Beltrán-Marcos *et al. Fire Ecology* (2024) 20:47
https://doi.org/10.1186/s42408-024-00276-w

Fire Ecology

ORIGINAL RESEARCH

Open Access

Fire regime attributes shape pre-fire vegetation characteristics controlling extreme fire behavior under different bioregions in Spain

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Abstract

Background Designing effective land management actions addressed to increase ecosystem resilience requires us to understand how shifting fire regimes are shaping landscapes. In this study, we aim to assess the link between fire regime and pre-fire vegetation biophysical characteristics (type, amount, and structure) in controlling extreme fire behavior across Atlantic-Transition-Mediterranean bioregions in Spain marked by different summer drought conditions and dominant plant regenerative traits. We used remote sensing metrics to estimate fire severity and pre-fire vegetation characteristics in eight study areas recently affected by large and highly severe wildfires under different environmental contexts. Furthermore, to account for fire regime attributes, we retrieved, for each target wildfire, the perimeter of the past wildfires that occurred between 1985 and 2022 and calculated fire recurrence, the time the since last fire (TSLF), and fire severity of previous wildfires (FSPW). The effect of fire regime attributes on pre-fire vegetation was examined using generalized linear mixed models (GLMMs).

Results During the study period, fire recurrence decreased significantly in all bioregions analyzed. Fire severity increased under Atlantic conditions and decreased under Mediterranean environmental context, where the time since the last fire was the highest. Pre-fire fuel type and amount were identified as primary drivers of fire severity, being both strongly modulated by fire regime but following distinct mechanisms depending on the environmental context of each bioregion. In Atlantic sites, more frequent past wildfires of low to moderate fire severity were associated with a greater dominance of fire-prone shrublands with moderate fuel amounts, which increases the risk of severe wildfires. Similar trends occurred in Transition and Mediterranean sites but under the previous occurrence of highly severe wildfires. Specifically, long times after highly severe wildfires (> 30 years) increased fuel amount in conifer-dominated ecosystems in all bioregions analyzed, heightening susceptibility to extreme fire behavior.

Conclusions Our findings highlight that fire-prone ecosystems need adaptative management strategies to mitigate the effects of fire regime changes, but these actions should be specific to the climatic and ecological context.

Keywords dNBR, Fire history, Fire severity, Fire recurrence, Fuel type, Fuel amount

Resumen

Antecedentes El diseño de acciones efectivas de manejo de tierras para incrementar la resiliencia de los ecosistemas, requiere que entendamos cómo el cambio en los regímenes de fuego está modelando los paisajes. En este

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estudio, buscamos determinar la relación entre el régimen de fuego y las características biofísicas de la vegetación pre-fuego (tipo, cantidad, estructura) en el control de fuegos de comportamiento extremo a través de las biorregiones Atlántica-Transicional-Mediterránea de España, marcadas por diferentes condiciones de sequía durante el verano y las características vegetativas de las especies de plantas dominantes. Usamos las mediciones de sensores remotos para estimar la severidad del fuego y las características de la vegetación en el pre-fuego, en ocho áreas afectadas por incendios grades y severos ocurridos bajo diferentes contextos ambientales. Además, para tener en cuenta los atributos del régimen de fuegos, recuperamos, para cada fuego seleccionado, el perímetro de los fuegos pasados que ocurrieron entre 1985 y 2022 y calculamos la recurrencia del fuego, el tiempo desde el último incendio (TSLF), y la severidad de los fuegos previos (FSPW). El efecto de los atributos del régimen de fuegos sobre la vegetación pre-fuego fue examinada usando modelos lineales generalizados (GLMMs).

Resultados Durante el período de estudio, la recurrencia del fuego decreció significativamente en todas las biorregiones analizadas. La severidad del fuego creció bajo condiciones Atlánticas y decreció bajo contextos ambientales Mediterráneos, donde el tiempo desde el último fuego fue el más alto. Los tipos de combustibles en el pre-fuego y su cantidad fueron identificados como los principales conductores de la severidad del fuego, siendo ambos fuertemente modulados por el régimen de fuego aunque siguiendo distintos mecanismos dependiendo del contexto ambiental de cada biorregión. En sitios Atlánticos, los fuegos pasados más frecuentes de moderada a baja severidad fueron asociados con una dominancia mayor de arbustales propensos al fuego con cantidades moderadas de combustible, lo cual incrementa el riesgo de incendios severos. Tendencias similares ocurren en sitios de Transición y Mediterráneos, aunque bajo la ocurrencia de fuegos altamente severos. Específicamente, tiempos largos luego de fuegos altamente severos (> 30 años) incrementaron la cantidad de combustible en ecosistemas dominados por coníferas en todas las biorregiones analizadas, elevando la susceptibilidad a fuegos de comportamiento extremo.

Conclusiones Nuestros resultados enfatizan que los ecosistemas propensos al fuego necesitan de estrategias de manejo adaptativo para mitigar los efectos de los cambios en los regímenes de fuegos, aunque esas acciones debieran ser específicas dentro de los contextos climáticos y ecológicos.

Background

In the Mediterranean Basin, the occurrence of increasingly larger and more severe wildfires is a concerning issue that recurs every year (Duane et al. 2021). This phenomenon is associated with the current levels of biomass accumulation prompted by land abandonment occurred across rural landscapes (Fernandes 2013), coupled with anthropogenic climate change (Turner 2010). Consequently, fire regime attributes (severity, extent, recurrence, fire-free interval, or fire return interval) are shifting (Pausas and Keeley 2021). These next-generation wildfires are extremely challenging, as they are very difficult to control, exceed suppression thresholds (Belval et al. 2020), and represent an unprecedented socio-economic and environmental threat (Wunder et al. 2021), putting populated areas (e.g., wildland-urban interface) at risk and compromising the resistance and resilience of forest ecosystems.

In fact, during the period 2017–2022, wildfires burnt 645,000 ha per year on average in southern European countries, including the most devastating wildfire seasons ever recorded in Spain (Chas-Amil et al. 2020; Fernández-Guisuraga et al. 2023a), Portugal (Rodrigues et al. 2023), or Greece (Giannaros et al. 2022) due to the overwhelming ecological and socio-economic impacts. The fire effects on ecosystems are defined by the concept of fire severity, a magnitude attribute of the fire regime that is intrinsically linked to fire behavior in extreme wildfires (Harris and Taylor 2017; Quintano et al. 2018; Fernández-García et al. 2022). It represents the degree of fire-induced ecological change in a system (Key and Benson 2006; Fernández-García et al. 2018) and is operationally quantified by the aboveground and belowground biomass loss in the ecosystem (Keeley 2009). Examining the drivers contributing to extreme wildfires is essential for designing appropriate pre-fire management strategies. These strategies focus on mitigating fire risk by reducing ecosystem vulnerability while strengthening ecosystem resistance and resilience (Basset et al. 2017; Fernández-Guisuraga et al. 2021a; Rodrigues et al. 2023). Primarily, the link between fire behavior and fire severity can be controlled by top-down (fire weather) or bottom-up (topography and pre-fire fuel characteristics) drivers (Harris and Taylor 2017; García-Llamas et al. 2019). Biophysical characteristics of pre-fire fuel, such as type, amount, or structure, are susceptible to being managed and have also showed to be crucial fire severity drivers in southern European fire-prone ecosystems (Fernández-Guisuraga et al. 2023b).

Despite the undeniable and well recognized relevance of pre-fire vegetation characteristics, other mechanisms need to be considered as drivers of extreme wildfires since they can provide a more complete overview of the potential ecosystem response to this type of disturbance (Fernández-Guisuraga et al. 2023b). In this sense, fire history has emerged as an important factor controlling fire severity because it determines not only fuel accumulation but also the composition and structure of fire-prone plant communities (Parks et al. 2014; Harris and Taylor 2017; García-Llamas et al. 2020), which have significant implications for land susceptibility to severe wildfires, in particular in the face of climate change (González-De Vega et al. 2016). In any case, up to the present moment, the complex relationship between fire legacies, pre-fire vegetation dynamics, and subsequent fire behavior (Parks et al. 2014; Steel et al. 2015) has not been unraveled. Most of the research carried out on this topic has focused on the evaluation of the direct effect of fire regime attributes on fire severity (Harris and Taylor 2017; García-Llamas et al. 2019, 2020), but the interactions between fire history and pre-fire vegetation characteristics that determine the behavior of unprecedented extreme wildfires under different environmental contexts are still to be understood.

Temporal fire regime attributes, including fire recurrence (number of fires in a given period), fire-free interval (time since last fire (TSLF)), and fire return interval (average period between fires), have been identified as key determinants of the composition, structure, and regeneration capacity of plant communities (Steel et al. 2015; Fernández-García et al. 2018). These attributes can modify ecosystem resilience by either promoting the dominance of different biological adaptations to fire (e.g., resprouting reproductive strategy, development of fire-resistant tissues, or serotiny; Fernández-García et al. 2020) or by leading to an increase in plant mortality and a decrease in regeneration in native forests (Huerta et al. 2022). In particular, a high fire recurrence may reduce fuel accumulation and woody vegetation cover (Bassett et al. 2017; Huerta et al. 2021). Conversely, areas where wildfires occur infrequently present a significant potential for fuel build-up and the dominance of species with low fire resistance (Steel et al. 2015; Gil-Tena et al. 2016), thereby increasing the likelihood of large and severe wildfires (Viedma et al. 2020). Despite this, the impact of fire recurrence on fire-prone landscapes is greatly influenced by environmental conditions and dominant regenerative plant traits (Pausas and Keeley 2014; Fernández-García et al. 2020). Specifically, in Mediterranean ecosystems characterized by warmer and drier climates, particularly during summer, frequent fires lead to a modification or even loss of post-fire recruitment capacity in obligated seeders, such as conifer species, especially when interacting with high-severity wildfires (Fernández-García et al. 2019). In such cases, a decline in plant photosynthetic capacity is also anticipated, either due to direct effects such as aboveground biomass consumption or indirect effects such as a decrease in nutrient availability, potentially diminishing long-term productivity (Keeley et al. 2012; Pausas and Keeley 2021). However, these changes are not as evident in humid regions, such as the Atlantic side of the Iberian Peninsula, where post-fire climate conditions quickly promote vegetation recovery (Fernández-García et al. 2018). Within this context, the role of fire severity of previous wildfires (FSPW) in post-fire vegetation recovery (Reyes and Casal 2008; Crotteau et al. 2013; Huerta et al. 2021, 2022) also needs consideration, as it strongly interacts with fire recurrence, impacting both plant community composition and structure, as well as ecosystem and landscape functioning (Bassett et al. 2017; San-Miguel et al. 2017). This interaction leads to the conversion of vegetation types and a decline in the diversity of fire-sensitive species (Fernández-García et al. 2020; García-Llamas et al. 2020). In this regard, fire severity may impede the development of species favored by undisturbed forest structures or promote vegetation types associated with open environments (e.g., shrubs or grass species). Compared to drier environments, these effects are less pronounced in highly productive settings, such as Atlantic sites (Pausas and Keeley 2014).

Few studies have examined the links among contemporary attributes of the fire regime (specifically fire size and proportion of area burned at high fire severity) and drivers of fire behavior in southern European countries (Fernández-Guisuraga et al. 2023b). In North America, some studies have assessed the relationships between fire legacies and the behavior of subsequent wildfires (Parks et al. 2014; Steel et al. 2015). Temporal attributes of fire regimes, including fire recurrence and TSLF, have been considered in recent research to determine their influence on ecosystem services provision in Spanish Mediterranean forests (Moghli et al. 2022). However, exploring how different environmental conditions influence vegetation responses and susceptibility to severe subsequent wildfire remains to be explored in the Mediterranean countries of Southern Europe. The main novelty of our research is that it could disentangle the complex interactions between fire regime attributes and pre-fire vegetation dynamics in different environmental contexts (in terms of regenerative traits of dominant species, soil type, altitude, fire history and climate) driving the behavior of the unprecedented extreme wildfire events that occurred in the Spanish Iberian Peninsula in the last decade (e.g., Chas-Amil et al. 2020; García-Llamas et al. 2020; Llorens et al. 2021; Fernández-Guisuraga et al. 2023a), providing valuable insights for adaptive pre-fire fire management strategies.

Based on the above, the main objective of this study is to assess the link between fire regime attributes and pre-fire vegetation characteristics in controlling extreme wildfire behavior in landscapes prone to severe wildfires in different bioregions (from Atlantic, wetter, to the Mediterranean, with drier conditions) of the Spanish Iberian Peninsula. Specifically, we aim to (i) analyze fire history trends across different environmental conditions over a 35-year period, (ii) determine which pre-fire vegetation characteristics drive fire severity under different environmental contexts, and (iii) explore how fire regime attributes (fire recurrence, time since last fire (TSLF), and fire severity of previous wildfire (FSPW)) shape pre-fire vegetation characteristics across landscapes prone to high fire severity in different bioregions. According to previous research, we hypothesize that different environmental contexts will imply substantial variation in both the effects of fire regime attributes on pre-fire fuel characteristics and subsequent fire behavior control (Keeley et al. 2012; Fernández-García et al. 2019; Huerta et al. 2021). In this sense, in Mediterranean ecosystems, where climate is becoming hotter and drier, higher fire severity is expected, and longer TSLF and no repeated severe wildfires are also expected, in line with previous observations across the Mediterranean Basin (Fernández-García et al. 2020; Pausas and Keeley 2021). This context would drive to the highest levels of fire risk due to increasing accumulation of biomass (Steel et al. 2015; Taboada et al. 2017; Fernández-Guisuraga et al. 2023b) and the dominance of flammable species (González-De Vega et al. 2016; Huerta et al. 2021). In contrast, in Atlantic ecosystems, it is expected that higher fuel accumulation rates would appear in shorter time periods (< 20 years), due to mild and humid environmental conditions that allow for early and rapid post-fire vegetation recovery (Fernández-García et al. 2019).

Materials and methods

Study sites

The study area comprises eight large wildfires (> 500 ha) that occurred during the period 2017–2022 along the Atlantic-Transition-Mediterranean bioregions in the Iberian Peninsula (Fig. 1; Table 1). These bioregions are characterized by different environmental contexts, including ecological (e.g., response to natural disturbances or soil types) and climatic (e.g., summer drought) conditions (EEA 2016). The target wildfires correspond to extreme events, in terms of extensive areas burned at high fire severity verified through field assessments (Llorens et al. 2021; Fernández-García et al. 2022; Huerta et al. 2022; Fernández-Guisuraga et al. 2023a), and feature a wide variety of vegetation types. Fire scars were delineated using Sentinel-2 post-fire satellite imagery displaying a false color composite (RGB; bands 12, 8 A and 4) at 1:10,000 scale (Fernández-García et al. 2022).

Atlantic wildfires were located in (i) Ponte Caldelas (Pontevedra province; 7° 57′ W 42° 2′ N) and in (ii) Carballeda de Avia (Ourense province; 4° 21′ W 42° 18′ N), both occurred in 2017 and burned a surface of 9789 ha and 5956 ha, respectively. Pre-fire landscapes feature a rugged topography, encompassing a landscape mosaic made of native broadleaf forests (e.g., *Castanea sativa* Mill., *Fagus sylvatica* L., and *Quercus* spp.) mixed with conifer forests and plantations of *Eucalyptus globulus* Labill., *Pinus pinaster* Ait., and *Pinus radiata* D. Don., heathlands (*Erica umbellata* Loefl. *ex* L.) and shrublands dominated by brooms (*Cytisus scoparius* L.) and gorses (*Ulex europaeus* L.), as well as transitional patches of woodland-shrubs mixed with grasslands and cultivated fields near to interface areas (Beltrán-Marcos et al. 2023). This study site is dominated by resprouter and facultative species as post-fire regenerative strategies (Fernández-García et al. 2020). Soils are siliceous with bedrock of granite and are classified as Cambisols (Jones et al. 2005). This bioregion is characterized by annual rainfall exceeding 1600 mm, and mean annual temperature of 12.65 °C (± 0.45 °C) (AEMET 2018), with less than 1 month of summer drought (Ninyerola et al. 2005).

To account for the transitional environmental conditions between the Atlantic and Mediterranean bioregions, two large wildfires were selected: (i) Cabrera wildfire (León province; 6° 38′ W 42° 14′ N) that occurred in 2017 and burned 9940 ha, covered by patches of shrublands (e.g., *Genista hystrix* Lange. or *Erica australis* L.), herbaceous vegetation, and forest ecosystems dominated by deciduous trees such as *Quercus pyrenaica* Willd., and (ii) O Barco de Valdeorras wildfire (Ourense province; 6° 30′ W 42° 15′ N) that occurred in 2022 and burned 12,591 ha dominated by broadleaved forests (*Castanea sativa* Mill., *Quercus pyrenaica* Willd., and *Quercus ilex* L.), conifer forests and plantations (*Pinus pinaster* Ait., *Pinus radiata* D. Don., and *Pinus sylvestris* L.), shrublands mixed with grasslands, and farmland. The relief in both cases is abrupt, with prominent crests and wide valleys. This study site presents a great variability of plant regenerative traits, with obligate resprouters, obligate seeders, and facultative seeders (plants with both mechanisms) species (Fernández-García et al. 2020). The soils, classified as Cambisols and Leptosols (Jones et al. 2005), are predominantly acidic and originated from siliceous lithologies (mainly slates and quartzite; Fernández-Guisuraga et al. 2021a). This bioregion is distinguished by a mean annual precipitation of 1100 mm and mean annual temperature of 9.7 °C (± 1.2 °C) (AEMET 2018), with a summer drought of 2 months (Ninyerola et al. 2005).

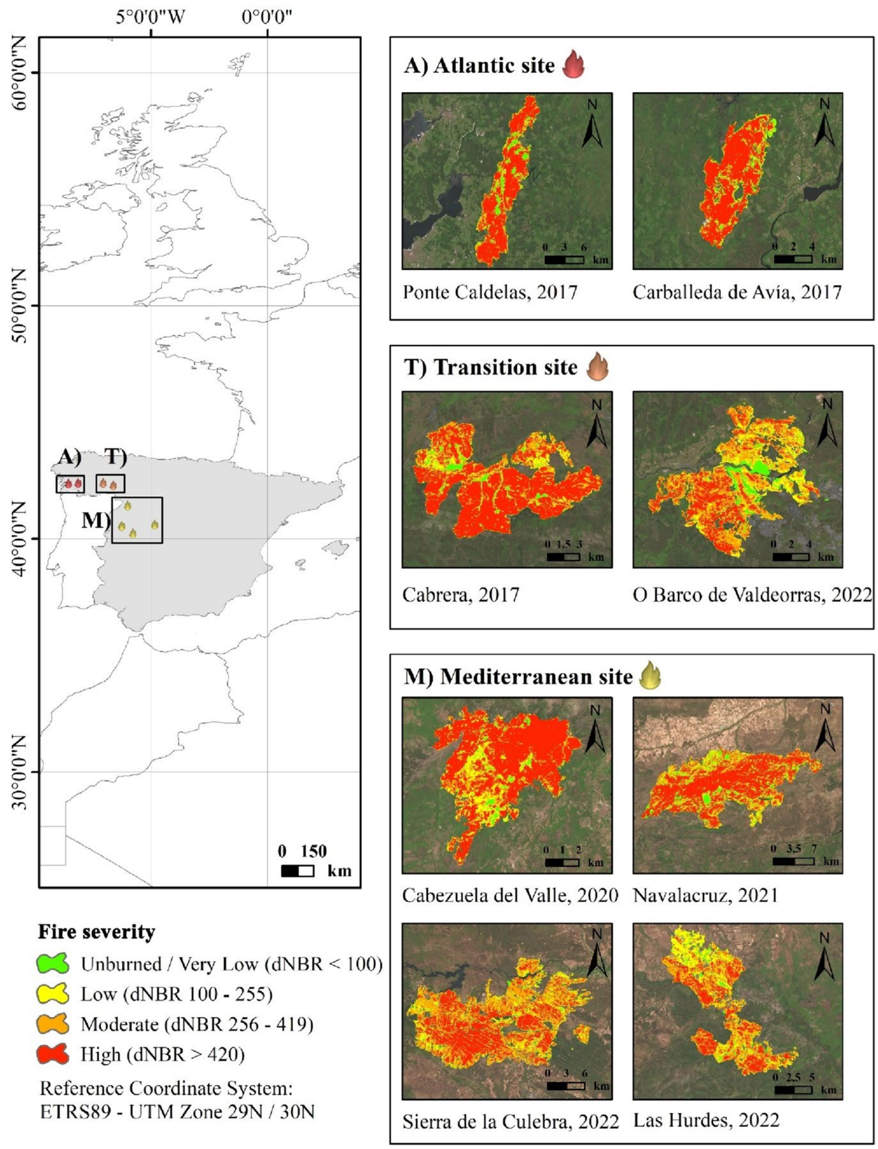

Fig. 1 Target wildfires that occurred in Spain across Atlantic (A)-Transition (T) - Mediterranean (M) bioregions. Fire severity was estimated through the difference of the normalized burn ratio (dNBR) computed from Sentinel-2 imagery and classified following the thresholds established by the European Forest Fire Information System (EFFIS)

Mediterranean wildfires were located in (i) Cabezuela del Valle (Cáceres province; 8° 14′ W 42° 25′ N), where fire burned 3949 ha in 2020, an area dominated by broadleaved forests (*Quercus pyrenaica* Willd and *Castanea sativa* Mill.), shrublands (*Cytisus multiflorus* (L′Hér.) Sweet., *Cistus ladanifer* L., and *Erica* spp.), and pasturelands; (ii) Navalacruz (Avila province; 7° 34′ W 42° 26′ 40 N), where the wildfire occurred in 2021, burned 22,444 ha of *Pinus sylvestris* L. and *Quercus il*ex L. forests, shrublands, pasturelands, and cultivated areas; (iii) Las Hurdes (Cáceres province; 7° 28′ W 41° 54′ N), in 2022 burning 11,927 ha; and (iv) Sierra de la Culebra (Zamora province) (8° 12′ W 41° 52′ N) where fire burned 25,228 ha in 2022. The landscape mosaic affected by the last two wildfires was dominated by heathlands (*Erica arborea* L. and *Erica australis* L.) and broomlands (*Genista florida* L.), as well as *Quercus pyrenaica* Willd., *Quercus ilex* L., *Pinus pinaster* Ait., and *Pinus sylvestris* L. forest stands. In this study site, post-fire regeneration is more related to plant regenerative traits associated with gemination (seed mass and heat-stimulated germination) (Fernández-García et al. 2020). All study Mediterranean wildfires show rugged topography

Table 1 Characteristics of the study wildfires

Fire location	Site	Fire size (ha)	Fire alarm date	MAP[a] (mm)	MADP10[a] (days)	MAT[a] (ºC)	MADT25[a] (days)	Altitude (m)	Soil WRB classification[b]
Carballeda de Avia	Atlantic	5956	17 October 2017	1610	49.4	12.2	64.2	234–987	LPha, CMmo
Ponte Caldelas		9789	16 October 2017	1763	58.3	13.1	67.2	21–729	LPha, CMmo
Cabrera	Transition	9940	21 August 2017	1102	29.5	8.5	80.8	849–1958	LPha, CMmo
O Barco de Valdeorras		12,591	15 July 2022	1014	37.9	10.9	74.5	320–1528	LPha, CMmo
Cabezuela del Valle	Mediterranean	3949	28 August 2020	904	41.2	12.1	109.6	630–1808	LPdy
Las Hurdes		11,927	11 July 2022	1309	39.2	13.4	119.5	472–1715	LPdy, CMmo
Navalacruz		22,444	14 August 2021	944	28.1	9.1	102.3	939–2153	LPdy, CMmo
Sierra de la Culebra		25,228	15 June 2022	805	27.8	10.5	85.7	746–1204	LVcr, CMmo

MAP Mean annual precipitation, *MADP10* Mean annual days with precipitation above 10 mm, *MAT* Mean annual temperature, *MADT25* Mean annual days with a temperature ≥ 25 ºC

[a] MAP, MADP10, MAT, and MADT25 were obtained from Spanish State Meteorological Agency (AEMET 2018)

[b] World Reference Base for Soil Resources classification according to Jones et al. (2005). Soil codes can be found in the database 106 World Soil Resources Reports (FAO 2014)

with steep slopes and wide valleys. Soils are acidic and derived from siliceous lithologies (mainly granitic and slate) with a reduced thickness and mostly classified as Leptosol (Jones et al. 2005). This bioregion presents a typically Mediterranean environmental context, with more than three months of warm dry summers (Ninyerola et al. 2005), precipitation ranging between 805 and 1309 mm, and mean annual temperature of 11.28 ºC (± 1.62 ºC) (AEMET 2018).

Data sources and processing

At each study wildfire location, fire severity and biophysical characteristics of pre-fire fuel (type, amount and structure) were retrieved through (i) Sentinel-2 multispectral instrument Level 1 C scenes from the Copernicus program operated by the European Space Agency ESA (https://sentinel.esa.int) and (ii) the fourth Spanish National Forest Inventory (4-SNFI; MTERD 2022), which uses the Spanish Forest Map at 1:25,000 scale as a cartographic base. Temporal and magnitude attributes of the fire regime over a 35-year period were obtained by mapped past fire scars within the perimeter of target wildfires through visual interpretation of Landsat imagery (Landsat 4–5, TM sensor; Landsat 7, ETM sensor; and Landsat 8, OLI sensor) available in the data catalogue (Collection 2——Level 1) of Google Earth Engine (GEE; Gorelick et al. 2017) (https://developers.google.com/earth-engine/datasets/catalog/landsat).

Fire severity

We acquired Sentinel-2 multispectral instrument Level 1 C (top-of-atmosphere reflectance) images in pre-fire and post-fire situations from Copernicus Open Access Hub (https://scihub.copernicus.eu/) for each study wildfire location. We selected cloud-free Sentinel-2 images with dates as close as possible to the fire alarm date (maximum time range of 1 month from pre-fire or post-fire situations) to avoid potential changes in vegetation status (e.g., phenological changes) (see Table SM1, in supplementary material, for further details). A cloud mask was applied in case there were no cloud-free images available until 1 month before or after the wildfire. The Sen2Cor processor integrated within the Sentinel Application Platform (SNAP) 7.0 version and a digital terrain model (DTM) at 25-m grid size from the Spanish Geographic Institute (IGN 2022) were used to correct Sentinel-2 imagery atmospherically and topographically, obtaining a final surface reflectance product (Level 2 A). This product features spectral data over the visible, near infrared (NIR), and shortwave infrared (SWIR) regions over thirteen bands with different spatial resolutions: three bands at 60 m, six bands at 20 m, and four bands at 10 m. The 60-m spatial resolution Sentinel-2 bands were discarded from further analysis because they are inadequate to deliver a proper canopy reflectance measurement (Fernández-Guisuraga et al. 2021b) and have been demonstrated to be strongly affected by atmospheric scattering of gasses and aerosols (Jia et al. 2016). Finally, we used the mean pixel value aggregation approach for down-sampling 10-m bands to 20 m (Fernández-García et al. 2022), ensuring adequate capture of the spatial and spectral information for land cover classification, pre-fire vegetation biophysical characteristics, and fire severity metric (Fernández-Guisuraga et al. 2021b).

Fire severity of the target wildfires in each study site was estimated through the difference of the normalized burn ratio (dNBR) index (López-García and Caselles 1991; Key and Benson 2006), which is computed as a measurement of ecological change (Keeley 2009). This bi-temporal spectral index is the most common benchmark method for assessing fire severity (Quintano et al. 2018), and widely used by the rapid damage assessment (RDA) module of the European Forest Fire Information System (EFFIS) to interpret the ecological impact in extensive burned areas using predefined thresholds (Table SM2). The index calculation is based on the reflectance from NIR and SWIR spectral regions in the pre- and post-fire Sentinel-2 imagery (Table SM3), and its performance has been extensively validated through field assessments with the Composite Burn Index (CBI; Key and Benson 2006), including several locations within the bioregions of our study (Garcia-Llamas et al. 2020; Llorens et al. 2021; Fernández-Guisuraga et al. 2023a). To account for potential variations in vegetation biophysical characteristics resulting from differences in phenology or precipitation between pre- and post-fire scenes (García-Llamas et al. 2020), we applied an offset term in the dNBR index for each target wildfire. This implementation enhances comparability among fire severity assessments in different wildfires (Miller and Thode 2007; Parks et al. 2018). The dNBR offset was determined by averaging the dNBR values from 1% of pixels within homogeneous and unburned areas located outside the wildfire perimeter but within a 1-km buffer (Miller and Thode 2007).

Pre-fire vegetation variables

Pre-fire Sentinel-2 multispectral images, atmospherically and topographically corrected, at a spatial resolution of 20 m, were used to retrieve pre-fire vegetation characteristics, accounting for fuel type, fuel amount, and fuel structure (see Table 2 for further details).

Fuel type was estimated as land cover class (LCC) by means of a support vector machine (SVM) classification algorithm on each pre-fire Sentinel-2 scene using ArcGIS 10.8. Five land cover classes were considered to classify (i) forests dominated by native broadleaf species, (ii) forests composed of conifer species, (iii) shrublands, which encompassed a diverse range of vegetation, including scrub (e.g., gorse, heath, or broom), small shrubs (e.g., creeping junipers or thorn scrub), and transitional areas from woodland, (iv) grasslands, including agricultural lands, actively cultivated crops, permanently irrigated regions, and natural grasslands, (v) and non-vegetated areas, considering those areas where vegetation cover is sparse, such as artificial surfaces, harvested farmlands (ploughed areas), recently burned areas (< 1 year), rock outcrops, and bare soil. These classes were used as groups of the categorical variable pre-fire fuel type. The SVM classification method is well-suited for satellite multi-band raster (Basheer et al. 2022) since it is not highly susceptible to noise, correlated bands, and unbalanced numbers of training polygons within each class (Huang et al. 2002). Nevertheless, to address potential generalization issues associated with unbalanced samples (Ustuner et al. 2016), we created separate datasets featuring 40 to 50 homogeneous polygons for each land cover class. Each dataset, delineated over each target wildfire location, comprised a minimum of 600 pixels per class for effective SVM classifier training. In each target wildfire, the classification accuracy was assessed using 250 validation points randomly stratified by land cover class, which corresponded to approximately 10% of the training

Table 2 Pre-fire vegetation variables used as predictors of fire severity

Group	Variable	Acronym	Data source
Fuel type	Land cover class	LCC	Pre-fire Sentinel-2 imagery
Fuel amount	Vegetation cover fraction	FCOV	Pre-fire Sentinel-2 imagery
	Fraction of absorbed photosynthetically active radiation	FAPAR	Pre-fire Sentinel-2 imagery
	Leaf area index	LAI	Pre-fire Sentinel-2 imagery
Fuel structure	Homogeneity of the pre-fire vegetation cover fraction	FCOV homogeneity	FCOV data
	Landscape Shannon's evenness index	SHEI	Land cover class data
	Mean distance to nearest neighbors (m)	MNNdist	Land cover class data
	Land cover patch size (ha)	Patch size	Land cover class data
	Perimeter-area ratio index	PA-ratio	Land cover class data
	Mean Shape Index	MSI	Land cover class data

pixel count. This validation dataset ensures a sufficiently representative sample to capture the spectral variability present in Sentinel-2 imagery using SVM algorithms (Topaloğlu et al. 2016). Classification accuracy was estimated by means of a confusion matrix from which user's and producer's accuracy (%), overall accuracy (OA; %), and the Kappa statistic were calculated. The 4-SNFI database, a set of field reference data (Garcia-Llamas et al. 2020; Fernández-Guisuraga et al. 2023a), and pre-fire aerial orthophotographs of very high spatial resolution (0.5 m) provided by Spanish National Geographic Institute (IGN 2022) were used to train and validate the SVM algorithm. We found, for all study areas, a global overall accuracy of 87.65% and a Kappa index of 0.85. No significant underestimation or overestimation of any of the classes was identified across the wildfires set (Table SM4).

Fuel amount variables were retrieved by means of a physical-based approach widely used for estimating pre-fire biomass quantity based on high spatial resolution satellite data (Viedma et al. 2020; Fernández-Guisuraga et al. 2023b). Specifically, we estimated the vegetation cover fraction (FCOV), the fraction of absorbed photosynthetically active radiation (FAPAR), and the leaf area index (LAI). FCOV has been frequently used to quantify vegetation greenness or amount of forest stands as environmental drivers in extreme wildfire events (Fernández-Garcia et al. 2023). FAPAR reflects the available light energy for plant productivity, being a fundamental variable regulating photosynthesis, transpiration, and energy balance (Ogutu et al. 2014). LAI is commonly used as a proxy for the amount of biomass in the forest canopy and also to explain fire behavior variability (Viedma et al. 2020; Fernández-García et al. 2022). We retrieved these products through the pre-fire Sentinel-2 Level 2 A scenes and the biophysical processor embedded into the SNAP software, which have shown the capacity to reliably capture the biophysical properties of the vegetation canopy by means of radiative transfer models (RTMs) (Jia et al. 2016).

Fuel structure metrics were calculated to assess the horizontal continuity of pre-fire vegetation. We measured five different metrics: homogeneity of the pre-fire vegetation cover fraction (FCOV homogeneity), landscape Shannon's evenness index (SHEI), mean distance to nearest neighbor (MNNdist), land cover patch size (patch size), perimeter-area ratio index (PA-ratio), and Mean Shape Index (MSI). FCOV homogeneity is a second-order texture variable of the FCOV input estimated by means of the ENVI 5.3 software. This variable has proven to be very effective for fuel continuity characterization in pre-fire situations (Fernández-García et al. 2022) as it reflects the texture and distance relationships among neighboring pixels (Warner 2011). To obtain directionally invariant FCOV homogeneity, we used a 64-level co-occurrence matrix, a 3×3 pixel kernel, and the average of four directions (0°, 45°, 90°, and 135°) (Fernández-García et al. 2022). The values of this variable range from 0 (completely heterogeneous) to 1 (completely homogeneous). SHEI was retrieved on the basis of the Pielou (1966) equation (Eq. 1) and calculated over the SVM land cover maps. It determines the diversity and continuity of pre-fire land cover classes using the *landscapemetrics* v2.0.0 (Hesselbarth et al. 2019) and *rgdal* v1.6.4 (Bivand et al. 2021) packages in R 4.0.4 (R Core Team 2023) and RStudio 2023.03.2+454.pro2 (RStudio Team 2023).

$$\mathrm{SHEI} = \mathrm{SHDI}/\mathrm{H}'_{\max} \tag{1}$$

where SHDI is the Shannon diversity index and $H_{\max}$ is the maximum value for SHDI (LN (richness). The remaining landscape configuration metrics (patch size, MNNdist, PA-ratio and MSI) were calculated from SVM pre-fire land cover maps using the vector-based Landscape Analysis Tools Extension (V-LATE 2.0; Lang and Tiede 2003) for the ArcGIS 10.8 software. We estimated (i) the patch size as the area (in ha) occupied by each land cover class polygon within the burned areas, (ii) the MNNdist as the mean distance between patches of the same land cover class in the pre-fire landscape, (iii) the PA-ratio as the mean shape for each land cover class patch estimated by the patch perimeter divided by patch area, and (iv) the MSI as the mean shape complexity which is adjusted for a square standard by a constant (Toosi et al. 2022). These variables describe the form, aggregation, and composition of the landscape patches, being pre-fire structural landscape metrics highly correlated with wildfire extent and fire severity (San-Miguel et al. 2017; Toosi et al. 2022).

Fire regime attributes

The Global Fire Atlas (Andela et al. 2019) and the EFFIS burnt area database (San-Miguel-Ayanz et al. 2012) were used to identify all previous wildfires ≥ 30 ha that occurred within the target areas during the period 2000–2022. This burned scar size corresponds to the wildfire detectability provided by MODIS and Sentinel-2 satellite imagery for the surveyed period (San-Miguel-Ayanz et al. 2012). Wildfires occurred during the period 1985–2000 were identified through monthly inspection of Landsat images using the LandsatLook tool (https://landsatlook.usgs.gov/) of the U.S. Geological Survey´s Earth Explorer server. LandsatLook allows rapid temporal visualization of burned scars by area of interest, sensor, date of acquisition, or cloud cover, through dynamic mosaics in composites of three user-defined spectral bands (Wulder et al. 2019). All perimeters recorded for the whole period (1985–2022) were manually digitized in ArcGIS 10.8 at 1:20,000 scale (minimum mapping unit of 0.04 km^2) above false color Landsat imagery (Fernández-García et al. 2020) and validated with data from the forest fire reports (1968–2015) available at the Spanish General Forest Fire Statistics database (MTERD 2023). This spatial database of wildfire scars was used to estimate temporal fire regime attributes (fire recurrence and time since last fire-TSLF) over the study period (1985 to the year of target extreme wildfire occurrence). Both attributes are frequently used as indicators of potential fire-induced ecological change (Parks et al. 2014) and as considered drivers of ecosystem resilience in southern Europe (Fernández-García et al. 2020). TSLF in study areas without fire recurrence (no wildfires in the study period) was set to one year higher than the time period analyzed: (year of last fire − 1985) + 1.

The fire severity of the previous wildfire (FSPW) within the target areas was retrieved in GEE (Gorelick et al. 2017) using the Landsat Collection 2 Level-1 imagery which included scenes from Landsat 4–5 TM, Landsat 7 ETM, and Landsat 8 OLI (https://developers.google.com/earth-engine/datasets/catalog/landsat). This set of 30-m spatial resolution scenes corresponds to a surface reflectance product with geometric and radiometric corrections covering a 35-year time range. Fire severity of each historical wildfire was computed using the dNBR index with the code provided by Parks et al. (2018) in GEE, adapted for initial assessments of fire severity. This approach also incorporates dNBR offset by quantifying the average value of unburned pixels. With the historical fire severity database for each study area, we obtained the fire severity of the previous wildfire (FSPW) within the target wildfire perimeter.

Data extraction and statistical analysis

Fire regime attributes (fire recurrence, TSLF, and FSPW), fire severity of the target wildfire, and pre-fire vegetation characteristics were extracted using a random sample of points separated at least 100 m from each other (i.e., maximum of one point per hectare). This distance has been considered appropriate to avoid spatial autocorrelation in fire severity assessments (Fernández-Guisuraga et al. 2021a; Fernández-García et al. 2022). To maintain consistency in the relationship between previous wildfires and the formation of pre-fire vegetation characteristics prone to extreme fire behavior, the initial dataset of 90,188 points was pruned by discarding areas corresponding to unburned patches within the perimeter (i.e., sampling points with dNBR values lower than − 100), burned areas during the same year of the occurrence of the target wildfires (2% of the total burned area under study), and areas potentially affected by disturbances other than wildfires (e.g., clearcutting). Finally, we also removed points established in patches categorized as forest plantations (e.g., *Eucalyptus globulus* Labill.) in the 4-SNFI (26.75% of the total points in the Atlantic site, 7.75% in the Transition site, and 17.60% in the Mediterranean site) to guarantee that post-fire landscape dynamics in the 35-year time series have not undergone significant man-made interventions. Following these criteria, the final dataset was comprised of 67,572 sampling points.

Trends of fire recurrence, total burned area, and fire severity over the 35-year period across different bioregions were evaluated by means of the non-parametric Mann-Kendall test (Mann 1945) and the Theil-Sen slope estimator (Sen 1968), respectively. One-way ANOVAs with pairwise multiple comparison test of means (Tukey HSD) were used to evaluate differences in fire regime attributes between bioregions. Statistical significance was fixed at the 0.05 level.

A prior data exploratory analysis to detect potential collinearity issues among pre-fire vegetation drivers (Table 2) was conducted through the computation of the Pearson's bivariate correlation coefficient. A threshold of $R > |0.7|$ was considered to identify groups of correlated variables from which we retained only the most ecologically relevant (García-Llamas et al. 2020; Fernández-Guisuraga et al. 2023a). Then, we examined the relationship between the uncorrelated pre-fire vegetation characteristics (predictors) and continuous dNBR values (fire severity; response variable) through a frequentist model averaging approach (FMA; Burnham and Anderson 2002). FMA computes weighted estimates for the parameters included in all the potential combinations of candidate models in the full model set (Nakagawa and Freckleton 2011). This approach avoids spurious predictor selection because it can robustly handle uncertainty in model parametrization (Burnham and Anderson 2002; Dormann et al. 2018). Candidate models in each study site ($n = 9498$ in the Atlantic; $n = 14{,}977$ in the Transition; $n = 43{,}097$ in the Mediterranean) were fitted using linear mixed models (LMMs). We considered linear and quadratic predictor terms as well as interaction effects between pre-fire LCC and all other variables. The identity of each target wildfire was included in the models as a random factor (Moghli et al. 2022). From the full model set, following the recommendation of Burnham and Anderson (2002), we retained those models with an Δ-value < 2 of the Akaike information criterion, obtaining a top model set to average. The performance of the averaged LMM was evaluated through the McFadden's pseudo-coefficient of determination (R^2) and the root-mean-square-error (RMSE). We followed the same approach to disentangle the influence of fire regime attributes (fire recurrence, TSLF, and FSPW; predictors) over the last 35 years on pre-fire vegetation characteristic (response variable) relevant in the previous analyses to explain fire severity variability. We considered interaction effects between all the predictors. Mixed effects multinomial regression models instead of LMMs were fitted when the response variable was categorical (e.g., pre-fire LCC). All analyses were computed in R 4.0.4 (R Core Team 2023) and. RStudio 2023.03. 2 + 454.pro2 (RStudio Team 2023) using the *trend* v1.1.6 (Pohlert 2023), *caret* v6.0-94 (Kuhn 2008), *lme4* v1.1-35.1 (Bates et al. 2015), and *mclogit* v0.9.6 (Elff 2022) packages.

Results

Fire history trends in different Spanish bioregions

During the 1985–2022 period, 746 wildfires ≥ 30 ha were identified within the study areas, 48.8% at the Atlantic site, 37.8% in the Transition site, and 13.4% in the Mediterranean site (Fig. 2A). The highest number of wildfires that occurred in the late 1980s and early 1990s in the three bioregions with a significant decrease in time. The total burned area had a decreasing trend in all study sites (Fig. 2B). Over the study period, fire severity showed an increasing trend in Atlantic and Transition areas (although not significant in the latter case) and a significant decrease in Mediterranean areas (Fig. 2C).

The particular environmental context of each bioregion explained variations in the temporal attributes of the fire regime (fire recurrence and TSLF; $F > 478.98$, p-values < 0.001) better than in fire severity ($F = 257.05$, p-value < 0.001) (Fig. 3). Fire recurrence diminished significantly from Atlantic (1.93 ± 1.00 times, maximum = 7) to Transition (1.81 ± 0.95, 7) and Mediterranean areas (1.10 ± 0.32, 3) during the last 35 years (Fig. 3A). Mean TSLF was higher in the Mediterranean (24.90 ± 10.19 years) than in Transition (14.92 ± 7.47) and Atlantic (18.57 ± 8.71) sites (Fig. 3B). Mean fire severity was lower in the Transition (232.04 ± 161.53) than in the Mediterranean (353.37 ± 210.70) and Atlantic (355.11 ± 215.69) areas (Fig. 3C). The highest fire severity value was observed in Atlantic areas (dNBR = 980.80) (Table SM5).

Pre-fire vegetation variables driving fire severity in the target wildfires under different bioregions

Pearson correlation analyses showed that all fuel amount variables (FCOV, FAPAR, and LAI) were positively and strongly correlated ($R > 0.7$) (Fig. SM1). High correlation was also observed between fuel structure variables related to patch metrics (patch size and PA-ratio). For

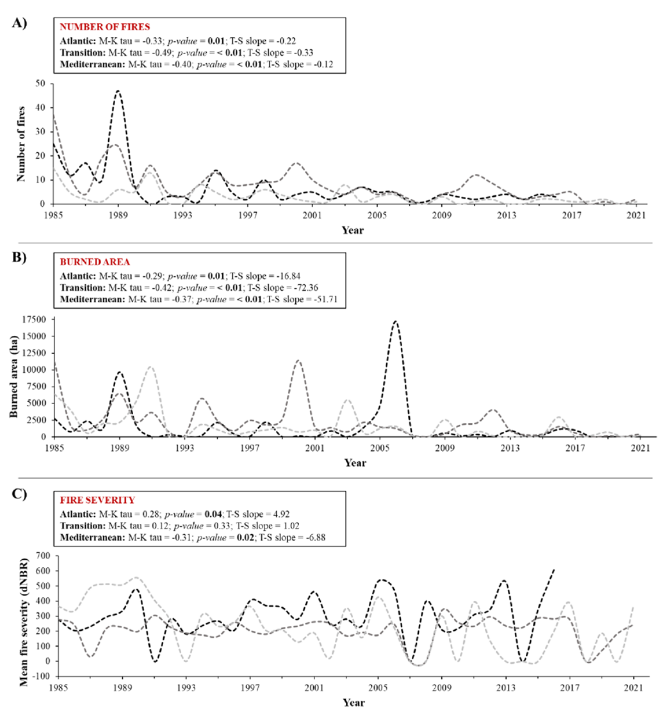

Fig. 2 Number of fires ≥ 30 ha (**A**), total burned area (**B**), and mean annual fire severity (**C**) in the study sites from 1985 to the year before the occurrence of the last wildfires under study (2016 in the Atlantic site, 2021 in the Transition and Mediterranean sites) with indication of the results of the Mann-Kendall (M-K) and Theil-Sen slope (T-S) tests

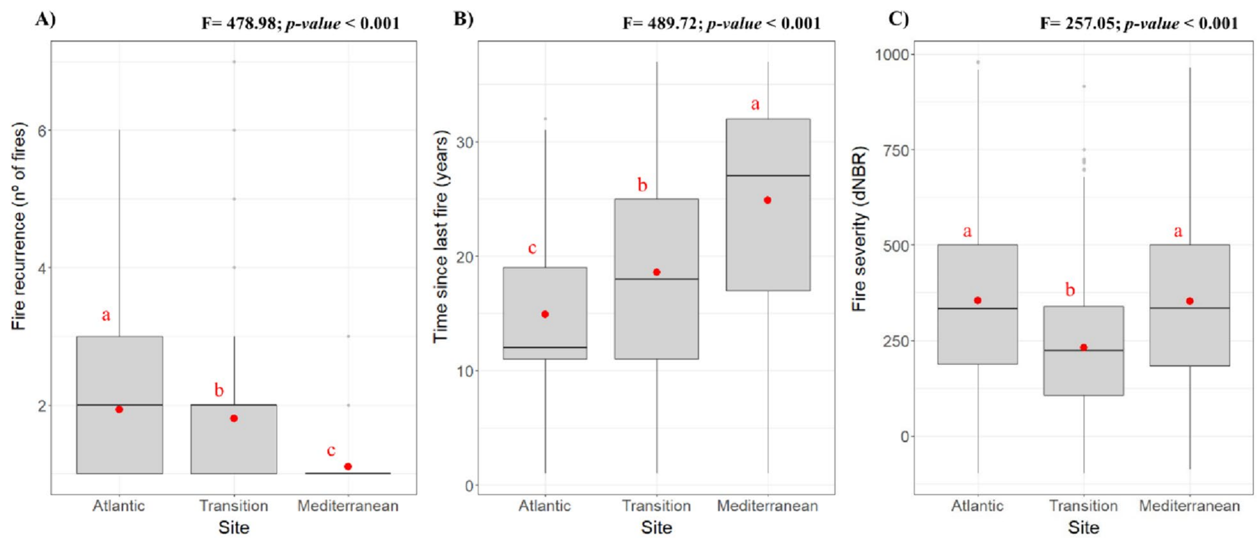

Fig. 3 Relationships between environmental contexts (sites) and **A** fire recurrence, **B** time since last fire, and **C** fire severity. The red dots represent the mean values, the black line indicate the median values, and different letters above bars denote significant differences along the Atlantic-Transition-Mediterranean bioregions at the 0.05 level

that reason, for subsequent analyses, we used pre-fire LCC, FAPAR, FCOV homogeneity, SHEI, MNNdist, PA-ratio, and MSI as uncorrelated fuel type, amount, and structure pre-fire vegetation predictors of fire severity with the highest ecological meaning.

Fire severity was satisfactorily predicted in each bioregion by FAPAR, pre-fire LCC, and their interaction (p-values < 0.05) (Table 3). Nevertheless, none of the fuel structure variables were retained in the models with FMA approach due to their low contribution. Models featured a higher fit in the Transition ($R^2 = 0.54$; RMSE = 152.91) than in the Mediterranean ($R^2 = 0.43$; RMSE = 145.65) and Atlantic ($R^2 = 0.33$; RMSE = 196.08) areas. The effect of FAPAR on fire severity was dependent on the ecosystem type (LCC) across all bioregions studied (Fig. 4). In Transition and Mediterranean areas, fire severity strongly increased with high fuel amount in conifer forests. In contrast, in Atlantic sites, maximum severity values occurred in shrubland ecosystems with intermediate pre-fire fuel amount. Based on these results, FAPAR and pre-fire LCC were selected as variables to be considered in the analyses of Predicting pre-fire vegetation characteristics through fire regime attributes across different bioregions section.

Predicting pre-fire vegetation characteristics through fire regime attributes across different bioregions

Fire recurrence, TSLF and fire severity of the previous wildfire (FSPW) were retained in the FMA of linear mixed model and explained significantly pre-fire FAPAR

Table 3 Results of the averaged linear mixed models depicting the effects of the pre-fire fuel type (LCC), fuel amount (FAPAR), and their interaction on fire severity for the target wildfires in Atlantic, Transition, and Mediterranean areas

Site	Model parameter	Df	Sum of squares	Mean of squares	*F*	*P*-value
Atlantic	FAPAR (polynomic^2)	2	1.69E+07	8.43E+06	96.10	< 0.001***
	LCC	4	8.73E+05	2.18E+05	2.49	0.0414*
	FAPAR (polynomic^2) * LCC	8	5.72E+06	7.15E+05	8.14	< 0.001***
Transition	FAPAR (polynomic^2)	2	6.47E+07	3.24E+07	1382.19	< 0.001***
	LCC	4	1.20E+06	3.01E+05	12.85	< 0.001***
	FAPAR (polynomic^2) * LCC	8	1.22E+07	1.52E+06	65.09	< 0.001***
Mediterranean	FAPAR (polynomic^2)	2	1.60E+08	8.01E+07	3776.53	< 0.001***
	LCC	4	2.94E+07	7.36E+06	346.75	< 0.001***
	FAPAR (polynomic^2) * LCC	8	8.28E+07	1.04E+07	487.79	< 0.001***

The significance of linear mixed model coefficients is represented by *** (p-value < 0.001), and * (p-value < 0.05)

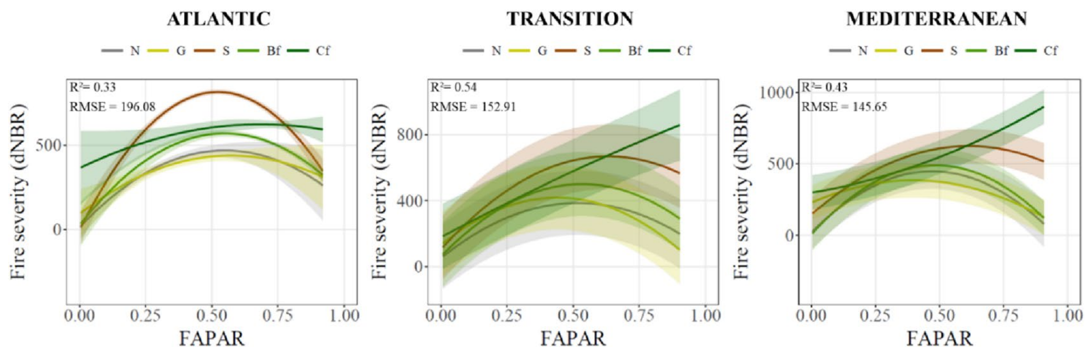

Fig. 4 Relationship between fire severity and pre-fire fuel amount (FAPAR) for the target wildfires as a function of land cover class (N, non-vegetated; G, grassland; S, shrubland; Bf, broadleaf forest; Cf, conifer forest) in Atlantic, Transition, and Mediterranean areas

variability as linear or quadratic predictors (p-values <0.001) across the different bioregions analyzed. However, interaction effects between fire regime attributes were only significant in Transition and Mediterranean areas (p-values <0.001) (Table 4). There was a significant relationship between fire regime attributes and FAPAR in Mediterranean ($R^2=0.32$; RMSE $=0.13$), Transition ($R^2=0.28$; RMSE $=0.16$), and Atlantic ($R^2=0.27$; RMSE $=0.18$) areas (Fig. 5). Under Atlantic conditions, the highest FAPAR values were associated with TSLF between 15 and 20 years and high values of FSPW, decreasing markedly with repeated wildfires occurring during the study period. Under Transition conditions, FSPW exerted, at short fire-free intervals (<10 years), a greater influence on FAPAR than fire recurrence, as evidenced by the strong interaction between this variable and TSLF. In this context, FAPAR increased towards longer TSLF, which dilutes the effects of both FSPW and fire recurrence (Fig. 5). Under Mediterranean conditions, the higher FAPAR values were mainly related to high TSLF (>15–20 years) in combination with low fire recurrence. There were no notable differences in the FAPAR variability shaped by FSPW at either short or long TSLFs.

Fire regime attributes were retained in the FMA of mixed effects multinomial regression models and also played a significant role as linear or quadratic predictors (and their interactions) in the estimation of pre-fire LCC across the different bioregions where the strength of the relationships was higher in the Transition site ($R^2=0.57$) than in the Atlantic ($R^2=0.35$) and Mediterranean ($R^2=0.41$) sites (Table 5; Fig. 6). There was variation in the control exerted by FSPW on the pre-fire LCC probability among the different bioregions. Native broadleaf forests were more likely to dominate in the Atlantic area as FSPW increased. The probability of shrubland emergence was associated with low values of FSPW. The same

Table 4 Results of the averaged linear mixed models depicting the effects of the fire regime attributes (FSPW, fire recurrence, and TSLF) and their interactions on pre-fire vegetation amount (FAPAR) for the target wildfires in Atlantic, Transition, and Mediterranean areas

Site	Model parameter	dF	Sum of squares	Mean of squares	F	P-value
Atlantic	FSPW (polynomic^2)	2	1.34E+00	6.70E−01	21.03	<0.001***
	Fire recurrence (polynomic^2)	2	1.58E+01	7.92E+00	248.43	<0.001***
	TSLF (polynomic^2)	2	7.82E+00	3.91E+00	122.64	<0.001***
Transition	FSPW	1	7.35E+00	7.35E+00	280.50	<0.001***
	Fire recurrence	1	6.19E−02	6.19E−02	2.36	0.124ns
	TSLF	1	7.46E+00	7.46E+00	284.51	<0.001***
	Fire recurrence * TSLF	1	1.09E+00	1.09E+00	41.64	<0.001***
	FSPW * TSLF	1	3.49E+00	3.49E+00	133.08	<0.001***
Mediterranean	FSPW (polynomic^2)	2	2.46E+00	1.23E+00	52.21	<0.001***
	Fire recurrence (polynomic^2)	1	7.76E−01	7.76E−01	32.91	<0.001***
	TSLF (polynomic^2)	1	6.18E−01	6.18E−01	26.19	<0.001***
	Fire recurrence (polynomic^2) * TSLF (polynomic^2)	4	3.77E+00	9.41E−01	39.92	<0.001***
	FSPW (polynomic^2) * TSLF (polynomic^2)	3	3.67E+00	1.22E+00	51.89	<0.001***

The significance of linear model coefficients is represented by *** (p-value < 0.001), and ns (p-value > 0.05)

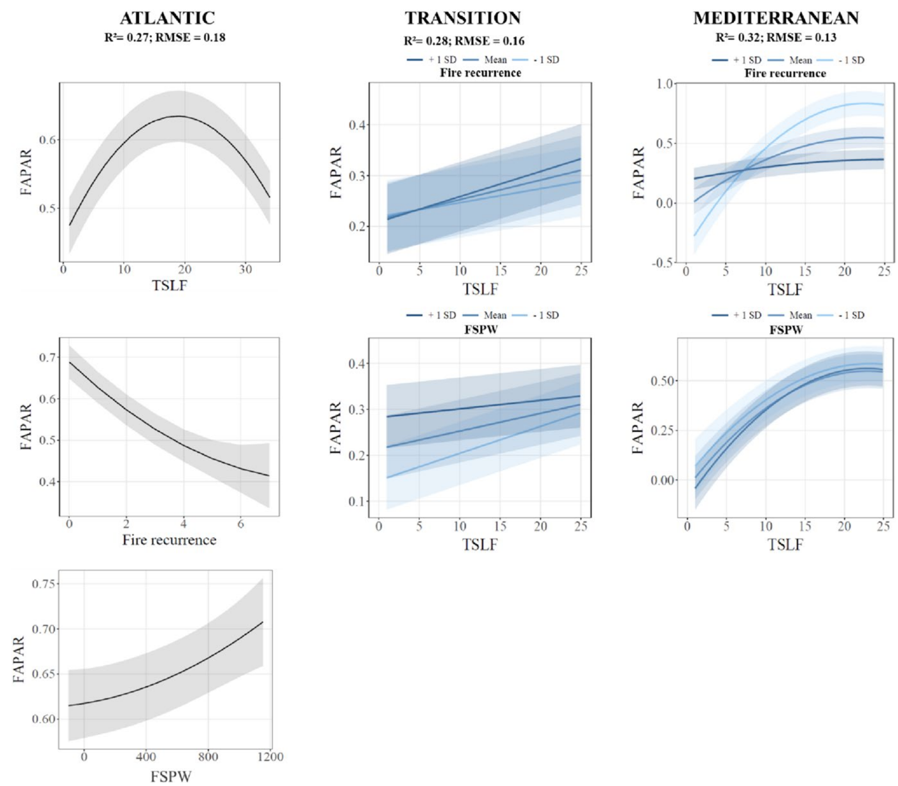

Fig. 5 Relationship between pre-fire FAPAR and fire regime attributes (FSPW, fire recurrence, and TSLF) for the target wildfires in Atlantic, Transition, and Mediterranean areas. The variation of the moderator variable (+ 1SD, mean, − 1SD) in the interaction is shown in different shades of blue

Table 5 Results of the averaged mixed effects multinomial regression models depicting the effects of the fire regime attributes (FSPW, fire recurrence, and TSLF) and their interactions on the pre-fire land cover class (LCC) probability for the target wildfires in Atlantic, Transition, and Mediterranean areas

Site	Model parameter	dF	LR chi-square	*P*
Atlantic	FSPW (polynomic^2)	4	261.06	< 0.001***
	Fire recurrence (polynomic^2)	4	281.99	< 0.001***
	TSLF (polynomic^2)	4	268.45	< 0.001***
	Fire recurrence (polynomic^2) * TSLF (polynomic^2)	4	259.12	< 0.001***
	FSPW (polynomic^2) * TSLF (polynomic^2)	4	38.40	0.0013**
Transition	FSPW	4	373.44	< 0.001***
	Fire recurrence	4	143.19	< 0.001***
	TSLF	4	154.11	< 0.001***
	Fire recurrence * TSLF	4	137.08	< 0.001***
	FSPW * TSLF	4	111.68	< 0.001***
Mediterranean	FSPW (polynomic^2)	4	814.37	< 0.001***
	Fire recurrence (polynomic^2)	4	513.14	< 0.001***
	TSLF (polynomic^2)	4	1745.44	< 0.001***
	Fire recurrence (polynomic^2) * TSLF (polynomic^2)	4	336.39	< 0.001***
	FSPW (polynomic^2) * TSLF (polynomic^2)	4	303.06	< 0.001***

The significance of multinomial regression model coefficients is represented by *** (*p*-value < 0.001), and ** (*p*-value < 0.01)

pattern was observed in the Mediterranean area but with the dominance of conifer forest under high FSPW. However, the Transition sites exhibited a clear dominance of shrubland ecosystems under any FSPW and only a slight increase in the likelihood of conifer forests with increase of FSPW. Short TSLF favored the dominance

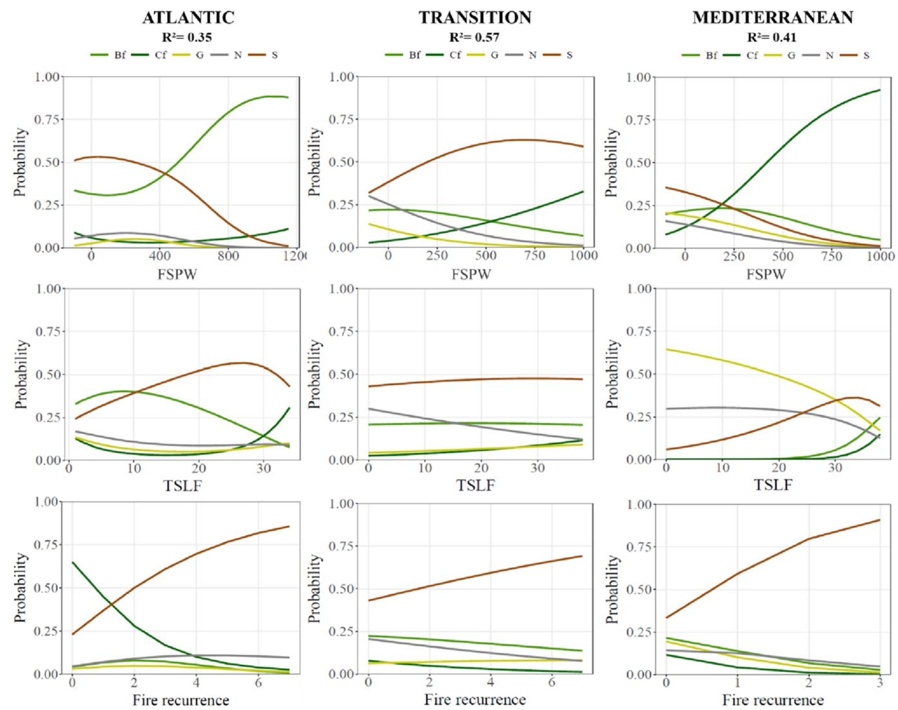

Fig. 6 Predicted probabilities of the pre-fire land cover class (LCC) for the target wildfires as a function of fire regime attributes (FSPW, fire recurrence, and TSLF) in Atlantic, Transition, and Mediterranean areas. N, non-vegetated; G, grassland; S, shrubland; Bf, broadleaf forest; Cf, coniferous forest

of fast-regenerating vegetation types in Atlantic areas, mainly shrublands and native broadleaf forests, while long TSLF favored the probability of conifer forest dominance in all bioregions analyzed, particularly after 30 years. In Mediterranean sites, tree-dominated LCC disappeared at short and medium TSLF levels, with a clear dominance of sparse vegetation types (i.e., grasslands and shrublands). Shrubland dominance increased with fire recurrence, following a similar pattern across all bioregions studied.

Altogether, our results suggest that the response of fire severity to pre-fire vegetation characteristics is strongly modulated by fire regime attributes but following different pathways depending on the environmental context of the bioregions analyzed (Fig. 7). In the Atlantic area, high fire severity may be driven by two mechanisms: (i) high fire recurrence of low to moderate severity wildfires may foster transitions to shrubland stable states with intermediate FAPAR values prone to high fire severity in subsequent wildfires; (ii) long TSLF periods after previous wildfires of high fire severity and low fire recurrence may promote the dominance of conifer stands prone to extreme fire behavior in areas with intermediate to high site productivity. In Transition and Mediterranean areas, other mechanisms exist: (i) long TSLF (> 30 years) after high-severity wildfires may enhance fuel build-up (high FAPAR values) in conifer-dominated ecosystems that are responsible for high fire severity levels in the target wildfires; (ii) high fire recurrence and TSLF over 15 years may promote shrublands of intermediate FAPAR values that are likely to undergo subsequent high-severity wildfires. The development of intermediate amounts of shrub-type fuels in Transition and Mediterranean sites is strongly related to fire severity of previous wildfires.

Discussion

We assessed the effects of fire activity over 35 years across Atlantic, Transition, and Mediterranean bioregions of the Spanish Iberian Peninsula on pre-fire fuel composition and amount, allowing the identification of direct and indirect control patterns of new situations prone to subsequent severe fire behavior. Our results shed light on the importance of fire regime attributes in modulating biophysical contexts that shape landscapes prone to high fire severity in the western Iberian Peninsula. Fire severity was found to be mainly influenced by pre-fire fuel characteristics, but this effect was strongly controlled by their interaction with fire recurrence, time since last fire, and fire severity of the previous wildfire under different environmental contexts. This understanding is essential for decision-making strategies targeted at mitigating the worst ecological effects of severe wildfires (Harris and

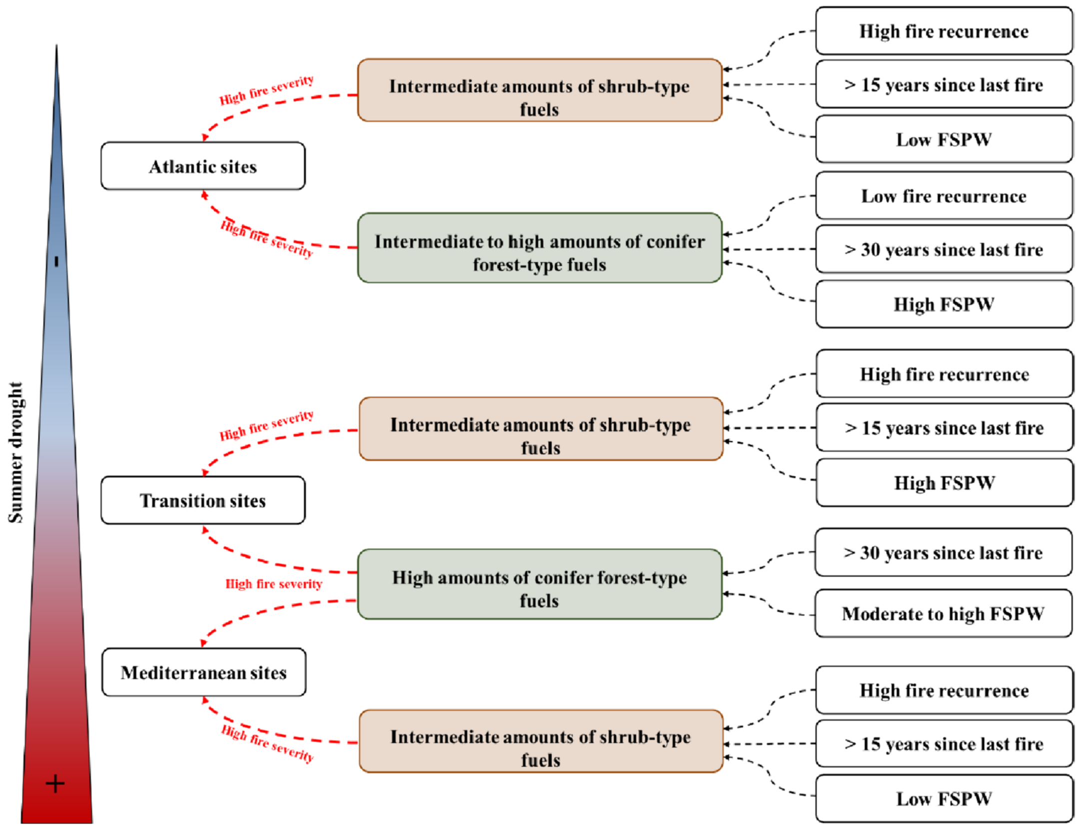

Fig. 7 Flowchart of the modulation of main high fire severity drivers by fire regime attributes under different environmental context (sites)

Taylor et al. 2017), which should be site-dependent (Kane et al. 2015) and consider ecosystem responses to future climate scenarios (Fernandes 2013).

Fire history dynamics in different Spanish bioregions

The well-known disruption of fire regimes in the Mediterranean Basin suggests an uncertain scenario in the functioning of fire-prone forest ecosystems (Pausas and Paula 2012; Taboada et al. 2017; Pausas and Keeley 2021). These include the expected harsher fire weather risk and longer fire seasons (Calheiros et al. 2021). In this sense, the worsening of fire effects on ecosystems would be likely to occur even in environmental contexts where fire activity is traditionally limited by unfavorable conditions in terms of type of fuel and rate of fuel accumulation (Vázquez et al. 2002). Nonetheless, we evidenced a reduction in fire occurrence and total burned area in all our study areas since the 1980s which may have led to a notably change in fuel build-up patterns and, subsequently, an increase in the likelihood of more intense and severe wildfires, in line with the findings of other authors (e.g., Fernandes 2013; Rodrigues et al. 2020; Boisramé et al. 2022). A downward trend in fire occurrence has also been reported over most of the northwestern region in Spanish where fire frequency has historically been higher (Rodrigues et al. 2020). The decrease in fire occurrence in all the bioregions analyzed is probably associated with an efficient wildfire suppression policy, mainly during the mid-90s when a total fire exclusion policy was enforced (Ruffault and Mouillot 2015; Rodrigues et al. 2020). However, we found contrasting tendencies in fire severity in our study sites, with an increasing trend in the Atlantic area, and a decreasing trend in the Mediterranean area. Despite the observed decrease in fire occurrence in the three bioregions, the ecological contexts of the Atlantic areas, where the rate of fuel build-up is higher (primarily of resprouting and facultative species; Fernández-García et al. 2020), may have contributed to the increased fire severity of repeated wildfires (Rodrigues et al. 2020). This can also reinforce positive fire-vegetation feedbacks that perpetuate fire-prone vegetation types that will generate new high-severity wildfires (Parks et al. 2014; Duane et al. 2021; Povak et al. 2023). Apart from the higher relative abundance of fast-recovering resprouting species after short fire-free intervals (Pausas and Keeley 2014), the increase in extreme fire weather conditions throughout an extended fire season observed by authors as Calheiros et al. (2021) might also promote a greater vegetation propensity to burn at high fire severity in the Atlantic bioregion.

Vegetation drivers of fire behavior across different bioregions

Our results showed that proxies for pre-fire fuel type and amount were the most relevant predictors of fire severity across different bioregions, which is in accordance with previous research (e.g., García-Llamas et al. 2019; Fernández-García et al. 2022). Conversely, structural variables related to fuel horizontal distribution, which have proven before to be relevant in fire extent modeling, were not found to be good predictors of fire severity (Fernandes et al. 2016).

Among pre-fire fuel amount variables, FAPAR, closely associated with site productivity (Fensholt et al. 2004), was the best predictor of fire severity (Viedma et al. 2020; Fernández-García et al. 2022). We reported a clear pattern of increasing fire severity towards intermediate and high pre-fire fuel amounts, depending on ecosystem type and environmental context of each bioregion. This fire behavior control has been documented by other authors (e.g., Fernández-Guisuraga et al. 2021a), who found that fire severity at fine spatial scales is largely determined by specific parameters related with the distribution of the fuel amount in the stand (e.g., canopy volume). Nevertheless, the role of pre-fire biomass amount in predicting the spatial variability of fire severity was stronger in Transition or Mediterranean areas, compared to Atlantic areas. This could be partly due to the importance of fire weather-type and topographic variables in determining high fire severity likelihood in the most humid and productive regions (weather-limited fire regimes) of the western Iberian Peninsula, especially in areas of elevated roughness and dissected terrain, as previously reported by other authors (Fernández-Alonso et al. 2017). In any case, here we have only considered variables that can be handled through management actions, such as pre-fire fuel. In addition, fine-scale fire weather data is not available at the spatial scale of the present study.

The distinct strength of fire severity predictions across different bioregions was not only due to pre-fire vegetation amount but also to the interaction with specific ecosystem types. Under Transition and Mediterranean environmental conditions, conifer forests with high FAPAR were the main drivers of extreme fire behavior. Previous studies (Fernández-Guisuraga et al. 2021a, 2023b) demonstrated that a high fraction of flammable fuel types (e.g., Mediterranean pine forests), typically with dense and tall understories that accumulate substantial dead plant material (Fernandes and Rigolot 2007), are prone to more severe fires, mainly because of ladder fire propagation and crowning potential (Kane et al. 2015; García-Llamas et al. 2020). Notwithstanding, maximum fire severity in the Atlantic area was found for intermediate pre-fire vegetation amount, with shrublands and conifer forests being the most affected land cover classes. In previous research (García-Llamas et al. 2019; Viedma et al. 2020), it has been highlighted that very dense live biomass reduces severe fire behavior, probably due to flammability limitations caused by high moisture loads under mesic environments (Busby and Holz 2022) and fire resistance of individuals in native mature forests (Gil-Tena et al. 2016). The above-mentioned pattern was clearly evident in shrublands in this study, but also in conifer forests, where fire-induced ecological effects stabilize or increase very slightly under intermediate site productivity. Moreover, in Atlantic areas, where humid climate promotes resprouting reproductive strategies (Reyes and Casal 2008), shrub-dominated ecosystems could be the most affected by fire at intermediate productivity sites.

Effects of fire regime attributes in shaping severe fire-prone landscapes in different Spanish bioregions

Fire regime attributes strongly modulated pre-fire vegetation characteristics and, thus, the fire behavior of subsequent wildfires, following distinct mechanisms across Atlantic-Transition-Mediterranean bioregions. First, our results indicated that long-term fire effects on ecosystems as measured by fire severity of previous wildfires (FSPW) have been a key element in the composition and productivity of landscapes prone to subsequent extreme wildfire disturbances, as previously reported in Sierra Nevada of California, United States (Steel et al. 2021). In this respect, our results revealed that the ecological impacts of previous wildfires have different implications in landscape composition and vegetation productivity under distinct environmental contexts. Productivity and vegetation recovery after fire (whether by obligate seeders, facultative seeders, or obligate resprouters) vary as a function of moisture and fertility conditions (Pausas and Keeley 2014), gap availability for seedling recruitment, and growth in highly competitive environments (Clarke et al. 2005, 2013; Fernández-García et al. 2020). For instance, as resource availability increases, namely moisture and nutrients, resprouting strategy after a wildfire disturbance confers competitive advantages over seeding strategy from lower to higher site productivity (Pausas and Keeley 2014).

Translating the above to specific environmental contexts, the highest post-fire competition intensity can be expected for resprouter species in the Atlantic bioregion (Fernández-García et al. 2020) according to the resource-productivity model proposed by Clarke et al. (2005). This may explain that native broadleaf forests are dominated by fast-recovering and low-flammability resprouter species (Reyes and Casal 2008) that were more likely to dominate after severe wildfires with high post-fire resource availability in our Atlantic study areas. Conversely, in Mediterranean environments with open post-disturbance habitats fostered by high severity wildfires, higher competition intensities in stands of seeding tree species (e.g., Peninsular pine species) over shrubby understory species can be expected according to the gap-dependent model (Keeley et al. 2016). This fact may be reinforced by the high level of serotiny of some pine species at the Mediterranean site (e.g., *Pinus pinaster* Ait.) that provides an effective post-fire seedling recruitment mechanism without the influence of competitive advantages exerted by shrub resprouter species in more densely vegetated areas (Keeley et al. 2016). Agreeing with our results, high post-fire conifer seedling recruitment after severe wildfires, together with long TSLF (>30 years), may be responsible for the accumulation of flammable fuels prone to subsequent high severity wildfires in the Mediterranean bioregion. The same mechanism may be also behind the high severity outcome at moderate to high FAPAR values in places dominated by facultative and seeder shrubs. Similarly, highly disturbed environments by past wildfires in the Transition site promote a high fuel accumulation of fire-adapted species even with short TSLF, mainly resprouting and facultative shrubs with high recovery rates (Fernández-García et al. 2020; Huerta et al. 2021), associated to transitions from forest to shrub-dominated ecosystems (Gil-Tena et al. 2016) with high fire severity likelihood in subsequent wildfires.

Regarding the temporal attributes of the fire regime, fire recurrence and TSLF had a strong effect on vegetation composition and productivity, besides potentially impairing other ecosystem functions and services that are highly related to the former through synergies or trade-offs (Moghli et al. 2022), such as biodiversity, soil fertility, or decomposition rates. Across all bioregions studied, high fire recurrence led to a marked reduction in the area occupied by forest ecosystems (both conifer and broadleaf dominated) and also to an increase of shrublands ecosystems that need less time (short TSLF) to recover to a pre-fire state after a wildfire disturbance (Taboada et al. 2017).

High fire recurrence may strengthen high fire severity feedbacks in shrubland ecosystems, particularly in the Atlantic and Transition areas dominated by resprouter and facultative species linked to high post-fire regrowth rates (Clarke et al. 2013; Pausas and Keeley 2014), as compared to the Mediterranean areas where seedling recruitment prevails (Fernández-García et al. 2020; Fernández-Guisuraga et al. 2020). For instance, in the Atlantic bioregion, moderate to high fire recurrence together with low disturbance intensity of past wildfires conduct to high shrub fuel build-up according to the resource-productivity model (Clarke et al. 2005), thus leading to extreme fire behavior of subsequent wildfires. In the Mediterranean bioregion, shrublands of intermediate FAPAR values, prone to high fire severity, are promoted by high fire recurrence and severity of previous wildfires, according to the gap-dependent model (Keeley et al. 2016). Conversely, low fire recurrence, coupled with long TSLF, may be accountable for a high accumulation of flammable fuels in conifer forests that are likely to undergo subsequent wildfires of high severity. These results are consistent with previous research demonstrating that long TSLF (>10–20 years) are necessary to ensure that Mediterranean conifer species regenerate after wildfire (Fernández-García et al. 2019). Instead, short TSLF (<10 years) foster the dominance of shrub and native broadleaved tree species in Atlantic and Transition areas, whereas low-biomass ecosystems such as grassland dominated the Mediterranean area. Furthermore, we found that maximum vegetation productivity in bioregions with opposite environmental conditions (i.e., Atlantic and Mediterranean sites) was reached in TSLF of around 20 years. Remarkably, long TSLF under Mediterranean conditions buffered the negative effects of fire recurrence and fire severity of previous wildfire on vegetation productivity, as reported by Moghli et al. (2022), who evidenced that long TSLF may buffer ecosystem functioning from recurrent wildfires. In the Transition area, the same TSLF buffer mechanism was evidenced for FSPW.

Management implications and research future scope

Our findings suggest that in fire-prone ecosystems adaptive management strategies addressed to reduce the accumulation of highly flammable fuels and avoid or minimize the consequences of changing fire regimes must be developed considering particular and local environmental contexts, as well as their historical relationship with fire (Fernandes 2013; García-Llamas et al. 2020).

In Atlantic areas, a decrease in fire frequency has been observed over the last 35 years with the consequent accumulation of high amounts of flammable fuels, promoting significant worsening of winter and spring fire activity (Rodrigues et al. 2020). In fact, climate change is exacerbating this scenario by raising the number of dry days with elevated temperatures (Calheiros et al. 2021) leading to more severe fires during these seasons. In this context, it would be relevant to consider the application of management measures for dense and mature shrublands prone to high severity wildfires, especially in landscapes under risk of homogenization (Fernández-Alonso et al. 2017; García-Llamas et al. 2019). Land management strategies in areas that have not burned for long periods of time must be a priority to promote heterogeneous mosaics of vegetation types to also encourage heterogeneous patterns of fire behavior and severity across the landscape (Fernandes 2013). Particularly, prescribed burning treatments and clearing tasks at short time intervals can be useful for creating uneven-aged patches in shrublands and constraint fire behavior with lower loads (Valkó et al. 2014). A resilient well-managed landscape mosaic will not only act as a fire regulation service (Sil et al. 2019) but will also increase the provision capacity of other ecosystem services to the rural populations (Moghli et al. 2022). In addition, it would be important to close the loop caused by previous high severe wildfires in long TSLF situations, also observed in less productive environments such as the Transition and Mediterranean sites. The dangerous build-up of conifer-type fuels tending to be associated with a very dense understory (Fernández-García et al. 2019) might be addressed by following various silvicultural treatments: (i) pruning and removing of low-height branches to raise canopy base height and avoid ladder fuels (Fernández-Guisuraga et al. 2021a), (ii) reducing fuel accumulation in the understory to moderate fire intensity and crowning potential (Fernandes 2013), (iii) thinning the stand to create open patches (García-Llamas et al. 2020; Viedma et al. 2020), and (iv) reforesting with more fire-resistant vegetation-types as native broadleaved species (e.g., *Quercus* spp.) (Pausas and Keeley 2021; Huerta et al. 2022). Moreover, fire-smart management should be considered in Transition and Mediterranean areas to avoid fuel-type conversion by tree-shrubland transitions observed in high fire recurrence situations (Gil-Tena et al. 2016; Fernández-García et al. 2019). Management strategies to reduce the fire occurrence could be focused on (i) decreasing surface fuel accumulation by recovery of traditional land uses (e.g., grazing or forage production) (Moghli et al. 2022), (ii) encouraging multi-species forest arrangement (Fernandes 2013; García-Llamas et al. 2019), and (iii) promoting native tree growth in place of the shrubby undergrowth community (Fernández-García et al. 2019; Huerta et al. 2022).

Our research approach is adequate to understand how the influence of pre-fire vegetation characteristics on fire behavior is modulated by their interactions with fire regime attributes, which is critical for providing a more complete picture of land-management policies and strategies in southern European countries (Fernandes 2013; Fernández Guisuraga et al. 2023b). However, caution is needed given the temporal uncertainty in fire regimes that may be generated by post-fire human interventions (e.g., altering patterns in fuel composition and arrangement), which may become dependent on the environmental context (Rodrigues et al. 2020). Furthermore, in the bioregions analyzed, variables related to fire weather (e.g., wind speed) or drought conditions in the pre-fire vegetation play a key role in controlling fire severity patterns (Busby and Holz 2022; Fernández Guisuraga et al. 2023b), implying a high degree of variation in fire behavior both spatially and temporally. In this sense, further research should be conducted to link fire regime dynamics with changes in climate conditions, land use, and socioeconomic factors, as these frequently imply substantial modifications in fuel settings (Pausas and Keeley 2021) and, consequently, in fire behavior. Further validation of these results on a larger number of burned areas is also recommended, which would allow capturing a wider heterogeneity, both in landscape dynamics and fire behavior, within each environmental context. The need for such validations in different scenarios resides in the attenuation of the effect of local driving patterns (e.g., extreme heat waves), as eventual extreme weather conditions may dampen the influence of landscape-scale variables (Calherios et al. 2021; Evers et al. 2022). Finally, eventual biases involving training data of SVM land cover classifications and the inherent uncertainty in model predictions should be considered. Despite the high overall accuracy of the SVM classifier in this study (OA $\approx$ 90%), SVM performance and generality can be improved by considering more specific training data (e.g., differentiating pixels belonging to distinct shrubland types or maturity stage) and allowing for individual representation of certain landscape features (Basheer et al. 2022), such as recently burned areas. Moreover, the evaluation of the generalization capacity of SVM models to new areas outside the training dataset in this study would also help to better contextualize our findings and extrapolate our results regarding pre-fire landscapes prone to extreme fire behavior to broader geographic regions.

Conclusions

The present study provides new evidence in characterizing the importance of fire history patterns in modulating biophysical characteristics that shape landscapes prone to high fire severity across Atlantic-Transition-Mediterranean bioregions in the western Iberian Peninsula. Our analysis revealed a decrease in fire occurrence in all bioregions but a rise in fire severity under the wetter and more productive areas such as Atlantic contexts. Pre-fire fuel type and amount were the most relevant drivers of fire severity in all the bioregions analyzed, being structural variables related to the fuel horizontal distribution not influential. In this context, fire regime attributes strongly modulated pre-fire vegetation characteristics, and thus the behavior of subsequent wildfires, but following distinct mechanisms depending on the environmental context. In Atlantic sites, high fire recurrence, even at low to moderate fire severities, may induce transitions to shrubland stable ecosystem states with intermediate fuel amount that are prone to high fire severity in subsequent wildfires and perpetuate fire-prone vegetation types. The same behavior was evidenced in shrublands of Transition and Mediterranean sites when the previous wildfires had burned at high fire severity. Under the three environmental contexts, long time since last fire after high-severity wildfire disturbances may enhance fuel build-up in conifer-dominated ecosystems prone to subsequent severe fire behavior. In Atlantic bioregion, this situation is favored in less mesic areas with intermediate site productivity. Altogether, our results suggest that adaptive management actions in fire-prone ecosystems addressed to mitigate the consequences of changing fire regimes must be specifically developed considering the specific environmental contexts.

Abbreviations

TSLF	Time since the last fire
FSPW	Fire severity of previous wildfires
MAP	Mean annual precipitation
MADP10	Mean annual days with precipitation above 10 mm
MAT	Mean annual temperature
MADT25	Mean annual days with a temperature ≥ 25 ºC
ESA	European Space Agency
SNFI	Spanish National Forest Inventory
TM	Thematic Mapper
ETM	Enhanced Thematic Mapper
OLI	Operational Land Imager
GEE	Google Earth Engine
SNAP	Sentinel Application Platform
DTM	Digital terrain model
NIR	Near infrared
SWIR	Shortwave infrared
dNBR	Differenced normalized burn ratio
CBI	Composite Burn Index
LCC	Land cover class
SVM	Support vector machine
FCOV	Fraction cover vegetation
FAPAR	Fraction of absorbed photosynthetically active radiation
LAI	Leaf area index
SHEI	Landscape Shannon's evenness index
MNNdist	Mean distance to nearest neighbors
PA-ratio	Perimeter-area ratio index
MSI	Mean Shape Index
RTM	Radiative transfer models
SHDI	Shannon diversity index
EFFIS	European Forest Fire Information System
FMA	Frequentist model averaging
LMM	Linear mixed models

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00276-w.

Supplementary Material 1.

Authors' contributions

D.B.M, s.s.s, J.M.F.G, and L.C conceived and designed the experiment. D.B.M, and J.M.F.G analyzed the data. D.B.M wrote the manuscript. S.S.S, J.M.F.G, J.C.A, and L.C revised the manuscript. S.S.S, J.M.F.G and L.C coordinated the study.

Funding

This study was financially supported by the Spanish Ministry of Science and Innovation in the framework of LANDSUSFIRE project (PID2022-139156OB-C21, PID2022-139156OB-C22) within the National Program for the Promotion of Scientific-Technical Research (2021–2023); by the Spanish Ministry of Science and Innovation and the Next-Generation Funds of the European Union (EU) in the framework of the FIREMAP project (TED2021-130925B-I00); by the Regional Government of the Principality of Asturias, the Foundation for the Promotion of Applied Scientific Research and Technology in Asturias (FICYT) and the European Regional Development Fund (ERDF) in the framework of the REWILDING project (AYUD/2021/51261); by the Regional Government of Castile and León in the framework of the IA-FIREXTCyL project (LE081P23); and by Portuguese funds through FCT-Portuguese Foundation for Science and Technology, project UIDB/04033/2020 (DOI:https://doi.org/10.54499/UIDB/04033/2020). David Beltrán-Marcos was supported by a pre-doctoral contract from the Regional Government of Castile and León co-financed by the European Social Fund (EDU/556/2019).

Availability of data and materials

The datasets generated and used during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Received: 17 January 2024 Accepted: 10 April 2024
Published online: 13 May 2024

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