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Resilience of Mediterranean communities to fire depends on burn severity and type of ecosystem

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Abstract

Background: Burn severity plays an important role in shaping vegetation recovery in Mediterranean ecosystems. In the present study, we aimed to evaluate the influence of burn severity on short-term vegetation resilience in different ecosystems. We selected the Cabrera wildfire (northwest Iberian Peninsula), which affected shrubland, heathland, broomland, and oak woodland ecosystems in 2017. Immediately after the fire, we established 249 field plots within the burned area, in which burn severity was quantified by the application of the Composite Burn Index, differentiating three burn severity categories: low, moderate, and high. Moreover, we fixed 136 plots in unburned areas at two different maturity stages: young (unburned for the last 10 years) and old (unburned for the last 20 years) vegetation. Two years after the wildfire, we evaluated the total percentage cover of vegetation in four vertical strata ranging from 0 to > 4 m, as well as the cover of each woody species and total herbaceous vegetation in the lowest stratum (0–0.5 m). Resilience of the 2017 burned areas was interpreted in terms of the difference in vegetation cover and species composition in relation to the two different maturity stages.

Results: The results showed that the lowest stratum was the most resilient in the short term. In fact, all ecosystems presented high resilience of this stratum in low-severity areas. In shrublands and heathlands, this was mainly the consequence of the regeneration of herbaceous vegetation, as the dominant woody species did not fully recover in any of the burned situations (at least 21% and 11% less cover in shrubland and heathland burned plots compared to areas of young vegetation). Specifically, the resilience of this stratum was higher in broomlands and oak woodlands, mainly under moderate and high severities. In these ecosystems, woody dominant species recovered with respect to young vegetation at the 0–0.5-m level. Despite this, burn severity had a negative impact on the short-term resilience of the uppermost strata in broomlands and oak woodlands (cover values close to 0%).

Conclusions: The effects of burn severity on short-term vegetation resilience differed among type of ecosystems and vertical strata, so these results may constitute a starting point for the evaluation of the influence of burn severity and vegetation composition and structure on ecosystem resilience.

Keywords: Burn severity, Mediterranean ecosystems, Recovery, Vegetation resilience, Wildfires

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Resumen

Antecedentes: La severidad de los incendios juega un papel importante en la forma en que se recupera la vegetación de los ecosistemas mediterráneos. En el presente estudio, nos enfocamos en evaluar la influencia de la severidad de los incendios en la resiliencia de la vegetación a corto plazo. Para ello seleccionamos el incendio de Cabrera (noroeste de la Península Ibérica), que afectó ecosistemas de aulagar, brezal, escobar y robledal en 2017. Inmediatamente después del fuego, establecimos 249 parcelas dentro del área quemada, donde la severidad del fuego se cuantificó mediante la aplicación del índice de quema compuesto (*Composite Burn Index)*, diferenciando tres categorías: baja, moderada y alta. Además, fijamos 136 parcelas en áreas no quemadas diferenciando dos estadios de madurez: vegetación joven (sin quemar en los últimos 10 años), y vegetación vieja (sin quemar en los últimos 20 años). Dos años después del fuego, evaluamos el porcentaje total de cobertura de la vegetación en cuatro estratos verticales en un rango desde 0 a > 4 m, así como la cobertura de cada especie leñosa y del total de la vegetación herbácea en el estrato más bajo (0–0,5 m). La resiliencia de las áreas quemadas se interpretó en términos de diferencia en la cobertura de la vegetación y en la composición de especies con respecto a los dos estadios de madurez analizados.

Resultados: Los resultados demostraron que el estrato más bajo fue el más resiliente en el corto plazo. En efecto, todos los ecosistemas presentaron una alta resiliencia en este estrato en las áreas quemadas a baja severidad. En los matorrales y brezales esto fue principalmente consecuencia de la regeneración de la vegetación herbácea, ya que las especies leñosas dominantes no se recuperaron en ninguna de las situaciones quemadas (los aulagares y brezales quemados presentaron al menos una cobertura un 21% y 11% menor que las áreas de vegetación joven). Específicamente, la resiliencia de este estrato fue más alta en escobares y robledales, principalmente bajo severidades moderadas y altas. En estos ecosistemas, las especies leñosas dominantes se recuperaron con respecto a la vegetación joven en el estrato de 0 a 0,5 m. A pesar de ello, la severidad de la quema tuvo un impacto negativo en la resiliencia de corto plazo en el estrato más alto de escobares y robledales (con valores de cobertura cercanos a 0%).

Conclusiones: Los efectos de la severidad de la quema en la resiliencia de la vegetación a corto plazo difirió entre los tipos de ecosistemas y los estratos verticales; por lo tanto estos resultados pueden constituir un comienzo para evaluar la influencia de la severidad de la quema, y de la composición y estructura de la vegetación en la resiliencia de los ecosistemas.

Background

Wildfires are a frequent disturbance in the Mediterranean Basin (Pausas et al. 1999, 2008), where they play an important ecological role acting as landscape modifying agents (Fernandez-Anez et al. 2021). In these areas, fire regimes have led many species to adapt to coping with fire (Balao et al. 2018; Rundel et al. 2018) and, therefore, Mediterranean ecosystems are often considered very resilient to wildfires (Calvo et al. 2008, 2013). In this context, the response to disturbances such as fire and the ability to maintain their structure and ecological processes under changing conditions determine the stability of ecosystems (Rykiel 1985; Mitchell et al. 2000; Orwin and Wardle 2004; Shade et al. 2012), which can be measured in terms of resistance and resilience (Lamothe et al. 2019). Resistance is defined as the ability of a system to withstand perturbations, while resilience is considered as the capacity to absorb changes and recover after disturbances, so that the ecosystem continues to maintain the same function and structure (Holling 1973; Pimm 1984; Walker et al. 2004; Sánchez-Pinillos et al. 2019; Steel et al. 2021). Specifically, there are mainly two ways of defining and understanding the concept of resilience: ecological and engineering resilience. Ecological resilience is the magnitude of disturbance that an ecosystem can withstand without altering its structure and processes, so that it is able to recover its original state (Gunderson 2000; Arani et al. 2021). Engineering resilience measures the capacity of an ecosystem to recover the characteristics present prior to the disturbance (Lloret et al. 2022), so this approach enables resilience to be studied in terms of the recovery of different ecosystem variables (Sánchez-Pinillos et al. 2019). Therefore, tolerance to change and, if it occurs, the degree in which pre-fire vegetation parameters are restored will define the stability of the system (Halpern 1988). In this context, disturbance regimes have important effects on plant communities, affecting both resistance and resilience (Enright et al. 2014). In the Mediterranean Basin, climatic variations, land use changes, and the subsequent increases in fuel amount and continuity act as the main drivers in the alteration of fire regimes (Moreno et al. 2014). All these drivers have relevant effects on burn severity, fire frequency, and burned area (Pausas 2004; Moreira et al. 2011; Pereira et al. 2016).

Severe wildfires cause important shifts in ecosystems, mainly because of the removal of vegetation (Key and Benson 2006) and the alteration of soil properties (Fernández-García et al. 2019a, 2019b). In fact, burn severity has relevant implications in the development and recovery of plant communities (Kimura and Tsuyuzaki 2011). In this sense, the higher consumption of vegetation forces plant communities to recover from an initial stage, exerting more negative effects on the ecosystem (González-De Vega et al. 2016). Thereafter, the effects of burn severity may persist after perturbation, influencing the post-fire response of plants (González-De Vega et al. 2018; Fernández-García et al. 2019c; Huerta et al. 2021), even conditioning vegetation resilience in subsequent fires (Collins et al. 2018).

High recurrence of fires also affects the secondary succession of the community, preventing the vegetation from advancing to more mature stages (Santana et al. 2010). Thus, it seems that high-recurrence fire regimes have exerted a significant effect on the dominant vegetation type in these areas. In this context, the presence of different reproductive strategies facilitates the post-fire recovery of vegetation, not only under fire regimes of high severity, but also after recurrent wildfires (Fernández-García et al. 2019d, 2020; García-Llamas et al. 2020; Fernández-García et al. 2021; Huerta et al. 2021). In such a way, many species have the ability to regenerate by vegetative resprout, a regenerative trait that could facilitate the regeneration of vegetation under high severity and recurrence fire regimes (Fernández-García et al. 2020). At the same time, post-fire recovery can be favored by the heat-stimulated germination of dormant seeds that are resistant to high temperatures (Lamont et al. 2019). Thanks to these adaptive traits, shrub vegetation tends to regenerate quickly after the fire even in high-severity situations, in some cases conditioning the recovery of tree species, which are usually less resilient to severe fires (Crotteau et al. 2013; González-De Vega et al. 2016; Minor et al. 2017). Therefore, it is common for tree vegetation to end up being replaced by shrub communities in areas that suffer severe and recurrent fires (Kowaljow et al. 2018; Stevens-Rumann and Morgan 2019).

Apart from fire regime parameters, environmental variables such as soil nutrient content and climatic conditions, as well as pre-disturbance vegetation characteristics, may condition the post-fire response of vegetation (Calvo et al. 2003; Fernández-García et al. 2020, 2021). Thus, vegetation recovery will be shaped by the successional stage of the community, which could also have an effect on the burn severity level reached during the fire (López-Poma et al. 2014). The successional stage of vegetation will condition the amount of fuel that can be consumed, its spatial continuity, and other characteristics such as humidity, which are highly related to the damage caused by the fire in the ecosystem (Baeza et al. 2002, 2007). In fact, the risk of severe wildfires increases with high vertical and horizontal fuel continuity, which is very frequent in young woodlands (Fernández-Guisuraga et al. 2021), so vegetation composition and structure determine ecosystem functions and post-fire resilience (González-De Vega et al. 2016).

Resilience can be measured by analyzing the recovery of vegetation variables such as the fraction of vegetation cover or species composition with respect to pre-disturbance situations (Halpern 1988; Wittenberg et al. 2007; Schaffhauser et al. 2008; Coop et al. 2016). The study of post-fire resilience is a highly relevant issue in the Mediterranean Basin, since it offers an approximation of the recovery of ecosystem services that are of value to society, and whose provisioning could be threatened as a consequence of current fire regimes and global change (Puerta-Piñero et al. 2012; Seidl et al. 2016). This approach can also constitute a support tool for the application of pre- and post-fire management strategies aimed at fire risk reduction and ecosystem recovery, which promote fire-resilient environments (Valdecantos et al. 2009; Fernandes 2013; González-De Vega et al. 2016). Many authors have focused on the analysis of vegetation resilience to wildfires in the Mediterranean Basin (Arianoutsou 2004; Kazanis and Arianoutsou 2004; Valdecantos et al. 2009; Puerta-Piñero et al. 2012) and the study of how it is conditioned by burn severity (Fernandez-Manso et al. 2016; González-De Vega et al. 2016). However, we found no evidence of studies evaluating short-term resilience as a function of burn severity in various types of Mediterranean ecosystems with respect to vegetation at different maturity stages.

The main objective of this study was to assess the effects of burn severity on short-term (2 years after fire) engineering resilience of vegetation in different forest ecosystems (shrubland, heathland, broomland, and oak woodland) in relation to two maturity stages: young vegetation, unburned at least in the last 10 years, and old vegetation, unburned at least in the last 20 years. Specifically, this research aimed to (1) analyze the recovery of the total vegetation cover by vertical strata as a function of burn severity with respect to young and old maturity stages and (2) evaluate how the specific composition of the lowest stratum (0–0.5 m) varies in areas burned at different severity levels in comparison with unburned areas.

We hypothesize that the development capacity of herbaceous vegetation during the first stages of post-fire succession (Calvo et al. 1999; Castro and Leverkus 2019), the high productivity and rapid growth of shrub species (Montès et al. 2004; Crotteau et al. 2013), and the presence of adaptive traits that make it easy for vegetation to regenerate after the fire (Calvo et al. 1991; Tárrega et al. 1992; Bellingham and Sparrow 2000; Calvo et al. 2003; Moreira and Pausas 2012; Clarke et al. 2013; Huerta et al. 2021) would favor the short-term recovery of the lowest stratum of vegetation even in high-severity situations (González-De Vega et al. 2018; Fernández-García et al. 2020; Huerta et al. 2021). However, understory and canopy vegetation may respond differently to fire, mainly because of variations in their function, structure, and productivity, which could affect their regeneration capacity (Meng et al. 2018). In this context, the loss of canopy after moderate-high-severity fires would condition vegetation to recover from a more primitive stage, with a subsequent reduction in short-term resilience (González-De Vega et al. 2016). On the contrary, less severe wildfires that leave remaining canopy vegetation would facilitate the recovery of the tree community (Graham et al. 2004).

Methods

Study area

The present study was conducted in the Cabrera mountain range, located in the province of León (NW Iberian Peninsula, Spain). This area was affected by a wildfire in summer 2017 that burned 9939 ha (Fig. 1).

This area has mountainous orography, with altitudes ranging from 836 to 1938 m. The climate is Mediterranean, with dry temperate summers (AEMET-IM 2011). Average annual temperature and precipitation are 9 °C and 700–800 mm, respectively (Ninyerola et al. 2005). The predominant lithologies in this area are slates, sandstones, and quartzites from the Ordovician period (GEODE 2021). Soils are acidic, with sandy loam and sandy clay loam texture, mainly classified as Lithic Leptosols and Humic Cambisols (IUSS-WRB 2015).

Fire regimes in the study area were previously described by Fernández-García et al. (2019d) (Additional file 1: Fig. 1.1). According to these authors, half of the area affected by the 2017 wildfire had burned in the

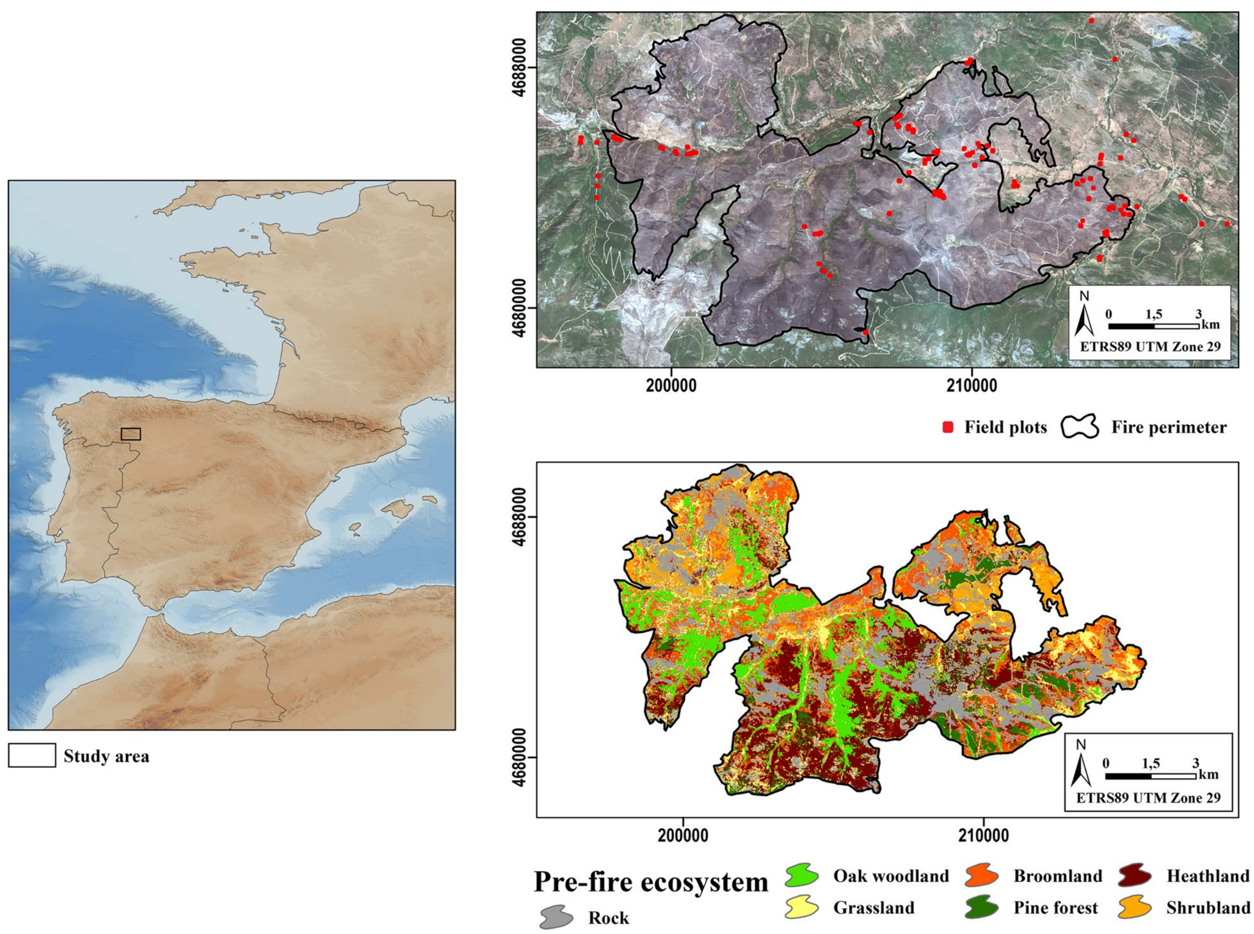

Fig. 1 Location of the study area in the Iberian Peninsula (left). The panels on the right show the fire perimeter and field plot location, represented on a post-fire RGB image (top) and pre-fire ecosystem classification (bottom)

previous 20 years. Four fire recurrence categories were identified in the 1984–2017 period, ranging from areas burned once to those burned four or more times, and the percentage of area occupied by each recurrence category was similar within the 2017 fire perimeter. Likewise, a similar distribution of fire severity categories was observed, although the highest severities were found in areas burned 15–20 years ago (Additional file 1: Fig. 1.1).

The diverse fire history in the Cabrera mountain range has led to different maturity stages of the dominant vegetation communities, which are mainly *Genista hystrix* Lange shrublands and *Erica australis* L. heathlands (García-Llamas et al. 2020). In fact, this area is characterized by a heterogeneous landscape, also dominated by *Cytisus scopariu*s (L.) Link broomlands and *Quercus pyrenaica* Willd. oak woodlands, with *C. scopariu*s, *E. australis*, and *Pterospartum tridentatum* (L.) Willk. as the main species of the understory vegetation (Fig. 1).

Field sampling

Field samplings were carried out 2 years after the 2017 wildfire, during the months of June and July 2019. We randomly established a total of 385 field plots (2 m × 2 m) (Fig. 1) (Huerta et al. 2021), covering areas burned in 2017, areas of young vegetation, unburned at least in the last 10 years, and areas of old vegetation, unburned at least in the last 20 years.

Burn severity was quantified in each 2017 burned plot using the Composite Burn Index (Key and Benson 2006), following the methodology adapted by Fernández-García et al. (2018). Different burn severity indicators (litter consumed, char depth and soil color, foliage consumed, char height, tree mortality, and canopy color) were visually evaluated from a score of 0 (unburned) to 3 (maximum burn severity) in 5 vertical strata of soil and vegetation. The average of all the evaluated strata was calculated to obtain the final score of the plot, differentiating three levels of burn severity: low, moderate, and high.

Vegetation field monitoring

Sampling plots were randomly distributed in accessible zones of the most characteristic ecosystems in this area (Fig. 1): *G. hystrix* shrublands (13 at low severity, 22 at moderate severity, 11 at high severity, 15 of young vegetation, and 22 of old vegetation), *E. australis* heathlands (16 at low severity, 27 at moderate severity, 28 at high severity, 20 of young vegetation, and 20 of old vegetation), *C. scoparius* broomlands (11 at low severity, 23 at moderate severity, 30 at high severity, 20 of young vegetation, and 20 of old vegetation), and *Q. pyrenaica* oak woodlands (19 at low severity, 23 at moderate severity, 26 at high severity, and 19 of young vegetation). Only young stands were considered in the oak woodland ecosystem, since most of the oak woodlands present in the study area had a pole stage structure, not reaching a clear structure of timber or old forest stage. In each plot, the total percentage cover of vegetation was visually estimated in different vertical strata: 0–0.5 m, 0.5–1 m, 1–4 m, and > 4 m. At the 0–0.5-m level, we evaluated separately the percentage cover of each woody species and the total cover of herbaceous vegetation in order to analyze the specific composition of each ecosystem as a function of burn severity.

Data analysis

The effect of burn severity on vegetation resilience was evaluated 2 years after the wildfire in each type of ecosystem. We carried out a preliminary analysis of the data to determine the distribution of the studied variables. Therefore, a Shapiro–Wilk normality test was performed, which showed that many of the variables followed a nonnormal distribution. Thus, we used generalized linear models by applying the *glm* function with a quasi-Poisson error distribution (*log* link function) to account for overdispersion. Model coefficients were obtained from the model summary, and the explained deviance and significance of model terms were obtained from the ANOVA (Fisher test) of the model. The statistical analyses were performed with R software (R Core Team 2021) using *car* (Fox and Weisberg 2019), *ggplot2* (Wickham 2016), and *sjPlot* (Lüdecke 2021) packages. We took burn severity categories as predictor variables: (1) low severity, (2) moderate severity, (3) high severity, (4) unburned in the last 10 years, and (5) unburned in the last 20 years. The response variable in the model was the percentage cover of vegetation for each vertical stratum: (1) 0–0.5 m, (2) 0.5–1 m, (3) 1–4 m, and (4) > 4 m. We assumed that differences were significant at a p value < 0.05.

We also performed a correspondence analysis in order to relate burn severity categories (low severity, moderate severity, high severity, unburned in the last 10 years, and unburned in the last 20 years) to the response of every woody species and the total of herbaceous vegetation in the lowest stratum (0–0.5 m) of each ecosystem. The correspondence analysis was performed using the mean cover values of every woody species and herbaceous vegetation for each burn severity category. This analysis was carried out with the statistical PAST 4.05 software (Hammer et al. 2001).

Results

Vegetation recovery by vertical strata

In the lowest stratum (0–0.5 m), young and old shrublands presented a total cover of 60–70% (Fig. 2). In this stratum, the total cover showed better post-fire recovery under the effect of high burn severity, even exceeding the cover of the oldest communities. In contrast, we observed

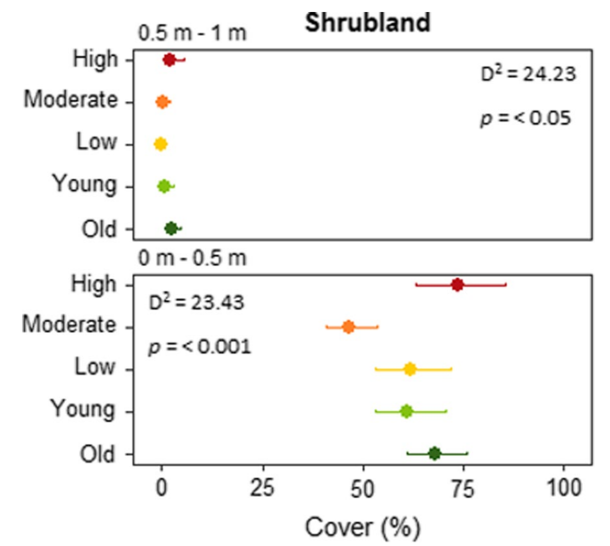

Fig. 2 Average cover (%) of vegetation and confidence intervals (±95%) for each burn severity category (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) at every vertical stratum present in the shrubland ecosystem (0–0.5 m and 0.5–1 m). D^2 values indicate the deviance explained by the generalized linear models; *p* values < 0.05 show the presence of significant differences between burn severity categories. Non-overlapping confidence intervals show the presence of significant differences between burn severity categories

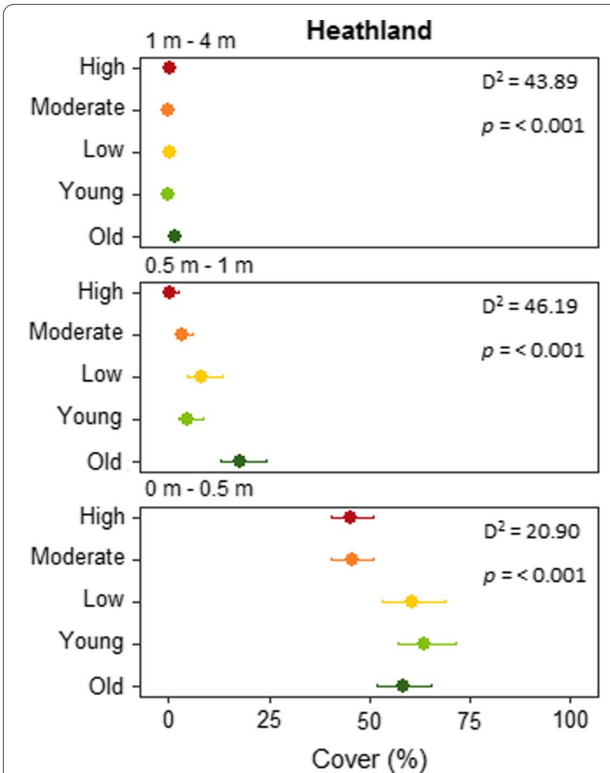

Fig. 3 Average cover (%) of vegetation and confidence intervals (±95%) for each burn severity category (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) at every vertical stratum present in the heathland ecosystem (0–0.5 m, 0.5–1 m, and 1–4 m). D^2 values indicate the deviance explained by the generalized linear models; *p* values < 0.05 show the presence of significant differences between burn severity categories. Non-overlapping confidence intervals show the presence of significant differences between burn severity categories

significantly lower recovery in areas of moderate severity ($p < 0.001$). Vegetation cover in the 0.5–1-m stratum was low in all situations, although it also increased in high-severity areas (Fig. 2, Additional file 2: Table 2.1).

In heathlands, the cover of young and old vegetation in the lowest stratum (0–0.5 m) was close to 60% (Fig. 3). In the 0.5–1-m stratum, old vegetation reached almost 20%, compared to the low cover of young vegetation. Vegetation exceeded 1 m high in old communities only. In the 0–0.5-m stratum, the total vegetation cover of heathlands burned at low severity was completely recovered 2 years after the fire, whereas it was significantly lower in moderate- and high-severity situations ($p < 0.001$). In the second vertical stratum (0.5–1 m), vegetation recovery significantly decreased with burn severity (Fig. 3, Additional file 2: Table 2.1).

In the lowest stratum (0–0.5 m) of the broomland ecosystem, young and old vegetation showed cover percentages of 80% and 70%, respectively. In this type of ecosystem, vegetation reached heights of 1–4 m, with covers of almost 50% in old communities. The cover of the younger vegetation showed a more pronounced reduction from the lower to the upper stratum (Fig. 4). Recovery in the 0–0.5-m stratum was high, especially under the moderate-severity situation, but without significant differences among burned, young and old communities. In the two upper strata, we did not observe recovery 2 years after the fire, with significantly lower cover values in burned areas (Fig. 4, Additional file 2: Table 2.1).

Young oak woodlands presented vegetation cover percentages close to 60% in the 0–0.5-m and 1–4-m strata. These values were around 30% and 20% in the 0.5–1-m and >4-m strata, respectively (Fig. 5). Recovery in the lowest stratum (0–0.5 m) was very high in all severity situations 2 years after the fire. In fact, we found significantly higher cover values in areas burned with moderate and high severities than in young oak woodlands ($p < 0.001$). In the second vertical stratum (0.5–1 m), there was a significant increase in vegetation recovery with burn severity ($p < 0.05$). The 1–4-m stratum did not show recovery in any of the burned situations ($p < 0.001$). In the uppermost stratum (>4 m), moderate and high

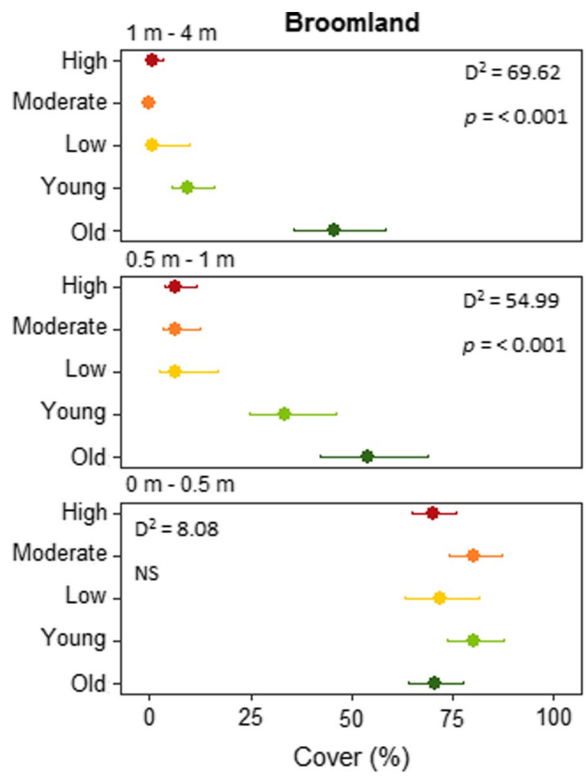

Fig. 4 Average cover (%) of vegetation and confidence intervals (± 95%) for each burn severity category (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) at every vertical stratum present in the broomland ecosystem (0–0.5 m, 0.5–1 m, and 1–4 m). D^2 values indicate the deviance explained by the generalized linear models; *p* values < 0.05 show the presence of significant differences between burn severity categories; NS indicates the absence of significant differences. Non-overlapping confidence intervals show the presence of significant differences between burn severity categories

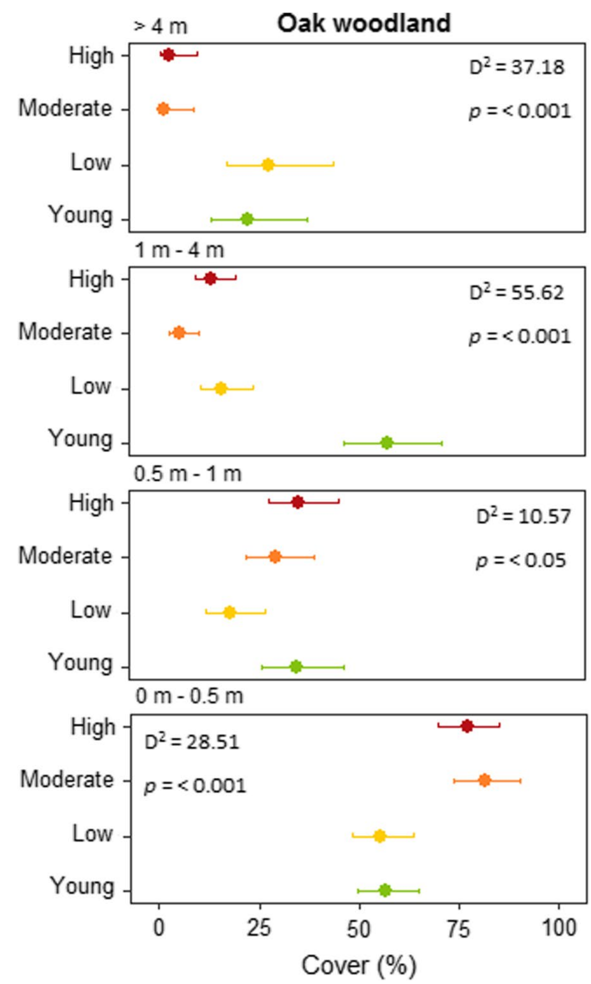

Fig. 5 Average cover (%) of vegetation and confidence intervals (± 95%) for each burn severity category (low severity, moderate severity, high severity, and unburned in the last 10 years (young vegetation)) at every vertical stratum present in the oak woodland ecosystem (0–0.5 m, 0.5–1 m, 1–4 m, and > 4 m). D^2 values indicate the deviance explained by the generalized linear models; *p* values < 0.05 show the presence of significant differences between burn severity categories. Non-overlapping confidence intervals show the presence of significant differences between burn severity categories

burn severities had a significant negative influence on vegetation cover ($p < 0.001$) (Fig. 5, Additional file 2: Table 2.1).

Changes in the specific composition of the 0–0.5-m stratum

The correspondence analysis performed for the lowest stratum of the shrubland ecosystem (Fig. 6a) showed that axis I discriminated between young and old vegetation and burned plots. Both young and old communities were associated with higher cover of the dominant species, *G. hystrix*, which did not recover 2 years after the fire (Table 1). Axis II separated moderate severity from low- and high-severity plots, characterized by higher percentages of herbaceous vegetation (Fig. 6a, Table 1).

In heathlands, we observed a relationship between young and old communities and the species *E. australis* and *P. tridentatum* (Fig. 6b). Neither of these species fully recovered in the short term. However, both increased their cover values with burn severity, especially *P. tridentatum*, which showed a strong association with more severely affected areas (Fig. 6b, Table 1). On the other hand, low-severity plots were related to the highest cover of herbaceous species (Fig. 6b, Table 1).

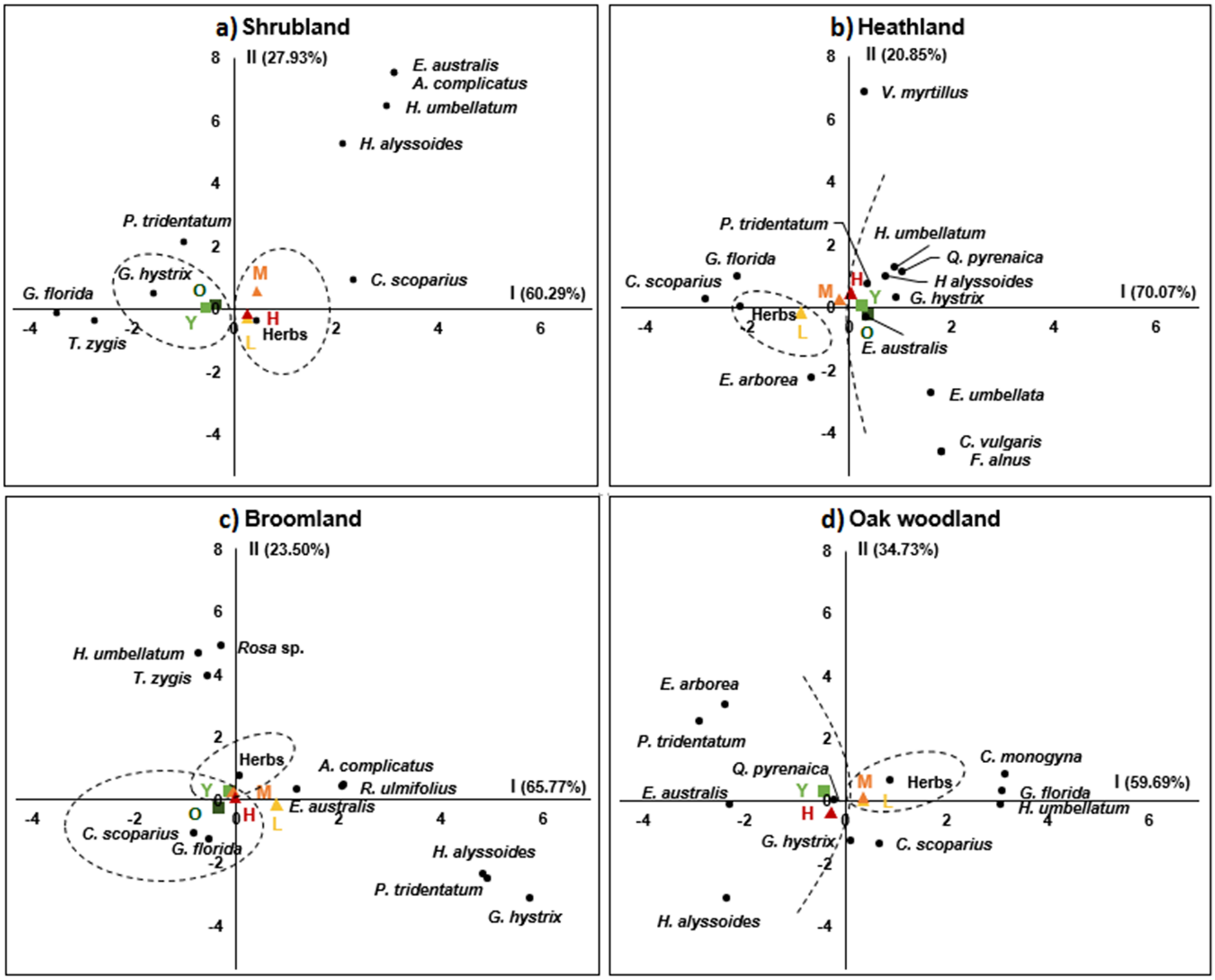

Fig. 6 Location of each woody species, herbaceous vegetation, and burn severity categories (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) in the plane defined by the first two axes of the correspondence analysis developed for the lowest stratum vegetation (0–0.5 m) in each ecosystem (**a** shrubland, **b** heathland, **c** broomland, and **d** oak woodland). L low severity, M moderate severity, H high severity, Y young vegetation, O old vegetation. Values in brackets correspond to the percentage of total variance explained by each axis. The average cover per burn severity category of each woody species and herbaceous vegetation in the 0–0.5-m stratum are shown in Additional file 3: Table 3.1

Young and, especially, old vegetation in the lowest stratum of the broomland ecosystem were associated with the presence of *C. scoparius* and *G. florida* species (Fig. 6c, Table 1). *C. scoparius* also showed a close relationship with high-severity plots (Table 1). In axis II, an association between young vegetation and moderate severity was observed since both situations presented high covers of herbaceous species (Fig. 6c, Table 1).

The correspondence analysis developed for the lowest understory stratum (0–0.5 m) of the oak woodland ecosystem (Fig. 6d) clearly differentiated low and moderate severities, associated with the high cover of herbaceous vegetation, from young vegetation and high-severity plots, characterized by a higher cover of the dominant species, *Q. pyrenaica* (Table 1).

Discussion

In the present study, we evaluated the influence of burn severity on short-term vegetation resilience in fire-prone Mediterranean ecosystems. We focused on a heterogeneous landscape in the Iberian Peninsula, dominated by four types of ecosystems (shrubland, heathland, broomland, and oak woodland) distributed in mosaic patches with various stages of regeneration in each one. This type of distribution is the consequence of different land uses, fire history, and environmental conditions

Table 1 Average cover values (%) for each burn severity category (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) of every woody species and herbaceous vegetation at the lowest stratum (0–0.5 m) in each type of ecosystem (shrubland, heathland, broomland, and oak woodland)

Vegetation	Burn severity	Shrubland	Heathland	Broomland	Oak woodland
Woody species					
Cytisus scoparius	HS	1.82 (4.92)	0.43 (1.90)	20.43 (17.18)	17.96 (19.74)
	MS	1.02 (4.53)	0.56 (1.61)	15.28 (13.49)	15.45 (16.34)
	LS	-	1.52 (2.82)	8.73 (19.59)	10.63 (9.17)
	YV	-	-	20.90 (18.44)	3.91 (7.92)
	OV	-	-	49.13 (41.05)	NA
Erica australis	HS	-	16.84 (10.39)	0.78 (2.08)	5.43 (9.56)
	MS	0.01 (0.05)	14.44 (9.38)	-	0.01 (0.05)
	LS	-	13.80 (13.26)	0.25 (0.75)	0.72 (3.15)
	YV	-	27.69 (19.37)	0.13 (0.56)	6.08 (14.63)
	OV	-	40.56 (14.30)	-	NA
Genista florida	HS	-	-	5.54 (11.92)	-
	MS	-	0.33 (1.68)	7.51 (15.26)	0.27 (1.30)
	LS	-	0.20 (0.40)	6.64 (10.97)	0.46 (1.73)
	YV	0.02 (0.06)	-	8.96 (22.42)	-
	OV	-	-	21.91 (33.59)	NA
Genista hystrix	HS	8.36 (3.92)	0.77 (2.05)	-	0.35 (1.71)
	MS	5.32 (5.53)	0.44 (1.93)	-	0.37 (1.19)
	LS	5.75 (5.73)	-	1.30 (2.89)	-
	YV	29.93 (24.20)	0.20 (0.89)	0.01 (0.06)	0.11 (0.46)
	OV	29.42 (14.70)	1.31 (3.71)	-	NA
Pterospartum tridentatum	HS	0.57 (0.75)	26.88 (17.05)	0.30 (1.15)	1.67 (2.48)
	MS	1.41 (2.61)	16.39 (9.24)	-	-
	LS	-	11.78 (10.12)	1.86 (4.15)	-
	YV	1.63 (4.31)	38.13 (14.78)	0.04 (0.17)	6.13 (11.02)
	OV	-	30.24 (13.94)	-	NA
Quercus pyrenaica	HS	-	0.04 (0.24)	-	46.94 (27.97)
	MS	-	-	-	40.26 (21.28)
	LS	-	-	-	27.04 (15.91)
	YV	-	-	-	48.09 (20.52)
	OV	-	0.04 (0.17)	-	NA
Herbaceous species	HS	65.27 (10.57)	7.46 (9.68)	42.98 (16.65)	14.72 (14.30)
	MS	36.43 (14.16)	9.78 (9.22)	59.70 (21.84)	39.65 (23.89)
	LS	57.79 (17.91)	26.55 (13.82)	42.27 (32.00)	21.74 (17.46)
	YV	41.33 (12.80)	5.48 (7.00)	71.75 (12.74)	23.53 (11.27)
	OV	43.64 (17.12)	2.76 (6.20)	58.19 (27.06)	NA

The values in brackets correspond to the standard deviation. A dash (-) indicates that the species is not present. Species that do not exceed 10% cover in any of the situations are not included in this table. All species are represented in Additional file 3: Table 3.1

LS low severity, *MS* moderate severity, *HS* high severity, *YV* young vegetation, *OV* old vegetation, *NA* not applicable

(García-Llamas et al. 2020). Based on our results, all studied ecosystems showed high recovery of the lowest vegetation stratum 2 years after the fire, mainly due to the rapid regeneration of herbaceous vegetation and the active regrowth of woody species. The highest resilience values were observed in broomlands and oak woodlands, since the cover in the lowest stratum of the dominant woody species was recovered at a high-severity level. Vegetation resilience tended to decrease from the lower to the upper strata, but the response to burn severity differed according to the dominant vegetation type.

At the 0–0.5-m level, herbaceous vegetation played a key role in the recovery of all studied ecosystems. In fact, many authors have already documented the rapid regeneration and dominance of herbaceous vegetation during the early stages of post-fire succession (Kazanis and Arianoutsou 1996; Calvo et al. 2002a, 2003; González-De Vega et al. 2016, 2018). Herbaceous vegetation is characterized by pioneer and fast-growing species (Castro and Leverkus 2019), which, after the fire, find favorable conditions to proliferate until woody vegetation begins to dominate (Calvo et al. 1999; Álvarez et al. 2009). In this sense, the growth of herbaceous vegetation is favored by the efficient uptake through surface roots of soil nutrients deposited by ashes, thermal stimulation of the soil seed bank, and decrease in competition for light due to open gaps in vegetation (Calvo et al. 2002b, 2003; Álvarez et al. 2009). Therefore, it is normal for the colonization of herbaceous species to occur early, even after moderate-high-severity fires (González-De Vega et al. 2018), while the dominance of woody vegetation is typical of advanced stages of post-fire succession (Calvo et al. 1999).

In our study area, shrublands are degraded communities dominated by *G. hystrix*. This is a facultative seeder species, with the ability to regenerate by vegetative resprout and by seeds (Pérez-Fernández and Lamont 2016). According to Bradbury et al. (2016), species with both reproductive mechanisms could experience better post-fire regeneration. Despite this, *G. hystrix* showed low short-term resilience in all severity situations. Therefore, the high regeneration of herbaceous species and slower recovery of shrub vegetation could lead to further degradation of this community, even compromising the resilience of these ecosystems adapted to frequent wildfires (Keeley 2005).

In heathlands, we observed that 2 years after the fire, *E. australis* had 50% cover present in the youngest communities. Besides, an elevated recovery of the species *P. tridentatum* was found under the effect of high severity in this ecosystem. Both species are typical resprouters (Cruz et al. 2003; Reyes et al. 2009), so they have storage organs from which carbohydrate and nutrient reserves are mobilized after fire in order to regenerate vegetatively (Moreira et al. 2012; Clarke et al. 2013). Thus, many authors have highlighted resprouting as a reproductive strategy that facilitates the post-fire regeneration capacity of vegetation (Calvo et al. 1998; Pausas and Vallejo 1999; Calvo et al. 2002a, 2002c; Lamont et al. 2011), as well as a good strategy to face severe disturbances (Clarke et al. 2013; Fernández-García et al. 2020; Huerta et al. 2021) and promote resilience (Nemens et al. 2019; Menges et al. 2021). In such a way, *E. australis* is able to resprout quickly after fire, but interspecific competition may affect its recovery (Calvo et al. 1998). In fact, *P. tridentatum* showed a higher percentage cover than *E. australis* in areas of high burn severity. Reyes et al. (2009) found that *P. tridentatum* is strongly stimulated by fire in the NW of the Iberian Peninsula, and its ability to resprout can be enhanced even in areas that suffer frequent wildfires. Thus, it seems that *P. tridentatum* and herbaceous species made an important contribution to the short-term recovery of heathland vegetation in high- and low-severity areas, respectively. Other studies demonstrated that *E. australis* begins to dominate from the third year onwards, since herbaceous cover starts to decrease, and competition with other woody species becomes stronger (Calvo et al. 2002a, 2005).

In general, vegetation in the lowest stratum of the broomland ecosystem seems to be more resilient in the short term. In this type of ecosystem, not only is it common to observe significant growth of herbaceous species as we found in the present study, but brooms also tend to show fast regeneration (Provendier and Balandier 2008), mainly due to the characteristic regenerative traits of these species (Bradbury et al. 2016; Huerta et al. 2021). *C. scoparius* and *G. florida* are Leguminosae species that can regenerate by vegetative resprout or by seeds and whose germination could be stimulated by high temperatures (Tárrega et al. 1992). Thus, we found that *C. scoparius* cover increased with burn severity, recovering with respect to the cover of the younger community. In spite of this, the reduction in vegetation covers observed from the lower to the upper stratum indicates that 2 years is not enough to achieve good recovery of the higher vegetation in this ecosystem, which makes the upper vertical strata less resilient in the short term.

In the oak woodland ecosystem, we observed high resilience in the two lowest strata, especially under moderate and high severities. Apart from the influence of herbaceous vegetation, this was mainly due to the rapid regeneration of *Q. pyrenaica*, whose cover increased with burn severity recovering with respect to young oak communities. The regeneration mechanism of this species, which is able to resprout by belowground buds located in the rhizome and roots, enhances post-fire regeneration during the early stages after disturbance (Calvo et al. 1991, 2003, 2005), even under conditions of high burn severity (Huerta et al. 2021). Furthermore, it must be considered that pre-fire fuel characteristics such as high oak density, which is typical in young stands, could have contributed to reaching high-severity levels in these areas, also conditioning the post-fire regeneration of the dominant vegetation (Baeza et al. 2002; Calvo et al. 2003; Fernández-García et al. 2019c; Fernández-Guisuraga et al. 2021). In fact, the high short-term resilience shown by the two lower strata in the most severely affected areas could be influenced by the remaining canopy gaps in the highest strata (Meng et al. 2018). Open spaces in the tree canopy would increase the availability of light for herbaceous and woody understory vegetation, accelerating the recovery processes in the lower strata (Bartels et al. 2016).

Thus, oak woodlands showed low resilience of the 1–4-m stratum of vegetation under all severity situations, but vegetation cover in low-severity areas of the uppermost stratum (> 4 m) exceeded the cover present in young communities. However, moderate- and high-severity areas did not show recovery of the > 4 m stratum 2 years after the fire. Therefore, vegetation resilience in the higher strata seems to be more negatively affected by the high burn severity levels reached by fire. In this context, low-severity wildfires are usually characterized by tree survival, leaving remaining vegetation at the canopy level, which makes it easier for vegetation in the upper strata to return to pre-fire situations (Graham et al. 2004; Keeley 2009). In contrast, severe fires normally consume most of the canopy vegetation (Key and Benson 2006; Keeley 2009; Fernández-García et al. 2018), so recovery should start from a more initial phase (González-De Vega et al. 2016), which could explain the lower short-term resilience of the higher strata in areas of moderate and high severity.

Our results indicated that burn severity, species composition, and vegetation structure had significant effects on short-term resilience in different fire-prone Mediterranean ecosystems. In general, we found that vegetation resilience decreased from the lowest to the highest strata. Specifically, all ecosystems presented high resilience of the lowest stratum in low-severity burned areas. Despite this, the cover of the main dominant species showed a tendency to increase in areas of high burn severity compared to low and moderate severities. In general, this can be attributed to plant functional traits adaptive to severe fires, as previously observed in the Cabrera mountain range (Huerta et al. 2021). In particular, reproductive strategies such as resprouting and heat-stimulated germination are considered a fitness advantage to face recurrent and severe wildfires (Lamont et al. 2011; Moreira and Pausas 2012; Fernández-García et al. 2020). Thus, the dominant woody vegetation type exerted a strong influence on the short-term response of vegetation, showing two main patterns of resilience. In shrublands and heathlands, resilience was more influenced by the regeneration of herbaceous vegetation than by the recovery of woody species. In broomlands and oak woodlands, the high recovery of the woody dominant species had an important effect on short-term resilience, especially under moderate and high severities.

Climate change may increase the vulnerability of ecosystems to suffer more severe, frequent, and large wildfires (Busby et al. 2020), affecting the potential losses caused by fire (Lecina-Diaz et al. 2021). Specifically, in the present study, we identified shrublands and heathlands as the least resilient ecosystems to high burn severity. Thus, knowledge of the short-term resilience of different fire-prone ecosystems is essential for implementing management strategies aimed at reducing the negative effects of wildfires and restoring burned areas (Pereira et al. 2021). These strategies can be oriented to reduce the susceptibility of ecosystems to severe fires, increase the adaptive capacity of the ecosystems, and mitigate the effects of wildfires in burned areas (Lucas-Borja et al. 2019; Lecina-Diaz et al. 2021).

Studying the short-term effects of burn severity on vegetation composition and structure in different fire-prone Mediterranean ecosystems provides an approximation of the most vulnerable vegetation types and the species that are more resilient to high-severity wildfires. This is necessary for the implementation of optimal management strategies aimed at reducing fire risk and increasing the resilience of fire-prone Mediterranean ecosystems, which is essential in the current framework of change (Valdecantos et al. 2009; Fernandes 2013).

Despite the large importance of acknowledging short-term vegetation resilience, this type of research may offer a limited approach and does not fully inform about ecosystem resilience, since woody species required longer periods to recover, especially the upper vegetation strata (Calvo et al. 1998, 1999). Therefore, we recommend complementing the present study with medium- and long-term analysis of vegetation resilience (Moya et al. 2018) in order to evaluate the global response of vegetation over time as a function of burn severity.

Conclusions

This study provides evidence of the influence of burn severity on short-term vegetation resilience in Mediterranean fire-prone ecosystems with different vegetation compositions and structures.

In general, the lowest stratum of vegetation was the most resilient 2 years after the fire. All the studied ecosystems showed high resilience of this stratum under low-severity situations. Despite this, the effect of burn severity on short-term resilience varied among type of ecosystems and vertical strata of vegetation. The recovery of the ecosystems in less advanced successional stages, such as shrublands and heathlands, was mainly determined by the rapid regeneration of herbaceous vegetation, since the dominant woody species did not recover at the short term.

A higher resilience of vegetation was observed in the lowest stratum of broomlands and oak woodlands, communities that represent more advanced successional stages in these areas. However, the two uppermost strata of these ecosystems showed lower short-term resilience, which was negatively affected by burn severity.

Therefore, these results demonstrated that ecosystem resilience varies not only with burn severity, but also with species composition and vegetation structure, aspects that should be taken into consideration for the implementation of fire management strategies, especially in areas affected by recurrent and severe fires.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-022-00156-1.

Additional file 1: Fig. 1.1. Maps of the fire perimeter showing: (a) time since last fire, (b) fire recurrence, and (c) burn severity (Fernández-García et al. 2019d).

Additional file 2: Table 2.1. Results of the generalized linear models showing the effects of burn severity (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) on the cover (%) of each stratum (0 – 0.5 m, 0.5 – 1 m, 1 – 4 m, and > 4 m) for every type of ecosystem (shrubland, heathland, broomland, and oak woodland).

Additional file 3: Table 3.1. Average cover values (%) for each burn severity category (low severity, moderate severity, high severity, unburned in the last 10 years (young vegetation), and unburned in the last 20 years (old vegetation)) of every woody species and herbaceous vegetation at the lowest stratum (0 – 0.5 m) in each type of ecosystem (shrubland, heathland, broomland, and oak woodland).

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Authors' contributions
S.H., E.M., V.F.-G., and L.C. conceived and designed the experiment. S.H., E.M., V.F.-G., and L.C. collected field data. S.H. analyzed the data. V.F.-G. assisted in the data analysis. S.H. wrote the manuscript. E.M., V.F.-G., and L.C. revised the manuscript. E.M. and L.C. coordinated the study. The authors read and approved the final manuscript.

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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
Nor applicable.

Competing interests
The authors declare that they have no competing interests.

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