following fuel characteristics: (*i*) fine fuel loading (*w;* $kg{\cdot}m^{-2}$ of dry weight); (*ii*) bulk density (*bd*, $kg{\cdot}m^{-3}$); (*iii*) surface area-to-volume ratio (σ; $m^2{\cdot}m^{-3}$); (*iv*) high heat content (*h;* $kJ{\cdot}kg^{-1}$); (*v*) minimum fuel moisture content (*FMC;* % of dry weight); and (*vi*) the gap between the understory and overstory layers (*uo gap;* m) as a measure of vertical fuel continuity.

We only considered fine fuels (i.e. leaves and branches of diameter up to 6.35 mm) because they are the most relevant for fire behavior and propagation (Fernandes and Loureiro, 2013; Rothermel, 1972; Scott and Reinhardt, 2002). We estimated fine fuel loading (*w*) in forest plots following the same procedures described in Sánchez-Pinillos et al., 2019 (see Appendix A for details). Tree fine fuel loading was computed as the product of foliar biomass, tree density, and a species-specific ratio relating the dry weight of leaves plus small branches (<6.35 mm) to the weight of leaves alone. The foliar biomass of each measured tree was calculated from an allometric equation relating foliar dry weight to dbh and a measure of competition in the plot. For shrub species, fine fuel loading was calculated by multiplying an estimate of the fine fuel loading for an average individual (obtained by allometric equations from the shrub height) by an estimate of shrub density (De Cáceres et al., 2019a). For any measured tree, we estimated its crown base heights using a model of tree crown ratio (Weiskittel et al., 2011) and divided its crown length and fine fuel loading between the understory and the overstory layers. The understory and overstory fine fuel loadings were obtained by adding tree/shrub loadings in each layer. Then, we calculated fuel depth (m) in each layer as the difference in height between the maximum crown top and minimum crown base, considering a threshold of 2 m to differentiate both strata. By dividing fuel loading by fuel depth in each layer, we calculated the average fine fuel bulk density (*bd*, $kg{\cdot}m^{-3}$). The gap between understory and overstory fuels was estimated by analyzing the stand's fuel bulk density profile (Reinhardt et al., 2006). Specifically, the understory-overstory gap (*uo gap*) was defined as the difference between canopy base height (the minimum height equal to or above 2 m with a bulk density larger than 0.04 $kg{\cdot}m^{-3}$) and understory top height (the maximum height lower or equal to 2 m with a bulk density larger than 0.04 $kg{\cdot}m^{-3}$) (Mitsopoulos and Dimitrakopoulos, 2007). Note that the definitions of canopy base height and understory top height differed between the calculation of *uo gap* (which focused on vertical continuity of fuel density beyond a threshold) and that of layer bulk density (which focused on the overall fuel density within layer).

Surface area-to-volume ratio (σ) describes the amount of surface available for exchanging heat. Thus, it is related to fire intensity and spread rate. Similarly, high heat content (*h*) is also associated with the energy provided by fuel. Species-specific values for these two characteristics were obtained from bibliographic sources. Minimum fuel moisture content (*FMC*) values for living understory and overstory species were obtained from the bibliography, complemented with additional field sampling carried out in summer for some species to get typical summer values. When compiling trait data, we prioritized attribute values referred to the fraction including both leaves and branches up to 6.35 mm, but we took values that referred to smaller branches or only leaves when this information was lacking. We defined species groups to provide parameter values for species without data (Appendix B). Average understory and overstory attribute values were calculated using tree/shrub loadings as weights (Fernandes, 2009).

Although some chemical compounds of fuels can also be a source of flammable gasses that increase fire intensity, their concentration is not well established in the bibliography and we decided not to include them. Similarly, we did not consider the fuel dead fraction in the analyses because the information compiled from bibliographic sources could not be representative for each plot, as this variable highly depends on local environmental conditions (Keane, 2015). Calculations of fuel characteristics were conducted using functions available in the 'medfate' R package, ver. 1.1.6 (De Cáceres et al., 2015).

2.4. Forest categories and climate factors

SNFI3 forest plots were independently classified according to the species composition in their overstory or understory to facilitate the interpretation of the spatial and temporal variation of species composition in both layers. To identify plots according to their overstory we defined dominance-based forest types. A given plot was considered dominated by one tree species when both the relative basal area (BA) and density of adult trees (dbh $>$ 7.5 cm) for the target species were higher than 80%. Similarly, a stand was considered co-dominated by two species if: (1) the relative BA and the relative density of adult trees belonging to each species i and j were between 20% and 80%; (2) the relative BA and the relative density of the sum of all adult trees belonging to both species i and j were higher than 80% (De Cáceres et al., 2019b). We identified 51 overstory types, of which 12 corresponded to stands dominated by one species, but only eight classes presented more than 50 plots (*P. uncinata*, *P. sylvestris*, *P. nigra*, *P. halepensis*, *F. sylvatica*, *Q. pubescens*, *Q. suber*, *Q. ilex*; Appendices C.3).

To classify plots according to their understory, we applied a cluster analysis based on the dissimilarity of species composition and abundance between each pair of plots. For that, we generated a squared symmetric matrix containing the percentage difference (i.e. Bray-Curtis dissimilarity) between each pair of plots. Using the dissimilarity matrix, we generated an initial partition by cutting the dendrogram generated by Ward's hierarchical clustering and refined this initial partition with the non-hierarchical clustering Partition Around Medoids (PAM). We considered partitions of different numbers of clusters (2 to 12) that were evaluated through the Silhouette analysis. The clustering procedure resulted in a classification of understory communities into nine classes (Appendices C.4): subalpine low scrubs and heaths understory (*subalpine*), mesophile sub-Mediterranean understory with evergreen and deciduous shrubs (*sub-Mediterranean*), xerophile continental (*xerophile continental*) and Mediterranean (*xerophile Mediterranean*) calcicolous understories with evergreen and small-leaved scrubs, xero-mesophile continental (*xero-mesophile continental*) and Mediterranean (*xero-mesophile Mediterranean*) understories, mesophile Mediterranean understory with evergreen and deciduous shrubs (*mesophile*), silicicolous Mediterranean understory with evergreen and ericoid shrubs (*silicicolous ericoids*), and a mixed group including eurosiberian and Mediterranean species (*mixed group*).

The low value (0.198) of the adjusted Rand index calculated for the overstory and understory types indicated a low level of correspondence between the two partitions. In general, every overstory type was associated with multiple understory classes and *vice versa*. Only the stands dominated by *Q. suber* showed silicicolous ericoids predominating over other classes, while this understory class was uncommon under other canopies (Appendices C.5).

Among the climate variables considered to explain the spatial and temporal variation of fuel characteristics, we included the average monthly temperature, the average annual precipitation, and the moisture index (calculated as the ratio between annual precipitation and annual potential evapotranspiration). Climatic data averages corresponded to the 1961–1990 period and were obtained from Ninyerola et al. (2005).

2.5. Spatial and temporal analyses of fuel characteristics

Values of fuel characteristics in the canopy and understory layers of all 6,633 SNFI3 plots were used to test the relationship between fuel characteristics in both overstory and understory layers, as well as between fuel characteristics and climate. For that, we used the non-parametric Wilcoxon test and Spearman's correlation analysis. We additionally used the same data to produce maps displaying the spatial distribution of fuel characteristics (Appendices D).

The subset of 6,561 plots presenting understory stratum (i.e. w_{und} greater than 0) was used to assess the correlations between fuel characteristics within the same vegetation layer (either overstory or understory) and across both layers (e.g. between w_{ove} and w_{und}). For that, we used principal component analysis (PCA) to summarize fuel data estimated for the SNFI3 survey. The influence of climate in fuel characteristics for both vegetation layers was investigated using redundancy analysis (RDA) following the two-step procedure described in (Legendre and Legendre, 1998). Specifically, we first fitted linear mixed models considering each fuel characteristic as the response variable and all climatic variables as fixed effects, with a previous standardization of all of them. We included administrative subdivisions (counties, n = 42) as random effects to account for the spatial autocorrelation. Given the high correlation of the moisture index with both temperature and precipitation, it was discarded from the models. The fitted values of the resulting models were then represented in an ordination space through PCA and the correlations of environmental variables with principal components were displayed using the envfit() function in the 'vegan' R package (Oksanen et al., 2017).

Finally, to assess the variation of fuel characteristics along the 25 years encompassed by the SNFI, we calculated the rate of change of each fuel variable in the 2,856 plots comparable between the SNFI2 and the SNFI4 for both overstory and understory layers. Analogous PCA and RDA analyses to those described above were applied to the matrix compiling the annual rate of change of fuel characteristics between surveys. Besides the multivariate analyses, we used Spearman correlation analyses to assess the relationships between fuel characteristics within and among canopy and understory classes in terms of temporal change and the influence of climate variables.

3. Results

3.1. Spatial variation of fuel characteristics in canopy and understory layers

The non-parametric Wilcoxon test indicated that all fuel characteristics were significantly different between the overstory and understory strata (Table 1; Appendices D.2). Fine fuel loading (w) and bulk density (bd) were negatively correlated between the understory and the overstory (Spearman's r = -0.28 and $p < 0.001$, r = -0.02, respectively, Fig. 2). The heat content (h) was the fuel property with the highest interlayer correlation (Spearman's r = 0.42, $p < 0.001$). However, almost 72% of plots had higher values for the understory than the overstory, given the general high heat content of many Mediterranean shrub species. The variable with more contrasted values between the overstory and the understory was minimum *FMC,* with most forest plots (94.1%) presenting lower values of minimum *FMC* in the understory.

The first and second axes of the PCA summarizing the variation in fuel characteristics explained 28.1% and 24.3% of the variation, respectively (Fig. 3a). Fuel characteristics were generally correlated within each vegetation layer, but different patterns were observed in each stratum (Fig. 3a; Table D.1). In contrast to the understory layer in which fine fuel loading correlates positively with most fuel characteristics, fine fuel loading in the overstory was negatively correlated with any other fuel characteristics, except the bulk density, which was highly correlated with fine fuel loadings in both strata. Thus, *Q. ilex* forests were characterized by high overstory bulk density and fine fuels while

Table 1
Comparison of fuel characteristics between the overstory and understory, considering the values for plots in the SNFI3. For each variable and vegetation stratum, the table shows average, standard deviation, percentiles 5% and 95%, and the percentage of plots for which the value in the understory layer is larger than in the overstory; non-parametric Spearman's correlation for each fuel variable between layers (rho, * *p-value* < 0.001) is also shown. The Two-sample Wilcoxon test between layers was significant for all fuel characteristics ($\alpha = 0.001$).

		Overstory (O)			Understory (U)			U > O	rho
	Units	Mean (sd)	P05	P95	Mean (sd)	P05	P95		
Fine fuel loading (*w*)	$kg \cdot m^{-2}$	0.66 (0.32)	0.23	1.28	0.46 (0.32)	0.05	1.07	32.7%	−0.28*
Bulk density (*bd*)	$kg \cdot m^{-3}$	0.06 (0.04)	0.03	0.14	0.23 (0.17)	0.03	0.55	87.7%	−0.02*
Surface area-to-volume ratio (σ)	$m^2 \cdot m^{-3}$	5210.3 (705.3)	4050.0	6050.0	5138.1 (759.6)	4128.9	6460.6	42.8%	0.30*
Heat content (*h*)	$kJ \cdot kg^{-1}$	20343.8 (828.5)	19317.3	22150.0	20840.4 (794.9)	19783.1	22266.5	71.8%	0.42*
Min. fuel moisture content (*FMC*)	% dw	86.38 (15.31)	65.74	110.33	64.2 (10.53)	50.43	86.1	5.86%	0.22*
Understory-overstory gap (*uo gap*)	m	1.20 (2.07)	0.00	5.6					

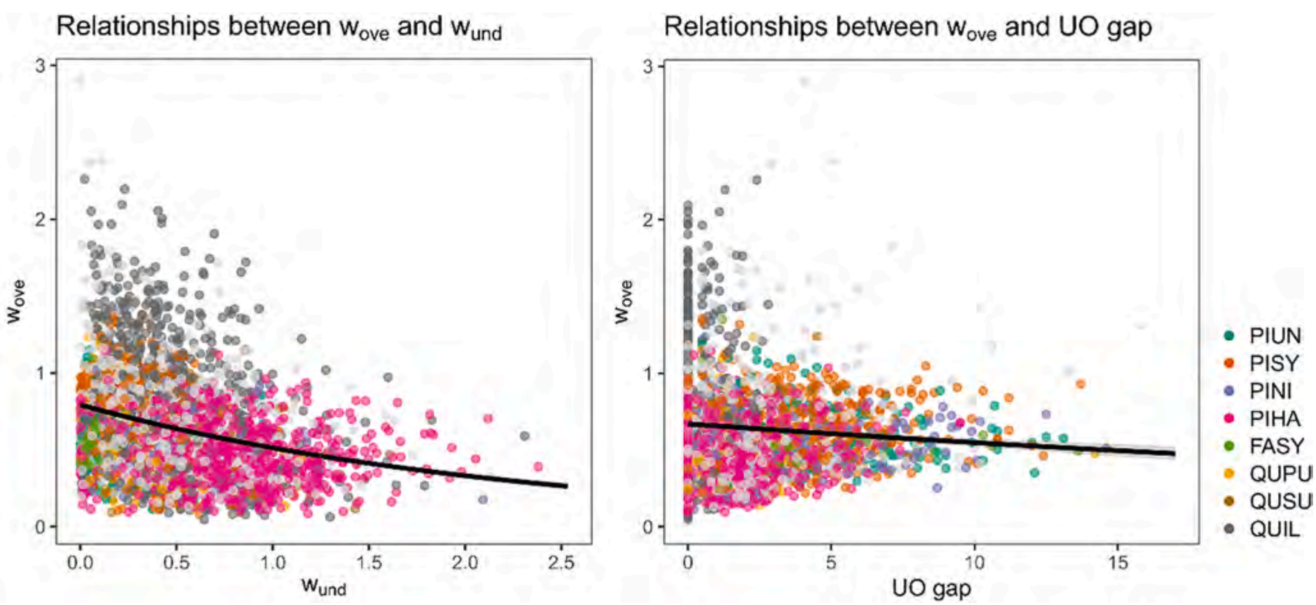

Fig. 2. Variation of understory fine fuel loading (w_{und}, $kg \cdot m^{-2}$) and understory-overstory gap (*UO gap*, m) in relation to the overstory fine fuel loadings (w_{ove}, $kg \cdot m^{-2}$). Both panels show predicted values of w_{ove} from generalized linear models using gamma distribution functions and w_{und} and *UO gap* as explanatory variables. Colors represent different overstory types (PIUN: *Pinus uncinata*, PISY: *P. sylvestris*, PINI: *P. nigra*, PIHA: *P. halepensis*, FASY: *Fagus sylvatica*, QUPU: *Quercus pubescens*, QUSU: *Q. suber*, QUIL: *Q. ilex*).

P. halepensis and *Q. suber* forests were characterized by high overstory heat content and understory fuel load, bulk density, heat content, and σ (Figs. 2 and 3a). *FMC* was negatively correlated with most fuel variables in the understory, indicating that some communities could be highly flammable and present a great potential to facilitate the spread of intense fires, depending on their combined values of low *FMC* and high *w*, σ, and *h*. In particular, silicicolous ericoids and xerophile understory types were the ones that better satisfied these flammability characteristics. Regarding the gap between the overstory and understory, it was positively related to overstory *FMC* (Table D.1). In this sense, forests dominated by mountain pines (*P. uncinata* and *P. sylvestris*) showed larger interlayer gaps and higher *FMC* than most forests, specifically those dominated by *Q. suber*, with high understory fine fuel loadings and continuous vertical structure (Fig. 2).

The first and second axes of the RDA explained 45.0% and 30.3% of the variation fitted by fixed factors in the mixed linear models, respectively (Fig. 3b). The overstory fine fuel loading (w_{ove}) and bulk density (bd_{ove}) were associated with high temperatures (non-significant for bd_{ove}) and precipitation. In the understory, temperature and precipitation had similar positive and negative effects, respectively, for both fine fuel loading and bulk density. The overstory surface area-to-volume ratio (σ_{ove}) and the heat content in both understory and overstory layers (h_{und}, h_{ove}) were significantly associated with low precipitation and low temperature in the overstory variables (σ_{ove}, h_{ove}). The temperature had a significant negative effect, together with precipitation, in FMC_{ove} and *uo gap*, reinforcing the effect of warm conditions on forest flammability (Tables D.4 and D.6).

3.2. Temporal variation of fuel characteristics in canopy and understory layers

In general, overstory and understory layers showed similar patterns of change for all fuel characteristics over the period between SNFI2 and SNFI4 (Table 2; Appendices D.2). In both strata, there was a significant but slight increase of fine fuel loading with time (*p-value* < 0.001), with higher values in the overstory than in the understory. Although significantly different from zero, increases in bulk density (*bd*) in the overstory and understory layers, respectively, were very small. The understory surface area-to-volume ratio (σ_{und}) and the overstory heat content (h_{ove}) significantly increased and decreased, respectively. However, it is important to note that the magnitude of the rate of change in these variables was very small if one accounts for the units (variations of −0.1% and −0.01% in relation to mean *h* and σ, respectively). *FMC* and *uo gap* slightly decreased and increased, respectively. Regarding the comparison between the overstory and understory layers, although the rate of change of all fuel characteristics (except *FMC*) was significantly different according to the two-sample Wilcoxon test, these differences were relatively small (Table 2) and the correlation between the rate of

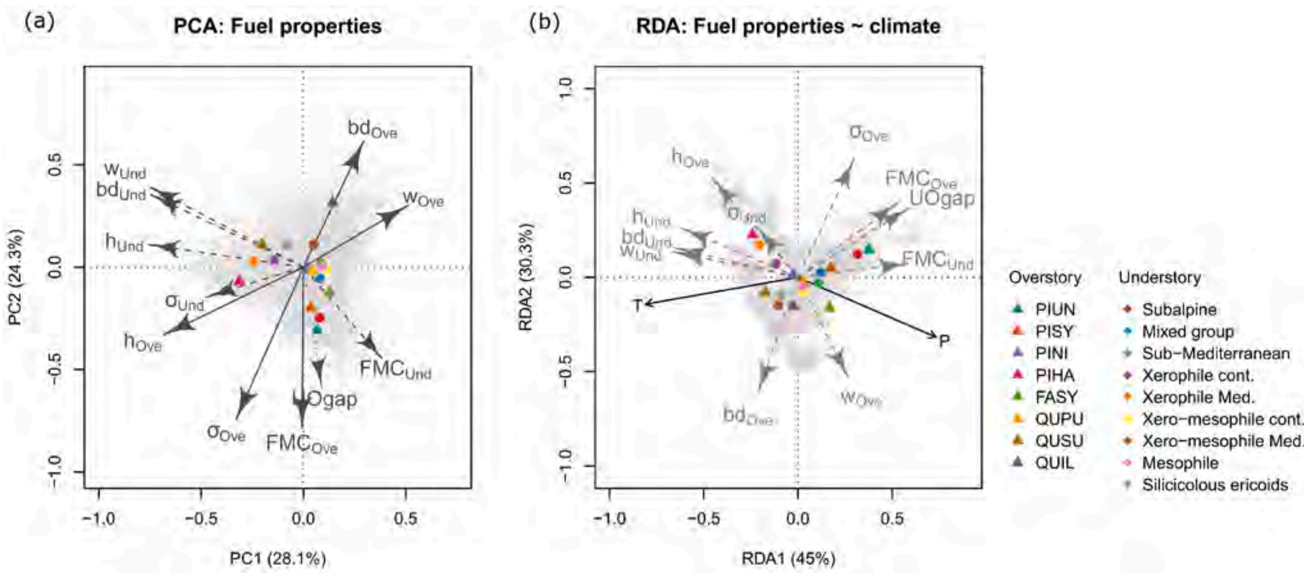

Fig. 3. (a) Principal Component Analysis summarizing overstory (*Ove*, solid arrows) and understory (*Und*, dashed arrows) fuel characteristics: loading (*w*), bulk density (*bd*), surface area-to-volume ratio (σ), heat content (*h*), minimum moisture content (*FMC*), and understory-overstory gap (*UOgap*). **(b)** Redundancy analysis relating fuel characteristics in both vegetation layers to environmental factors: temperature (T), precipitation (P). Grey dots indicate individual forest plots. Colored triangles and dots indicate the mean values of each forest type.

Table 2
Comparison of the rate of change of fuel characteristics between the SNFI2 and SNFI4 and overstory (O) and understory (U). For each variable and vegetation stratum, the table shows the average, standard deviation, percentiles 5% and 95%, and the percentage of plots for which the value in the understory is larger than in the overstory; non-parametric Spearman's correlation for each fuel variable between layers (rho, * *p-value* < 0.001) is also shown. Wilcoxon test was performed to test average differences from zero for each variable and layer (significance values: ** $\alpha = 0.001$; * $\alpha = 0.01$). The two-sample Wilcoxon test between layers was significant for all fuel characteristics ($\alpha = 0.001$) except *FMC*.

		Overstory (O)			Understory (U)			U > O	rho
	Units	Mean (sd)	P05	P95	Mean (sd)	P05	P95		
Fine fuel loading (*w*)	$kg \cdot m^{-2} \cdot year^{-1}$	0.01 (0.012) **	−0.01	0.03	0.005 (0.012) **	−0.01	0.02	41.76%	−0.03
Bulk density (*bd*)	$kg \cdot m^{-3}$	$5 \cdot 10^{-4}$ (0.002) **	−0.002	0.002	0.002 (0.007) **	−0.01	0.01	66.77%	0.06*
Surface area-to-volume ratio (σ)	$m^2 \cdot m^{-3} \cdot year^{-1}$	1.40 (16.925)	−22.41	31.70	5.92 (37.163)**	−55.11	66.85	55.51%	0.15**
Heat content (*h*)	$kJ \cdot kg^{-1} \cdot year^{-1}$	−3.08 (13.922) **	−27.80	13.57	−2.45 (31.799)	−57.72	45.81	54.07%	0.12**
Min. fuel moisture content (*FMC*)	% $dw \cdot year^{-1}$	−0.02 (0.252) **	−0.42	0.35	−0.06 (0.461)**	−0.96	0.55	49.67%	0.01
Understory-overstory gap (*uo gap*)	$m \cdot year^{-1}$	0.01 (0.085) **	−0.12	0.16					

change in both layers was very weak for all characteristics.

The first and second axes of the PCA applied to the matrix of changes in fuel characteristics explained 21.2% and 17.2% of the variation, respectively (Fig. 4a). Most understory communities showed a gradual increase in flammable characteristics parallel with a decrease in *FMC*, which only increased in silicicolous ericoids and xero-mesophile Mediterranean communities. In contrast to the result of static analyses, the change in fine fuel loading was poorly correlated between both strata (Table 2).

The mixed models used to construct the RDA associating the rate of change of fuel characteristics between SNFI2 and SNFI4 with climate indicated a weak power of these variables to predict the rate of change of fuel characteristics (Fig. 4b, Table D.7). Only the rates of change in bd_{ove}, σ_{ove}, σ_{und} and h_{ove} were significantly related to climate variables (bd_{ove}, σ_{ove}, h_{ove}: low temperature and precipitation, σ_{und}: low precipitation; Table D.7).

4. Discussion

4.1. Spatial distribution of overstory and understory fuel characteristics

Our analyses revealed that the overall forest vulnerability to fire is highly dependent on the species assembling each stratum, i.e., the overstory and the understory. In agreement with our hypothesis, the variation of fire hazard was primarily explained by fuel characteristics in the understory. In general, the understory showed higher bulk density, high heat content, and lower fuel moisture content than the overstory. These fire-promoting characteristics of the understory are strengthened by positive (*bd, h,* σ) and negative (*FMC*) correlations with the fine fuel understory loading. Moreover, the relationships between this latter variable and shorter interlayer gaps emphasize the role of the understory in promoting crown fires (Nunes et al., 2019), and therefore, driving the overall fire hazard.

In addition to the differences in fuel characteristics between strata, our assessments revealed remarkable spatial variations driven by climate characteristics. Forests in the warmest and driest regions of our study area were the most flammable. The low water availability and the relatively warm temperatures generate open structures that promote shrubby understories of shade-intolerant species well adapted to drought (Coll et al., 2011). That is the case of *P. halepensis* stands rich in species such as *Salvia rosmarinus, Quercus coccifera, Erica multiflora, Ulex parviflorus* or *Cistus* spp, which are drought-tolerant, but also highly flammable species (Pausas et al., 2012). The low moisture content of many of these shrubs facilitates fire ignitions, while the small leaves and thin twigs characteristic of these species contribute to increasing the fine fuel loadings and the surface area-to-volume ratios (Bowman et al., 2014; Saura-Mas and Lloret, 2007). These characteristics, together with the high heat contents of xerophile understory communities, facilitate

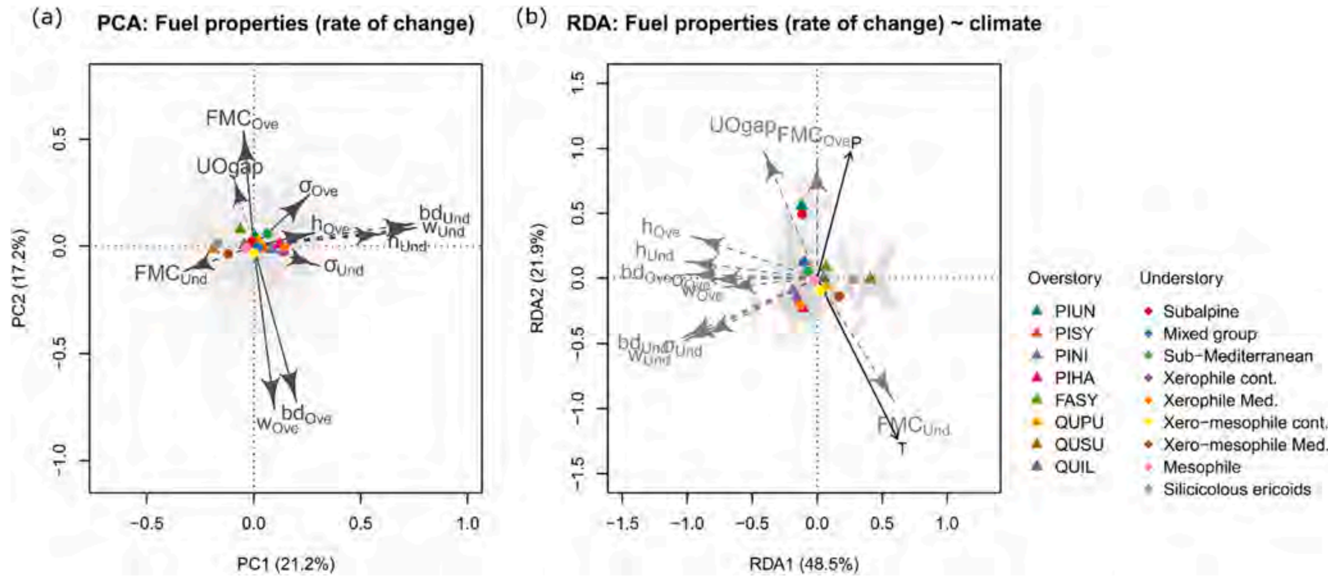

Fig. 4. **(a)** Principal Component Analysis summarizing the rate of change of fuel characteristics in the overstory (*Ove,* solid arrows) and understory (*Und,* dashed arrows) layers: change in loading (*w*), bulk density (*bd*), change in surface area-to-volume ratio (σ), change in heat content (*h*), change in minimum moisture content (*FMC*), and change in understory-overstory gap (*uogap*). **(b)** Redundancy analysis relating the rate of change of fuel characteristics in both vegetation layers to environmental variables: temperature (T), precipitation (P). Grey dots indicate individual forest plots. Colored triangles and dots indicate the mean values of each forest type. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the spread of high-intensity fires. In addition, although the low fuel loadings, bulk density, and the generally low cover of canopy trees in dry environments suggest a relatively reduced risk of crown-to-crown fire (Alvarez et al., 2012), the higher speed of surface wind in these open stands further facilitates the fire spread in the surface. The relatively elevated fire hazard of these drought-driven open stands with fire-prone understories agrees with previous studies on the spatial distribution of historical wildfires in the study area (Díaz-Delgado et al., 2004; González and Pukkala, 2007; Lecina-Diaz et al., 2014).

Mesic lowland areas dominated by *Q. suber* and *Q.ilex* showed lower canopy flammability than *P. halepensis* stands with xerophile understory communities. However, the fire hazard of these forests highly depended on the understory. Whereas *Q. ilex* forests may present a highly variable understory depending on the past management and their environmental conditions, *Q. suber* often coexists with silicicolous understories dominated by *Erica arborea, Cistus,* and genistoid species. The strong correlation between *Q. suber* and silicicolous ericoids is explained by the common ecological requirements and their ability to occupy poor soils, reinforced by the intense human management focused on cork extraction and the intentional promotion of species as *E. arborea* in the understory to supplement yields through secondary products (Guitart et al., 2020; Mundet et al., 2018). The species characterizing the silicicolous understory are, in general, extremely flammable because of their high heat content, high surface area-to-volume ratio, and low *FMC* (Dehane et al., 2017). Besides, the abundance of the multi-stemmed shrub *E. arborea* substantially increases the understory flammability through its small leaves, high fuel loading, bulk density, and relatively high height that reduces the gap with the overstory (Curt et al., 2011). In contrast to dry *P. halepensis* stands, forests dominated by *Q. suber* and silicicolous ericoid understories have not been stricken by large wildfires recently. Nevertheless, despite being a highly resilient system (Pausas, 1997), our results indicate a greater vulnerability of these forests to fire under potential drier conditions.

High precipitations and low temperatures were associated with high canopy fuel loadings and bulk density, low understory fuel loadings and bulk density, and high minimum understory fuel moisture content. Whereas in the temperate and relatively wet regions of the Pyrenees and Pre-Pyrenees, many forests are dominated or co-dominated by multi-stemmed oak stands resulting from past anthropic disturbances (mainly thinning for firewood and charcoal production), at higher altitudes, monospecific coniferous forests (*P. uncinata*, *P. sylvestris, Abies alba* Mill.) are more frequent. These differences in the stand composition and structure imply notable differences in forest flammability, mainly explained by the large interlayer gaps in many even-aged coniferous stands (Sánchez-Pinillos et al., 2019) and the highly-compacted litter composed of short thin needles. Accordingly, fire incidence has been much lower at the highest altitudes, affected by small surface or litter fires (González et al., 2007).

4.2. Overstory and understory fuel characteristics over time

Overstory and understory layers had significantly different rates of change in all fuel properties. However, our results showed that the annual variation of most fuel characteristics was very small during the time window considered. Fine fuel loadings and bulk density in both layers slightly increased over time as expected due to forest growth in absence of disturbances and silvicultural treatments. In this sense, the gradual increase in the abundance of broadleaf species in some Mediterranean and sub-Mediterranean pine forests during the last decades (Carnicer et al., 2013; Vayreda et al., 2013) contributed to a significant increase in fine fuel loadings and ladder fuels. This is explained by the combination of species with complementary light ecology which increases canopy space-filling (Pretzsch, 2014; Sánchez-Pinillos et al., 2019). Besides, the greater presence of broadleaf species generally reduced overstory high heat contents. The relatively higher rate of change of fine fuel loadings in the overstory than in the understory can be explained by the interception of light by the upper strata, limiting its availability, and therefore, development of lower strata (Rodríguez-Calcerrada et al., 2008; Valladares and Guzmán, 2006). These results may also be accentuated by the working definition of the understory layer in this study, which was considered up to a height of 2 m. Similarly, the overall increase in the gap between overstory and understory layers, particularly in mountain forests, can be explained by the primary growth of trees in relatively young forests and the reduction in the understory growth due to the shading effect and the ontogenetic growth reduction as individuals become senescent. This trend, however, is expected to slow down or even reverse in the long term, as trees reach their maximum height or successional dynamics promote diversification and the growth of saplings in the understory (Sánchez-Pinillos et al., 2019).

In contrast to the static analyses, the rate of change of fuel characteristics in our study area was rather small and weakly related to climate. We cannot reject, however, future differences among regions as climate warming rises. In this sense, our study suggests increasing forest flammability as annual precipitation decreases, promoting the development of understories dominated by xerophilous species with lower *FMC*.

4.3. Limitations and potential applications

Our study aimed to shed light on the spatial and temporal variation of fuel characteristics across a climatically diverse Mediterranean region. Still, some caveats to our approach need to be acknowledged. First, we excluded from our analyses the plots with evidence of intense forest management or disturbances in the past three decades through the percentage of stumps and dead trees. We could not control, however, silvicultural practices on the understory for not being registered in the SNFI. Although the large dataset used in our analyses could partially mitigate such effects, we strongly recommend future studies in smaller study areas or with smaller data sets to account for potential treatments of the understory. Second, we focused on climatic variables as general predictors of the distribution of fuel characteristics across space. Whereas our results showed the great complexity of fuel distribution at the stand and landscape scales, they cannot be used as a proxy to predict fire behavior as a function of fire hazard. Assessing fire behavior would require running realistic fire behavior models at the stand scale (e.g. Parsons et al., 2011) under a set of environmental conditions (Ager et al., 2011). The information provided in this study may be highly valuable to develop future custom fuel models adapted to Mediterranean forests and reproduce wildfire spread patterns (Salis et al., 2016). Nevertheless, additional effort is still necessary to characterize the dead fuel fraction in the understory and fuel properties of litter and downed dead wood, whose effects could either increase or decrease the understory influence on fire behavior (Keane, 2015).

4.4. Conclusions and management implications

Our study supports the hypotheses that living fuels in forests are significantly different across vegetation layers and at large spatial scales, highlighting the importance of understory fuels in the overall flammability of Mediterranean forests. While some commonly used fuel classifications benefit of well-known vegetation and environmental categories (e.g. Scott and Burgan, 2005), our findings agreed with the limitations provided by Keane (2013) for these 'association' approaches and remarked the necessity of considering the spatial variability of fuel characteristics across different vegetation strata. The support of our hypothesis emphasizes the need to complement canopy structural characteristics (e.g. canopy base height or bulk density) with understory fuel characteristics when assessing fire risk or defining fire mitigation policies.

Moreover, although forest management widely recognizes the role of the understory on the vulnerability of the whole stand, our results stressed the need to distinguish between understory communities and dominant tree species in the overstory (Keane, 2013). In this sense, management guides promoting different treatments based on species composition of vegetation layers entail valuable tools to guide forest owners and managers to reduce forest vulnerability to fire (Piqué et al., 2017). Selective and low-intensity thinning should be prioritized over clearcutting and high-intensity thinning to avoid the development of dense, shade-intolerant, and flammable understories. These practices can be also complemented with pruning and the removal of the understory through mechanical treatments, prescribed fires, or prescribed grazing (Agee and Skinner, 2005; Casals et al., 2016, 2009), particularly in warm regions with high fire hazard where we found the highest sensitivity to fire. Altogether, our findings constitute critical information on forest vulnerability to fire under different climatic conditions and highlight the urgent need of developing fuel management policies accounting for the fuel characteristics of different vegetation strata by incorporating species-specific information.

CRediT authorship contribution statement

Martina Sánchez-Pinillos: Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Visualization. **Miquel De Cáceres:** Conceptualization, Methodology, Investigation, Data curation, Writing - review & editing. **Pere Casals:** Methodology, Investigation, Writing - review & editing. **Albert Alvarez:** Writing - review & editing. **Mario Beltrán:** Writing - review & editing. **Juli G. Pausas:** Writing - review & editing. **Jordi Vayreda:** Writing - review & editing. **Lluís Coll:** Conceptualization, Writing - review & editing.

Declaration of Competing Interest

None.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119094.

References

Agee, J.K., Skinner, C.N., 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. 211, 83–96. https://doi.org/10.1016/j.foreco.2005.01.034.
Ager, A.A., Vaillant, N.M., Finney, M.A., 2011. Integrating Fire Behavior Models and Geospatial Analysis for Wildland Fire Risk Assessment and Fuel Management Planning. J. Combust. 2011, 572452 https://doi.org/10.1155/2011/572452.
Alvarez, A., Gracia, M., Castellnou, M., Retana, J., 2013. Variables that influence changes in fire severity and their relationship with changes between surface and crown fires in a wind-driven wildfire. For. Sci. 59, 139–150. https://doi.org/10.5849/forsci.10-140.
Alvarez, A., Gracia, M., Retana, J., 2012. Fuel types and crown fire potential in Pinus halepensis forests. Eur. J. For. Res. 131, 463–474. https://doi.org/10.1007/s10342-011-0520-6.
Ameztegui, A., Coll, L., 2013. Unraveling the role of light and biotic interactions on seedling performance of four Pyrenean species under environmental gradients. For. Ecol. Manage. 303, 25–34.
Baeza, M.J., De Luís, M., Raventós, J., Escarré, A., 2002. Factors influencing fire behaviour in shrublands of different stand ages and the implications for using prescribed burning to reduce wildfire risk. J. Environ. Manage. 65, 199–208. https://doi.org/https://doi.org/10.1006/jema.2002.0545.
Bowman, D.M.J.S., French, B.J., Prior, L.D., 2014. Have plants evolved to self-immolate? Front. Plant Sci. 5, 1–9. https://doi.org/10.3389/fpls.2014.00590.
Carnicer, J., Coll, M., Pons, X., Ninyerola, M., Vayreda, J., Peñuelas, J., 2013. Large-scale recruitment limitation in Mediterranean pines: The role of Quercus ilex and forest successional advance as key regional drivers. Glob. Ecol. Biogeogr. 23, 371–384. https://doi.org/10.1111/geb.12111.
Casals, P., Baiges, T., Bota, G., Chocarro, C., de Bello, F., Fanlo, R., Sebastià, M.T., Taull, M., 2009. Silvopastoral Systems in the Northeastern Iberian Peninsula: A Multifunctional Perspective. In: Rigueiro-Rodróguez, A., McAdam, J., Mosquera-Losada, M.R. (Eds.), Agroforestry in Europe: Current Status and Future Prospects. Springer, Dordrecht, pp. 161–181. https://doi.org/10.1007/978-1-4020-8272-6_8.
Casals, P., Valor, T., Besalú, A., Molina-Terrén, D., 2016. Understory fuel load and structure eight to nine years after prescribed burning in Mediterranean pine forests. For. Ecol. Manage. 362, 156–168. https://doi.org/10.1016/j.foreco.2015.11.050.
Castagneri, D., Esposito, A., Bovio, G., Mazzoleni, S., Seneca, U., Catalanotti, A.E., Ascoli, D., 2013. Fuel vertical structure affects fire sustainability and behaviour of

prescribed burning in Spartium junceum shrublands. Ann. For. Sci. 70, 863–871. https://doi.org/10.1007/s13595-013-0327-3.

Coll, L., González-Olabarria, J.R., Mola-Yudego, B., Pukkala, T., Messier, C., 2011. Predicting understory maximum shrubs cover using altitude and overstory basal area in different Mediterranean forests. Eur. J. For. Res. https://doi.org/10.1007/s10342-010-0395-y.

Cruz, M.G., Alexander, M.E., Wakimoto, R.H., 2004. Modeling the likelihood of crown fire occurrence in conifer forest stands. For. Sci. 50, 640–658. https://doi.org/10.1093/forestscience/50.5.640.

Curt, T., Schaffhauser, A., Borgniet, L., Dumas, C., Estève, R., Ganteaume, A., Jappiot, M., Martin, W., N'Diaye, A., Poilvet, B., 2011. Litter flammability in oak woodlands and shrublands of southeastern France. For. Ecol. Manage. 261, 2214–2222. https://doi.org/10.1016/j.foreco.2010.12.002.

De Cáceres, M., Casals, P., Gabriel, E., Castro, X., 2019a. Scaling-up individual-level allometric equations to predict stand-level fuel loading in Mediterranean shrublands. Ann. For. Sci. 76 https://doi.org/10.1007/s13595-019-0873-4.

De Cáceres, M., Martín-Alcón, S., González-Olabarria, J.R., Coll, L., 2019b. A general method for the classification of forest stands using species composition and vertical and horizontal structure. Ann. For. Sci. 76 (40), 1–19. https://doi.org/10.1007/s13595-019-0824-0.

De Cáceres, M., Martínez-Vilalta, J., Coll, L., Llorens, P., Casals, P., Poyatos, R., Pausas, J. G., Brotons, L., 2015. Coupling a water balance model with forest inventory data to predict drought stress: the role of forest structural changes vs. climate changes. Agric. For. Meteorol. 213, 77–90. https://doi.org/10.1016/j.agrformet.2015.06.012.

De Luis, M., Baeza, M.J., Raventós, J., González-Hidalgo, J.C., 2004. Fuel characteristics and fire behaviour in mature Mediterranean gorse shrublands. Int. J. Wildl. Fire 13, 79–87. https://doi.org/10.1071/WF03005.

Dehane, B., Hernando, C., Guijarro, M., Madrigal, J., 2017. Flammability of some companion species in cork oak (Quercus suber L.) forests. Ann. For. Sci. 74, 60. https://doi.org/10.1007/s13595-017-0659-5.

Díaz-Delgado, R., Lloret, F., Pons, X., 2004. Spatial patterns of fire occurrence in Catalonia, NE Spain. Landsc. Ecol. 19, 731–745. https://doi.org/10.1007/s10980-005-0183-1.

Dimitrakopoulos, A.P., 2002. Mediterranean fuel models and potential fire behaviour in Greece. Int. J. Wildl. Fire 11, 127–130.

FAO, 2005. Wildland Fire Management Terminology [WWW Document]. Term Portal. URL http://www.fao.org/faoterm/en/.

Fernandes, P.M., 2009. Combining forest structure data and fuel modelling to classify fire hazard in Portugal. Ann. For. Sci. 66, 415. https://doi.org/10.1051/forest/2009013.

Fernandes, P.M., Loureiro, C., 2013. Fine fuels consumption and CO2 emissions from surface fire experiments in maritime pine stands in northern Portugal. For. Ecol. Manage. 291, 344–356. https://doi.org/10.1016/j.foreco.2012.11.037.

Fernandes, P.M., Loureiro, C., Botelho, H.S., 2004. Fire behaviour and severity in a maritime pine stand under differing fuel conditions. Ann. For. Sci. 61, 537–544. https://doi.org/10.1051/forest.

Fernandes, P.M., Vega, J.A., Jiménez, E., Rigolot, E., 2008. Fire resistance of European pines. For. Ecol. Manage. 256, 246–255. https://doi.org/10.1016/j.foreco.2008.04.032.

González, J.R., Pukkala, T., 2007. Characterization of forest fires in Catalonia (north-east Spain). Eur. J. For. Res. 126, 421–429. https://doi.org/10.1007/s10342-006-0164-0.

González, J.R., Trasobares, A., Palahí, M., Pukkala, T., 2007. Predicting stand damage and tree survival in burned forests in Catalonia (North-East Spain). Ann. For. Sci. 64, 733–742. https://doi.org/10.1051/forest:2007053.

Guitart, L., Ojosnegros, M., Rosell, M., 2020. Bruc, un recurs menystingut amb moltes possibilitats. In: Beltrán, M., Monserrate, A. (Eds.), XXXVII Jornades Tècniques Silvícoles. Emili Garolera.

Keane, R.E., 2016. Spatiotemporal variability ofwildland fuels in Us Northern rocky mountain forests. Forests 7. https://doi.org/10.3390/f7070129.

Keane, R.E., 2015. Wildland fuel fundamentals and applications. pringer International Publishing, Cham, Switzerland.

Keane, R.E., 2013. Describing wildland surface fuel loading for fire management: A review of approaches, methods and systems. Int. J. Wildl. Fire 22, 51–62. https://doi.org/10.1071/WF11139.

Keeley, J.E., Bond, W.J., Bradstock, R.A., Pausas, J.G., Rundel, P.W., 2012. Fire in mediterranean ecosystems: Ecology, evolution and management.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J., Bradstock, R.A., 2011. Fire as an evolutionary pressure shaping plant traits. Trends Plant Sci. 16, 406–411. https://doi.org/10.1016/j.tplants.2011.04.002.

Lecina-Diaz, J., Alvarez, A., Retana, J., 2014. Extreme Fire Severity Patterns in Topographic, Convective and Wind-Driven Historical Wildfires of Mediterranean Pine Forests. PLoS ONE 9. https://doi.org/10.1371/journal.pone.0085127.

Legendre, P., Legendre, L., 1998. Numerical Ecology, 2nd ed. Elsevier Science B.V., Amsterdam. https://doi.org/10.1017/CBO9781107415324.004.

Majasalmi, T., Rautiainen, M., 2020. The impact of tree canopy structure on understory variation in a boreal forest. For. Ecol. Manage. 466, 118100 https://doi.org/10.1016/j.foreco.2020.118100.

Messier, C., Parent, S., Bergeron, Y., 1998. Effects of Overstory and Understory Vegetation on the Understory Light Environment in Mixed Boreal Forests. J. Veg. Sci. 9, 511–520. https://doi.org/10.2307/3237266.

Ministerio de Agricultura Alimentación y Medio Ambiente, 2019. Cuarto Inventario Forestal Nacional (IFN4).

Ministerio de Medio Ambiente, 2007. Tercer Inventario Forestal Nacional (IFN3). Dirección General de Conservación de la Naturaleza, Madrid, Spain.

Ministerio de Medio Ambiente, 1996. Segundo Inventario Forestal Nacional (IFN2). Dirección General de Conservación de la Naturaleza, Madrid, Spain.

Mitsopoulos, I.D., Dimitrakopoulos, A.P., 2007. Canopy fuel characteristics and potential crown fire behavior in Aleppo pine (Pinus halepensis Mill.) forests. Ann. For. Sci. 64, 287–299. https://doi.org/10.1051/forest:2007006.

Molina, J.R., Rodriguez y Silva, F., Herrera, M.A., 2011. Potential crown fire behavior in Pinus pinea stands following different fuel treatments. For. Syst. 20, 266. https://doi.org/10.5424/fs/2011202-10923.

Mundet, R., Baiges, T., Beltrán, M., Torrell, A., 2018. Guía de recomendaciones y medidas de adaptación al cambio climático en la gestión de Quercus suber.

Ninyerola, M., Pons, X., Roure, J., 2005. Atlas Climático Digital de la Península Ibérica. Metodología y aplicaciones en bioclimatología y geobotánica. Universidad Autónoma de Barcelona, Bellaterra.

Nocentini, S., Coll, L., 2013. Mediterranean forests: human use and complex adaptive systems. In: Messier, C., Puettmann, K.J., Coates, K.D. (Eds.), Managing Forests as Complex Adaptive Systems. Building Resilience to the Challenge of Global Change. The Earthscan Forest Library (series). Routledge., NY, USA, pp. 214–243.

Nunes, L., Álvarez-González, J., Alberdi, I., Silva, V., Rocha, M., Rego, F.C., 2019. Analysis of the occurrence of wildfires in the Iberian Peninsula based on harmonised data from national forest inventories. Ann. For. Sci. 76 https://doi.org/10.1007/s13595-019-0811-5.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package. R package version 2.4-2.

Parsons, R.A., Mell, W.E., McCauley, P., 2011. Linking 3D spatial models of fuels and fire: Effects of spatial heterogeneity on fire behavior. Ecol. Modell. 222, 679–691. https://doi.org/10.1016/j.ecolmodel.2010.10.023.

Pausas, J.G., 1997. Resprouting of Quercus suber in NE Spain after fire. J. Veg. Sci. 8, 703–706. https://doi.org/10.2307/3237375.

Pausas, J.G., Alessio, G.A., Moreira, B., Corcobado, G., 2012. Fires enhance flammability in Ulex parviflorus. New Phytol. 193, 18–23.

Pausas, J.G., Keeley, J.E., 2014. Abrupt Climate-Independent Fire Regime Changes. Ecosystems 17, 1109–1120. https://doi.org/10.1007/s10021-014-9773-5.

Pausas, J.G., Keeley, J.E., Schwilk, D.W., 2017. Flammability as an ecological and evolutionary driver. J. Ecol. 105, 289–297. https://doi.org/10.1111/1365-2745.12691.

Pausas, J.G., Paula, S., 2012. Fuel shapes the fire–climate relationship: evidence from Mediterranean ecosystems. Glob. Ecol. Biogeogr. 21, 1074–1082. https://doi.org/10.1111/j.1466-8238.2012.00769.x.

Piqué, M., Vericat, P., Beltrán, M., 2017. ORGEST: Regional guidelines and silvicultural models for sustainable forest management. For. Syst. Vol 26, No 2 (2017)DO - 10.5424/fs/2017262-10627 26.

Pretzsch, H., 2014. Canopy space filling and tree crown morphology in mixed-species stands compared with monocultures. For. Ecol. Manage. 327, 251–264. https://doi.org/10.1016/j.foreco.2014.04.027.

Reinhardt, E., Lutes, D., Scott, J., 2006. FuelCalc: A Method for Estimating Fuel Characteristics. In: Andrews, P.L., Butler, B.W., Comps. (Eds.), Fuels Management-How to Measure Success: Conference Proceedings. Proceedings RMRS-P-41. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station., Portland, OR., pp. 273–282.

Rodríguez-Calcerrada, J., Mutke, S., Alonso, J., Gil, L., Pardos, J.A., Aranda, I., 2008. Influence of overstory density on understory light, soil moisture, and survival of two underplanted oak species in a Mediterranean montane Scots pine forest. Investig. Agrar. Sist. y Recur. For. 17, 31–38.

Rothermel, R.C., 1972. A mathematical model for predicting fire spread in wildland fuels. USDA For. Serv. - Res. Pap, INT USA.

Salis, M., Arca, B., Alcasena, F., Arianoutsou, M., Bacciu, V., Duce, P., Duguy, B., Koutsias, N., Mallinis, G., Mitsopoulos, I., Moreno, J.M., Pérez, J.R., Urbieta, I.R., Xystrakis, F., Zavala, G., Spano, D., 2016. Predicting wildfire spread and behaviour in Mediterranean landscapes. Int. J. Wildl. Fire 25, 1015–1032.

San-Miguel-Ayanz, J., Durrant, T., Boca, R., Libertà, G., Branco, A., Rigo, D. De, Ferrari, D., Maianti, P., Artés-Vivancos, T., Costa, H., Lana, F., Löffler, P., Nuijten, D., Christofer, A., Leray, T., 2018. Forest Fires in Europe, Middle East and North Africa 2017, EUR 29318. ed. https://doi.org/10.2760/663443.

Sánchez-Pinillos, M., Cáceres, M. De, Ameztegui, A., Coll, L., 2019. Temporal dimension of forest vulnerability to fire along successional trajectories. J. Environ. Manage. 248, 109301 https://doi.org/10.1016/j.jenvman.2019.109301.

Sandberg, D.V., Ottmar, R.D., Cushon, G.H., 2001. Characterizing fuels in the 21st Century. Int. J. Wildl. Fire 10, 381–387.

Sande Silva, J., Rego, F., Fernandes, P., Rigolot, E., 2010. Towards Integrated Fire Management - Outcomes of the European Project Fire Paradox. Eur. For. Inst. Research Rep. 244.

Santana, V.M., Baeza, M.J., Vallejo, V.R., 2011. Fuel structural traits modulating soil temperatures in different species patches of Mediterranean Basin shrublands. Int. J. Wildl. Fire 20, 668–677.

Saura-Mas, S., Lloret, F., 2007. Leaf and shoot water content and leaf dry matter content of Mediterranean woody species with different post-fire regenerative strategies. Ann. Bot. 99, 545–554. https://doi.org/10.1093/aob/mcl284.

Saura-Mas, S., Paula, S., Pausas, J.G., Lloret, F., 2010. Fuel loading and flammability in the Mediterranean Basin woody species with different post-fire regenerative strategies. Int. J. Wildl. Fire 19, 783–794. https://doi.org/10.1071/WF09066.

Scott, J.H., Burgan, R.E., 2005. Standard Fire Behavior Fuel Models: A Comprehensive Set for Use with Rothermel' s Surface Fire Spread Model, Gen. Tech. ed. Department of Agriculture, Forest Service, Rocky Mountain Research Station., Fort Collins, CO: U.S.

Scott, J.H., Reinhardt, E.D., 2002. Estimating canopy fuels in conifer forests. Fire Manag. Today 62, 45–50.
Scott, J.H., Reinhardt, E.D., 2001. Assessing crown fire potential by linking models of surface and crown fire behavior. USDA For. Serv. - Res. Pap. RMRS-RP 1–62. https://doi.org/10.2737/RMRS-RP-29.
Simeoni, A., Salinesi, P., Morandini, F., 2011. Physical modelling of forest fire spreading through heterogeneous fuel beds. Int. J. Wildl. Fire 20, 625–632.
Stephens, S.L., Moghaddas, J.J., Edminster, C., Fiedler, C.E., Haase, S., Harrington, M., Keeley, J.E., Knapp, E.E., Mciver, J.D., Metlen, K., Skinner, C.N., Youngblood, A., 2009. Fire treatment effects on vegetation structure, fuels, and potential fire severity in western U.S. forests. Ecol. Appl. 19, 305–320. https://doi.org/10.1890/07-1755.1.
Valladares, F., Guzmán, B., 2006. Canopy structure and spatial heterogeneity of understory light in an abandoned Holm oak woodland. Ann. For. Sci. 63, 749–761.
Van Wagner, C., 1987. Development and Structure of the Canadian Forest Fire Weather Index System. Canadian Forest Service, Petawawa National Forestry Institute., Chalk River, ON, Forestry Technical Report.
Van Wagner, C., 1977. Conditions for the start and spread of crown fire. Can. J. For. Res. 7, 23–34.
Vayreda, J., Gracia, M., Martinez-Vilalta, J., Retana, J., 2013. Patterns and drivers of regeneration of tree species in forests of peninsular Spain. J. Biogeogr. 40, 1252–1265. https://doi.org/10.1111/jbi.12105.
Weise, D.R., Wright, C.S., 2014. Wildland fire emissions, carbon and climate: Characterizing wildland fuels. For. Ecol. Manage. 317, 26–40. https://doi.org/10.1016/j.foreco.2013.02.037.
Weiskittel, A.R., Hann, D.W., Kershaw, J.R., Vanclay, J.K., 2011. Forest Growth and Yield Modeling. John Wiley & Sons Ltd., Chichester, UK.
Werth, P.A., Potter, B.E., Clements, C.B., Finney, M.A., Goodrick, S.L., Alexander, M.E., Cruz, M.G., Forthofer, J.A., Mcallister, S.S., 2011. Synthesis of knowledge of extreme fire behavior: Volume I for fire managers. USDA For. Serv. - Gen. Tech. Rep. PNW-GTR I, 144. https://doi.org/10.2737/PNW-GTR-854.
Westerling, A.L., Bryant, B.P., Preisler, H.K., Holmes, T.P., Hidalgo, H.G., Das, T., Shrestha, S.R., 2011. Climate change and growth scenarios for California wildfire. Clim. Change 109, 445–463. https://doi.org/10.1007/s10584-011-0329-9.