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Interpreting the shifts in forest structure, plant community composition, diversity, and functional identity by using remote sensing-derived wildfire severity

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Abstract

Background Wildfires are increasingly impacting ecosystems worldwide especially in temperate dry habitats, often interplaying with other global changes (e.g., alien plant invasions). Understanding the ecological consequences of wildfires is crucial for effective conservation and management strategies. The aim of this study was to investigate the impacts of wildfire severity on plant community (both the canopy trees and herbaceous layer) and alien plant invasion, combining field observations and remotely sensed data.

We conducted an observational study in the Karst forests (North-East Italy) 1 year after the large wildfire which affected the area in 2022. We assessed the impact through 35 field plots (200 m^2 each) distributed among different fire severity (i.e., the loss of organic matter) classes assessed using the differenced normalized burn ratio (dNBR) calculated from satellite images. In each plot, tree species, diameter, vitality, resprouting capacity, and seedling density were measured. In addition, herb species richness (taxonomical diversity) was quantified, and plant cover was visually estimated. Functional diversity was also assessed considering six functional traits retrieved from databases.

Results Some woody species (e.g., *Quercus pubescens*) showed a higher resistance to the fire (i.e., lower mortality rate), while others showed a higher resilience (i.e., recovery after fire through resprouting or seedlings, e.g., *Cotinus coggygria*). The transition to a shrub-dominated community (i.e., *Cotinus coggygria*) where fire severity was the highest underlines the dynamic nature of the post-fire succession. We detected a significant variation in the herbaceous plant community composition, diversity, and functional identity (i.e., community-weighted mean of trait) along the fire severity gradient. In particular, high-fire severity areas exhibited higher species richness compared to low-severity or unburned areas. Total alien plant cover increased with fire severity, while native cover remained constant. We also found shifts in species that enhance traits related to germination potential and growth strategy.

Conclusions Our results highlight the vulnerability of the forest stands to an increase in wildfire severity, resulting in significant mortality and changes in tree community structure. This study contributes to the understanding

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of ecological processes after wildfires using a novel remote sensing approach in a temperate forest, emphasizing the need for conservation strategies aimed at mitigating high severity wildfires.

Keywords Biological invasion, Forest community, Functional traits, Herbaceous community, Karst landscape, Remote sensing approach, Vegetation dynamics

Resumen

Antecedentes Los incendios de vegetación están impactando incrementalmente en los ecosistemas de todo el mundo, especialmente en hábitats templado-secos, interactuando frecuentemente con otros cambios globales (i.e., invasiones de especies exóticas). El entender las consecuencias ecológicas de los fuegos de vegetación es crucial para una estrategia efectiva de manejo y conservación. El objetivo de este estudio fue investigar los impactos de la severidad del fuego en comunidades vegetales (tanto en el dosel de árboles como en el estrato herbáceo) y la invasión de exóticas, mediante la combinación de observaciones de campo y datos derivados de sensores remotos Condujimos un estudio observacional en los bosques de Karst (en el noreste de Italia), un año después de un incendio que afectó el área en 2022. Determinamos su impacto a través de 35 parcelas de campo (de 200 m^2cada una) distribuidas entre diferentes clases de severidades (i.e., calculada mediante imágenes satelitales). En cada parcela, se determinaron las especies de árboles, sus diámetros, vitalidad, capacidad de rebrote, y se midió la densidad de plántulas. Asimismo, fue cuantificada la riqueza de especies herbáceas (diversidad taxonómica), y estimada visualmente la cobertura de plantas. La diversidad funcional fue también determinada considerando seis características funcionales tomadas de las bases de datos.

Resultados Algunas especies arbóreas (e.g., *Quercus pubescens*) mostraron una alta resistencia al fuego (i. e. bajas tasas de mortalidad), mientras que otras mostraron una alta resiliencia (i. e. recuperación post fuego a través de rebrotes o plántulas, como por ejemplo *Cotinuscoggygria*). La transición hacia comunidades dominadas por arbustos (i. e. *Cotinus coggygria*), donde la severidad del fuego fue mayor, subraya la naturaleza dinámica de la sucesión post fuego. Detectamos una variación significativa en la composición, diversidad, e identidad funcional (i. e. promedio sopesado por características de las especies), a través del gradiente de severidad. Particularmente, áreas con alta severidad de fuego exhibieron una riqueza de especies más alta que áreas quemadas a baja severidad, o no quemadas. La cobertura total de especies exóticas se incrementó con la severidad del fuego, mientras que la cobertura de nativas permaneció constante. Encontramos también cambios en especies que aumentan las características relacionadas con el potencial de germinación y la estrategia de crecimiento.

Conclusiones Nuestros resultados subrayan la vulnerabilidad de los rodales forestales a un incremento en la severidad de los incendios, resultando en una mortalidad significativa y cambios en la estructura forestal. Este estudio contribuye al entendimiento de procesos ecológicos luego de incendios, usando una aproximación novedosa para un bosque templado, enfatizando la necesidad de desarrollar estrategias de conservación cuyo objetivo sea mitigar los incendios de alta severidad.

Background

Wildfires represent one of the most influential ecological disturbance agents affecting ecosystem distribution, properties, and functions over geological periods (Bowman et al. 2009). Fires trigger changes in primary productivity of the ecosystems and shape local plant communities by altering the ecological succession, nutrient cycle, and light availability of the sub-canopy layer, resulting in new available niches (Sousa 1984; Glenn-Lewin et al. 1992).

Plant species differ in their fitness (i.e., survival and/or reproductive success) as a consequence of adaptation to varying fire regimes (Cavender-Bares et al. 2004). Tree species can be classified into five groups according to their response strategy to fire (Moris et al. 2022): (i) resisters, which survive frequent surface fires thanks to their thick and insulating bark; (ii) embracers, which recover quickly from the canopy seed bank; (iii) avoiders, which are easily killed but live where fires are infrequent; (iv) resilient (i.e., used as synonyms of endurers), which are able to resprout after the event; (v) colonizers, which establish on burned areas following the long-distance seed dispersal.

Anthropogenic climate change is causing an increase in the frequency and severity of extreme fire events due to changes in local, regional, and global weather parameters that drive fire behavior (Clarke et al. 2013; North et al. 2015; Sharples et al. 2016; Bowman et al. 2017; Tedim et al. 2018). This trend is expected to increase in the future (Liu et al. 2010; Jolly et al. 2015) because of climate change projection. In recent years, for example, there have been increasing media reports of major fires disasters: the wildfires in Chile in 2017, Portugal in 2018, California in 2021, Brazil in 2019, Australia in 2019–2020, and Siberia in 2022–2023.

Prior to 2012, around 65,000 fires occurred in Europe every year, burning around half a million hectares of wild and forested land (San-Miguel-Ayanz et al. 2012), mainly in the Southern Mediterranean countries. In the Mediterranean basin, there is evidence that fires were common during the late Quaternary (Carrión et al. 2003), and fire was likely common prior to the Quaternary as most plant species evolved adaptive mechanisms to persist and regenerate after disturbance events such as recurrent fires (Pausas et al. 2004; Pausas and Verdú 2005). Although for fire adapted habitat wildfire can benefit from these events, the main concern of recent years regards the increasing frequency of this phenomenon. Fire frequency in Europe has been increasing in the last decades due to climate change (Senf and Seidl 2021; Patacca et al. 2023), socio-economic factors, and especially rural abandonment (Mancini et al. 2018; Colonico et al. 2022), in which the interplay causes an increase in biomass resulting in an increase in available fuel in the environment (i.e., higher severity). Indeed, these processes caused an increased flammability at the landscape scale due to an accumulation of fuel (e.g., dead biomass in forests) and its continuity (Moreira et al. 2011; Pausas and Fernández-Muñoz 2012; Badeau et al. 2024), thus calling for an active monitoring and prevention effort (Corona et al. 2015; Spadoni et al. 2023).

An increase in wildfire frequency and/or severity, defined as the loss of organic matter (Keeley 2009), will have major economic impacts, will increase plant and seed mortality, and may drive changes in species composition, dominance, and spatial distribution towards species adapted to more frequent and intense fires (Segura et al. 1998; Morrison 2002; Penman and Towerton 2008). Changes in soil properties are expected to strongly interplay with the plant community assemble, as observed in other ecosystems (Trotta et al. 2024). Besides habitat disruption, another adverse consequence of wildfire on vegetation is the potential to promote the ingression of new species into landscapes (Keeley 2006). A common consequence of wildfire in the northern hemisphere is the regression of ecosystems to more juvenile seral stages with an evident simplification of their structural complexity (Poldini et al. 2018), while in the southern hemisphere, the response depends on the various vegetation across regions (see Lehmann et al. 2014). This leads to a rapid establishment of herbaceous species shifting from forest specialist towards plants with a ruderal adaptive strategy, the majority of which can be alien (Ivanova et al. 2014; Trotta et al. 2023b). Alien species are a topic of global concern in terms of ecosystem preservation as they have shown their potential to alter ecosystem processes (Root et al. 2003; Raizada et al. 2008); decrease native species abundance and richness via competition, predation, hybridization, and indirect effects (Blackburn et al. 2004; Gaertner et al. 2009; Boscutti et al. 2020; Vitti et al. 2020; Trotta et al. 2023c); change native community structure (Hejda et al. 2009); alter nutrient cycling (Pellegrini et al. 2021); impact landscape perception (Pejchar and Mooney 2009); and alter the fire regimes of the ecosystem invaded (D'Antonio and Vitousek 1992; Brooks et al. 2004).

Remote sensing (RS) has been largely used to assess landscape change (Sellers et al. 1995; Vuerich et al. 2024; Cingano et al. 2024). Over the last decades, new satellite sensors (e.g., Sentinel-2 MSI, Landsat-8 OLI/TIRS) have been providing valuable data at increasingly higher temporal, spatial, and spectral resolutions. This growing variety and quality of remotely sensed data enables a wide range of fire-related applications, from detecting fire occurrence (Wooster et al. 2021) and severity (Keeley 2009; Veraverbeke et al. 2011) to monitoring post-fire recovery (Frazier et al. 2013). Satellite-derived spectral vegetation indices based on the ratio between short-wave infrared (SWIR) and near infrared (NIR) wavelengths have demonstrated a good capability in characterizing post-fire forest severity and dynamics, with strong correlations with field-based measurement (Keeley 2009; Cardil et al. 2019; Gibson et al. 2022). In particular, the normalized burn ratio (NBR) has become one of the most widely accepted spectral indices to assess burn severity (Lutes et al. 2006; Eidenshink et al. 2007; Escuin et al. 2008; French et al. 2008; Avetisyan et al. 2023; Jodhani et al. 2024). The difference between NBR of the vegetation pre-fire and post-fire is expressed as delta NBR (i.e., hereafter dNBR), but its potential use as a tool to assess the functional response of the vegetation community to fire has not been widely explored.

The functional response of a plant community to a wildfire can be used to study the response to the new environment and to the disturbance across taxa (Donato et al. 2009). Traits related to regeneration strategies (i.e., seed longevity, germination, growth form) and competition (i.e., growth rate, shade tolerance) are a well-known proxy to determine the functional response of the community (Noble and Slatyer 1980). Wildfire is a well-recognized ecological disturbance able to alter the structure and composition of vegetation communities, whose magnitude (i.e., fire severity) can greatly shape the impacts on both the herbaceous and tree forest layer (Bond et al. 2005; Bowman et al. 2009). Thus, determining the functional response of the plant community by combining field and remote sensing approaches appears crucial, especially in areas prone to repeated fire events where not all the species are adapted.

Our research hypothesis posits that varying fire severities (i.e., expressed as varying dNBR values) elicit differential responses in plant vegetation (i.e., both understory and tree layer), leading to a potential shift in community composition, functional response, and the potential for alien plant invasion in the Karst region. We expect that traits typical of ruderal and alien species will be advantageous for species colonizing ecosystems severely affected by wildfire. We also expect different tree species to respond differently to wildfire severity, especially in terms of resilience and resistance, but without knowing the specific species response. We also suppose a higher invasion of alien species with increasing levels of disturbance (i.e., high wildfire severity). Through our findings, we aim to provide valuable insights for biodiversity conservation, ecosystem management, and planning in the Karst landscapes. Indeed, the Karst region in Italy and Slovenia, as it is happening in other habitat, is becoming more and more prone to wildfires (Šturm and Podobnikar 2017). However, despite this higher susceptibility, the potential impact of such disturbances on vegetation dynamics as well as on the resistance and resilience of Karst ecosystems has not been completely understood.

Material and methods

Study area and the 2022 fire

The Karst region is a limestone plateau with an average elevation of 334 m above sea level located in between Italy and Slovenia, world famous for its peculiar topography and geological phenomena (Cucchi et al. 2015). Being at the boundary between Mediterranean Sea, the Alps, and the Dinaric mountains, the area is characterized by a high level of biodiversity, hosting a large number of protected animal and plant species under the protection of the European Habitat directive 92/43/EEC. For these reasons, most of the Italian Karst area is included in the Natura 2000 protected sites network. The most representative forest stands are composed by mixed-broad leaves species of temperate areas such as downy oak (*Quercus pubescens* Willd.), hophornbeam (O*strya carpinifolia* Scop.), and manna ash (*Fraxinus ornus* L.) with the occurrence of European smoketree (*Cotinus coggygria* Scop.). Artificial black pine stands (*Pinus nigra* J.F. Arnold) are also present as remnants of the large reforestation program launched by the Austro-Hungarian Empire at the beginning of the last century. These stands are characterized by the presence of senescent pines in the upper layer and mixed broadleaf species in the understory layer. Most of the areas are not subjected to forestry management since the forest establishment. Alien species such as black locust (*Robinia pseudoacacia* L.) and tree of heaven (*Ailanthus altissima* (Mill.) Swingle) are widespread especially in disturbed areas (i.e., both natural or human induced disturbance) and close to settlements. Karstic dry grasslands, characterized by *Centaurea rupestris* L. and *Carex humilis* L., are also common in the area even though they have been disappearing in the last decades due to agricultural abandonment and natural forest expansion.

The climate is Pannonian continental with average temperatures in January and July of 4.0 °C and 22.9 °C respectively, with an annual average of 13.1 °C. However, temperatures are milder at lower altitude, along the sea. Rainfall ranges between 900 and 2000 mm per year depending on the altitude. The soil is extremely drained and classified in the family of red Mediterranean soils.

The 2022 wildfire broke out following an extremely dry and hot summer. It started on July 15 and was extinguished on July 29 with a total burnt area of around 4000 ha between Italy and Slovenia (Čahojová et al. 2024) (Fig. 1). Even though wildfires are common in the area (190 fires occurred within the Italian Karst since 1970 most of which were less than 1 ha in area (Autonomous Friuli Venezia Giulia Region 2023), the 2022 wildfire can be considered an extreme event for the area due to its extent. For the purposes of the current research, we limited our study area to the burnt patch in the municipality of Doberdò del Lago (Italy, 500 ha), the municipality that was the most effected in Italy.

Fire severity calculation and sampling design

The severity of the 2022 wildfire was assessed using the dNBR index (Fig. 1). Such an index was calculated using Sentinel-2 images (Level-2A, tile T33TUL), taken on July 2 (pre fire) and August 16 (post fire) respectively, through the Semi-Automatic Classification Plugin (SCP) in the QGis software using the NIR band (8A) and the SWIR (12) (EFFIS 2020), both with a resolution of 20×20 m. The severity map was then classified according to the European Forest Fire Information System (EFFIS) fire severity classes (Lutes et al. 2006). Non-burned vegetation shows very high reflectance in the NIR, and low reflectance in the SWIR portion of the spectrum, while recently burned areas show low reflectance in the NIR and high reflectance in the SWIR. Applying the difference between the before and after wildfire RS data allow to calculate the difference NBR (dNBR or ΔNBR; Lutes et al. 2006; Miller and Thode 2007; Miller and Quayle 2015).

Using EFFIS map of fire severity, we randomly selected 30 points distributed proportionally to the area of each EFFIS class (class 1: 15 plots; class 2: 10 plots; class 3: 5 plots). In addition, 5 reference plots were selected in the

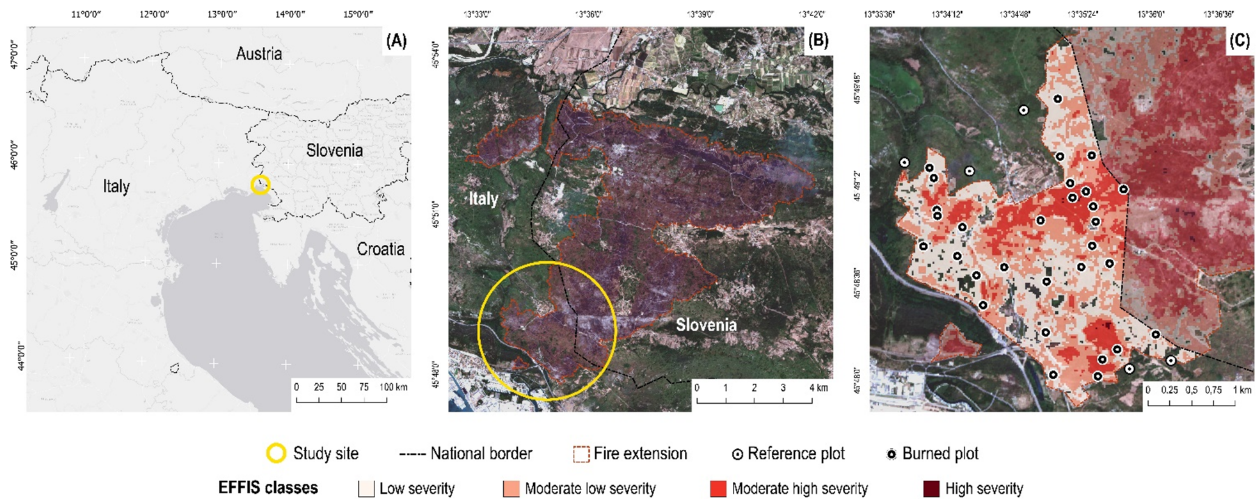

Fig. 1 Study area and sampling design. Localization of the Karst (**A**), the 2022 wildfire area (**B**), and the study area and sampling plots classified according to EFFIS severity classes (**C**) are represented

surrounding forest stands not subjected to any fire in the last decades (i.e., since 1965) and representing the vegetation before the fire events.

In each of the 35 selected points, we established a permanent circular plot of 200 m^2 (8 m of radius; Maringer et al. 2020), where the tree and understory data were collected. A permanent sampling network was developed, through a picket located in the center of each plot with the GPS position recorded.

Tree and understory data collection

In all plots, diameter at breast height (1.30 m; DBH) of all tree and shrub stems larger than 2 cm was recorded in the summer of 2023 and the species identified. Each stem was also classified as alive or dead. Aboveground mortality was then calculated as the ratio between dead and total stems (alive + dead). Resprouting stems from each stump were counted and their average height measured. The number of tree seedlings divided for species and their average height were measured within a subplot of 2 m radius centered in each plot.

For the herbaceous layer (i.e., all herbaceous species and only woody species with less than 50 cm of height), the cover of each plant species was visually estimated as cover percentage for the whole 200 m^2 plot (Rapson 2018). Taxonomy and nomenclature followed Bartolucci et al. (2018) and Galasso et al. (2018) for native and alien species, respectively. Taxonomic diversity of the herbaceous layer was assessed using species richness (i.e., number of species). Functional identity of each community was quantified using six functional traits per species expected to be ecologically relevant and to respond to major environmental changes due to fire disturbance (Cornelissen et al. 2003), namely light demand, nutrient demand, life-span, specific leaf area (SLA), seed mass (i.e., for individual seed), and seed number (i.e., number of seed for each individual plant). According to literature, those are the traits which are expected to be affected by fire severity (Cornelissen et al. 2003; Müller et al. 2007). These traits were derived from "Flora Indicativa" (Landolt et al. 2010) and the "LEDA Traitbase" (Kleyer et al. 2008). The functional identity of the community was assessed calculating the community-weighted mean (CWM) of each trait, relying on the occurrence and abundance (i.e., cover value) of each species.

Statistical analyses

All the statistical analyses were performed in R environment (R Core Team 2022). Differences in mortality (i.e., percentage of dead trees) of the four most common species (i.e., *F. ornus*, *C. coggygria*, *Q. pubescens*, and *O. carpinifolia*) with dNBR were tested using generalized linear mixed-effects models (GLMM) with binomial distribution with the "glmer" function (p-value $\leq$ 0.05) of the "lme4" R package (Bates et al. 2015). Model included stem mortality as dependent variable and fire severity (dNBR), species, and their interaction as fixed effects, using the plot id as a random factor to adjust the model degree of freedom. We first tested the full model, and, where not significant, we manually backward simplified the model (summary of the full model reported in Table S2).

Differences in resprouting and recruitment were tested using linear mixed models (LMM), using the plot id as a random factor to adjust the model degree of freedom. For these variables (i.e., resprouting percentage and new seedlings), we considered the interaction significant between species and dNBR, given the proximity to 0.05 of the *p*-value (respectively 0.056 and 0.081). The number of recruitments was linear-transformed using square root to improve the model. Pairwise comparisons were performed using the function "emtrends" of the "emmeans" R package (Lenth 2022) to test the different response between species.

The effects of fire severity (dNBR) on the species richness and abundance (i.e., species cover) of native and alien species (i.e., alien status) were tested using linear mixed-effects models (LMM; $p < 0.05$), with the plot id included as random factor (Zuur et al. 2009). Significance was assessed using the ANOVA test and the R^2 using the "rsq.lmm" function of the "rsq" package (Zhang 2023). Both species richness and abundance were transformed with a Z-transformation, to better compare the trend between alien and native species. Both linear and non-linear trend (i.e., log-transformed fire severity) were tested. Non-linear relationships were kept when model diagnostics were better.

Changes in the understory species composition across all plots were inspected by Kruskal's non-metric multidimensional scaling (NMDS) unconstrained ordination (Wildi 2017). To highlight the relationships between species composition, forest parameters, and functional traits, a further fitting of environmental variables was performed. All the multivariate analyses were performed in the "vegan" package (Oksanen et al. 2024).

To test the effects of fire severity on the community functional identity of the selected traits (i.e., CWM of each trait), we used linear models (p-value ≤ 0.05). Significance was assessed using the ANOVA test and the R^2 in the summary function. Data normality was tested with the Shapiro–Wilk's test, and the homoscedasticity was visually tested with the residuals of the model. Given that most of the results exhibit a logistic trend, the dNBR index was used as log-transformed index. All graph visualization was performed using "visreg" (Breheny and Burchett 2017) or "ggplot2" package (Wickham 2016).

Results

A total of 21 species (19 native and 2 alien species) were recorded in the tree layer (i.e., both canopy and subcanopy). The most common native trees were *Fraxinus ornus* (found in 100% of the surveyed plots, 24 individuals on average per plot), *Cotinus coggygria* (91%, 24 individuals on average per plot), *Quercus pubescens* (77%, 5 individuals on average per plot), and *Ostrya carpinifolia* (63%, 4 individuals on average per plot). Two alien tree species were recorded: *Robinia pseudoacacia* (3% of the surveyed plot) and *Hesperocyparis arizonica* (3% of the surveyed plot). The analysis of dendrometric data showed that stem density, basal area, and mean diameter of dead stems increased with fire severity (Table 1). On the other hand, the average diameter of living trees did not differ between EFFIS classes, except for the high-severity class, where almost no living stems were measured.

We counted 202 species in the understory, 183 of which were native and 19 alien. The most common native species were *Asparagus acutifolius* (94%), *Sesleria autumnalis* (91%), *Brachypodium rupestre* (77%), *Rubus ulmifolius* (74%), and *Sonchus oleraceus* (69%). The most occurrent alien species were *Erigeron canadensis* (63%), *Senecio inaequidens* (37%), and *Phytolacca americana* (26%). A complete list of all the species and their frequencies in the sampling plots is reported in the tab supplementary materials (Table S1).

The percentage of stem mortality of all sizes showed a positive and significant relationship (p-value < 0.001) with fire severity (expressed as increasing values of dNBR) (Fig. 2a), regardless of the species (i.e., *p*-value of the interaction between dNBR and species = 0.75; Table 2a). Among the four most frequent tree species, *Quercus pubescens* exhibited the lowest mean overall stem mortality, while the other three species (*Fraxinus ornus, Cotinus coggygria* and *Ostrya carpinifolia*) did not show any significant difference (Fig. 2b).

The percentage of resprouting stumps across species in each plot was positively correlated with wildfire severity, showing a logistic increase of resprouting as dNBR increased ($R^2 = 0.21$, p-value $= 0.056$; Table 2b; Fig. 2c) with different responses among the four most common tree species. *Cotinus coggygria* showed

Table 1 Main dendrometric parameters in the surveyed plots by EFFIS class and control (mean ± s.d.)

EFFIS class	n. plots	Alive stems			Dead stems		
		N ha-1	m2 ha-1	davg (cm)	N ha-1	m2 ha-1	davg (cm)
Control	5	4846 ± 3030	25.11 ± 7.53	10 ± 6	458 ± 370	1.16 ± 0.86	5 ± 3
Low and moderate low severity	15	1668 ± 1283	12.89 ± 8.63	9 ± 5	3638 ± 1703	7.52 ± 3.01	6 ± 2
Moderate high severity	10	358 ± 399	5.04 ± 6.24	10 ± 8	3502 ± 1059	13.55 ± 8.84	7 ± 3
High severity	5	30 ± 67	0.01 ± 0.02	0 ± 1	3323 ± 1281	15.53 ± 8.03	8 ± 2

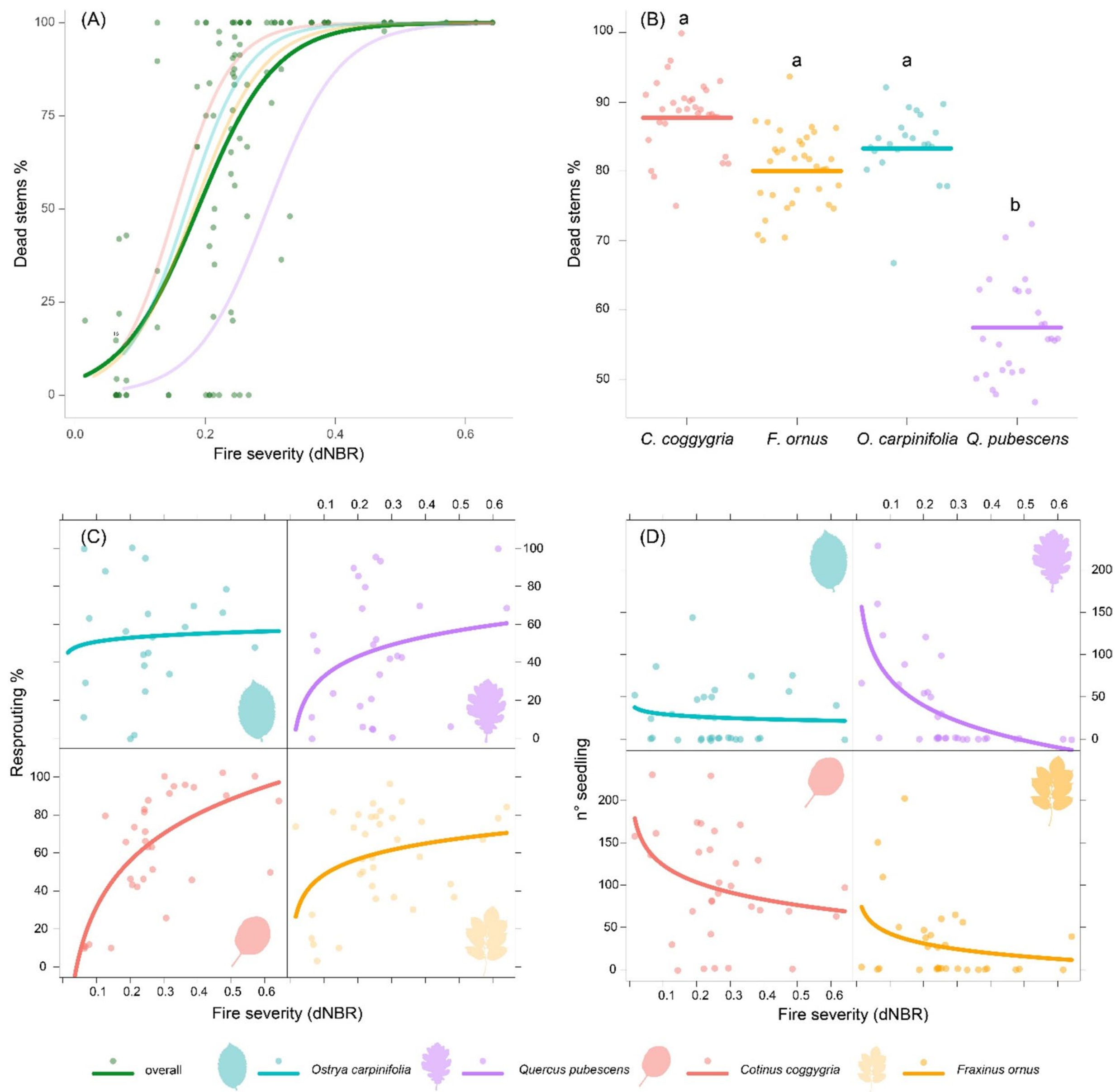

Fig. 2 Effect plots of the tested models. **A** Percentage of dead stems of the 4 most common tree species. In the graphs are displayed the 4 curves, one for each species considered (i.e., *F. ornus*, *C. coggygria*, *O. carpinifolia*, *Q. pubescens*) with colored line, while the solid green line represents the overall mortality. **B** The difference in mortality percentage between species. **C** Relationship between percentage of plants with resprouting and logarithm of dNBR of the 4 species considered. **D** Relationship between square root of number of seedling (i.e., recruitment potential) and dNBR of the four most frequent species

the highest resprouting capacity as the fire severity increases, while *Ostrya carpinifolia* had almost no increase (p-value = 0.055). *Quercus pubescens* was characterized by the lowest value of resprouting percentage (p-value = 0.021), while the other 3 species had no difference.

On the contrary, the number of new seedlings (i.e., species recruitment) decreased with increasing the fire severity ($R^2 = 0.37$, p-value = 0.081; Fig. 2d; Table 2c) with *Quercus pubescens* characterized by a greater decrease when compared with *Ostrya carpinifolia* (p-value = 0.064). *Cotinus coggygria* was the species with the highest mean value of new seedling (p-value < 0.001), while the other 3 species showed no differences. We found 13 new woody alien trees of

Table 2 ANOVA of the "GLMM" and of "LMM" models. The *p*-value is highlighted in bold when *p*-value < 0.05. We considered as significant also the *p*-value obtained in the (b) and (c) model with the interaction of dNBR and the species, given the proximity with 0.05

		numDF	Deviance	Resid. Dev	*p*-value
Tree mortality	(Intercept)	113		990.4	**0.004**
(a)	dNBR	112	48.03	51.00	**< 0.001**
	Species	109	17.54	33.46	**< 0.001**
		numDF	**denDF**	***F*-value**	***p*-value**
Resprouting	(Intercept)	1	75	315.15	**< 0.001**
(b)	log(dNBR)	1	33	12.45	**0.001**
	Species	3	75	1.87	0.143
	log(dNBR):species	3	75	2.64	**0.056**
N° of seedlings	(Intercept)	1	88	113.12	**< 0.001**
(c)	log(dNBR)	1	31	14.45	**< 0.001**
	Species	3	88	16.23	**< 0.001**
	log(dNBR):species	3	88	2.32	**0.081**

Table 3 ANOVA of the linear mixed models. The *p*-value is highlighted in bold when *p*-value < 0.05

		numDF	denDF	*F*-value	*p*-value
Species richness (*Z* trans-formed)	(Intercept)	1	33	< 0.001	1.000
(a)	log(dNBR)	1	33	23.951	**< 0.001**
	Status	1	33	< 0.001	1.000
Plant abundance (*Z* trans-formed)	(Intercept)	1	33	0.611	0.440
(b)	log(dNBR)	1	33	4.247	**0.047**
	Status	1	29	0.464	0.501
	log(dNBR):Status	1	29	6.573	**0.016**

Ailanthus altissima across all plots, with a mean height of 18 cm and a mean cover of 0.15%.

Fire severity also affected plant diversity independently of species status (i.e., native vs alien species showed no statistically significant difference, Table 2a). Species richness significantly increased with fire severity ($R^2 = 0.43$; *p*-value < 0.001; Table 3a; Fig. 3a).

Plant cover was affected by the interaction between fire severity and plant exotic status (Table 3b): alien cover was increased by high value of dNBR reaching a plateau at the highest severity values, while native cover remained stable (Fig. 3b). A summary for each full model is reported in the supplementary material (Table S2).

Species composition analysis revealed the presence of one major species turnover gradient indicated principally by the axis of the NMDS1, mainly related to the wildfire severity (Fig. 4). Along this gradient, the species composition showed a shift from species usually present in (i) mature forest habitats (i.e., *Ruscus aculeatus*, *Polygonatum odoratum*), to (ii) a transitional stage dominated by species typical of open forests and ecotones between forests and the karst dry grasslands (i.e., *Sesleria autumnalis*, *Dictamnus albus*), to (iii) species typically belonging to karst dry grasslands (i.e., *Centaurea jacea*, *Allium carinatum*, *Pentanema spiraeifolium*), and, finally, when the severity reached its maximum, (iv) to ruderal stage, often dominated by alien species (i.e. *Erigeron canadensis*, *Erigeron sumatrensis*). The environmental variables fitted to the two NMDS axes also showed a significant relationship between the understory species composition and main forest structure. More specifically, where tree stem mortality and resprouting were higher, the understory showed a high species richness as well as alien and annual species frequency. Along the NMDS2, it was also possible to note a gradient of nutrient availability, favoring more acquisitive species (i.e., high values of SLA).

Given the low frequency and data availability about the alien plant functional traits, the functional identity of the community (i.e., community-weighted mean of each trait CWM) was assessed without considering the status of the species.

We found a significant effect of fire severity on the selected traits of the understory community (Table 4). In particular, the community exhibited a higher nutrient indicator value where severity of wildfire was higher ($R^2 = 0.36$; Fig. 5a). The same trend was observed for light indicator value ($R^2 = 0.49$; Fig. 5b). High values of fire severity induced a decrease in plant community life span, as shown by the rapid increase in the percentage of annuals species ($R^2 = 0.54$; Fig. 5c). Similar trends were found for the community mean of SLA, which logistically

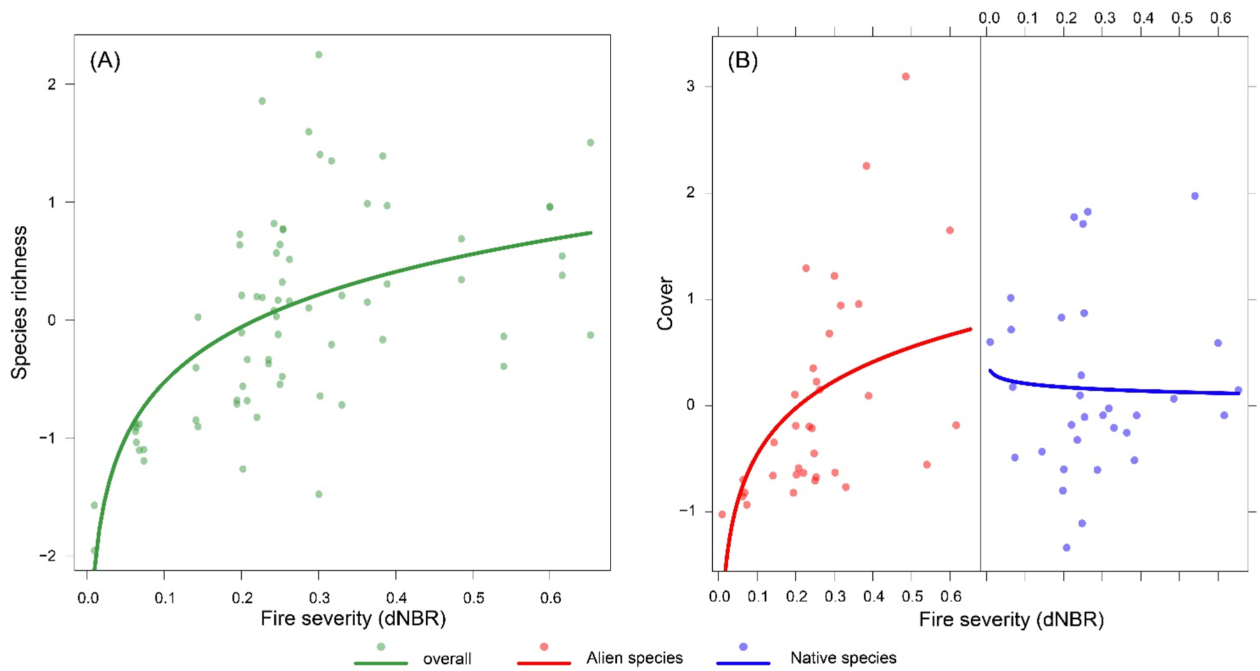

Fig. 3 **A** Relationship between species richness (*Z* transformed) and the logarithm of dNBR. **B** Relationship between plant cover (*Z* transformed) and logarithm of dNBR divided for species status (i.e., alien or native)

increases with increasing fire severity ($R^2 = 0.19$; Fig. 5d). In addition, the community mean of reproductive traits (i.e., seed number and seed mass) were affected by fire severity that selected communities producing more seeds ($R^2 = 0.47$; Fig. 5e) and with a lower mass ($R^2 = 0.15$; Fig. 5f).

Discussion

Remote sensing-derived fire severity was able to predict the gradual changes that occurred in a Karst forest ecosystem, shedding light on the complex ecological processes triggered by fire. We showed that wildfire severity increases the mortality and decreases resprouting of the tree layer. Our findings also suggested that fire is able to create new available niches, triggered by changes in light availability and soil nutrients, favoring the spread of annual, acquisitive species such as native ruderal and invasive alien species.

The species surveyed in the forest layer were consistent with previous research in the Karst, highlighting that the study area well-represents the forest association *Ostryo-Quercetum pubescentis*, previously described as the zonal vegetation (climax) of the supra-Mediterranean Karst (Favretto and Poldini 1985). The low frequency of alien trees (i.e., alien woody species above 1.3 m height) recorded in our sample plots (i.e., both burned and the external reference plots) can be linked to the ecological integrity and maturity of the selected forest stands and to the absence of previous large-scale disturbance events (Langmaier and Lapin 2020; Trotta et al. 2023a). In contrast, although native species dominate the herbaceous layer, the occurrence of several alien species in the burned areas highlighted the ongoing pressure of biological invasions in the area (Motard et al. 2015; Čahojová et al. 2024).

Our results showed that the response to fire severity by the tree layer is species-dependent. As expected, wildfire severity directly impacts the mortality of tree and shrub stems (Woolley et al. 2011). Overall, the studied stands seem to be resistant at low severity, but, once the severity is too high, the stem mortality raises logistically to the 100% (Fig. 2a). Among the four most frequent and abundant tree species, *Quercus pubescens* appeared to be the most resistant species (Fig. 2b), consistently to previous studies (Falk et al. 2022). This species reaches higher heights, and the crown is therefore protected from surface fires; moreover, thicker bark insulates better the cambium (Pellegrini et al. 2017; Nemens et al. 2019; Cansler et al. 2020). In the burned area, the tree resprouting ability was promoted by fire, but species response was specific and contrasting (Fig. 2c). *Fraxinus ornus* and *Quercus pubescens* increase their resprouting ability with fire severity; the resprouting of *Ostrya carpinifolia* was not stimulated by increasing severity. The shrub species *Cotinus coggygria*, on the other hand, showed the highest stem mortality but concurrently the

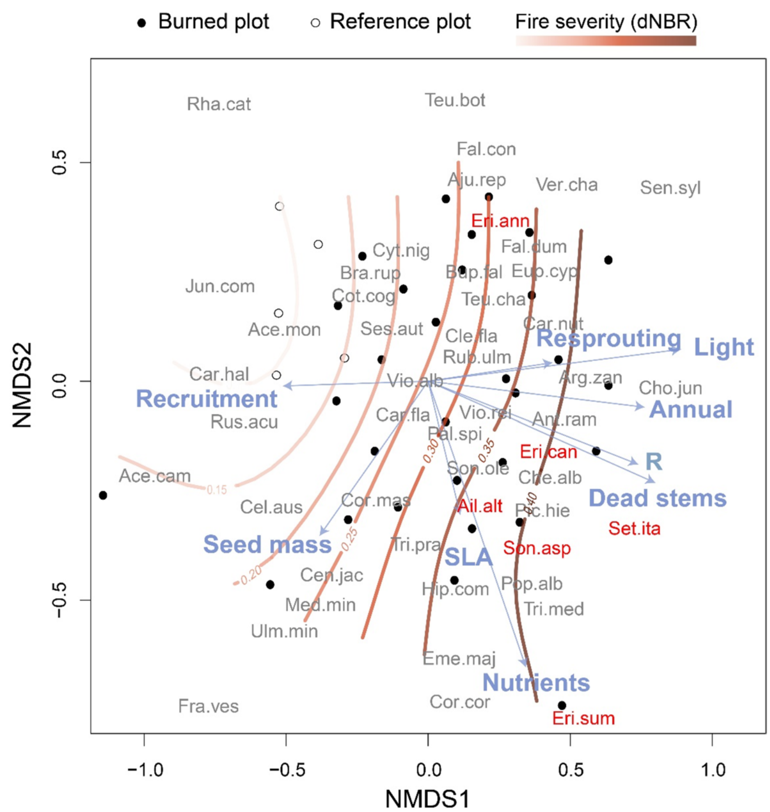

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of the study. The red line represents the isoline of dNBR values. A selection of species was plotted according to species scores. Alien species are reported in red and native species in gray. The dots represent the site location (i.e., green unburned areas while orange burned areas). Significant correlation of Landolt's indicator values (Nutrients, Light), functional traits (SLA = specific leaf area, seed mass, annual = annual species), and collected parameters (R = species richness, resprouting, recruitment, trees' death). The reference for the species code is reported in Table S1

Table 4 ANOVA of the linear models. The *p*-value is highlighted in bold when *p*-value < 0.05

		Df	Sum.sq	Mean.sq	*F*-value	*p*-value
Nutrients	Residuals	33	0.56158	0.017018		
(a)	log(dNBR)	1	0.31360	0.313602	18.428	**< 0.001**
Light	Residuals	33	1.0498	0.03181		
(b)	log(dNBR)	1	1.0201	1.02012	32.068	**< 0.001**
Percentage annuals species	Residuals	33	867.43	26.29		
(c)	log(dNBR)	1	1011.78	1011.78	38.491	**< 0.001**
SLA	Residuals	33	137.01	4.152		
(d)	log(dNBR)	1	31.82	31.820	7.6642	**0.0092**
Seed mass (mg)	Residuals	32	19,878.9	621.2		
(e)	dNBR	1	3359.9	3359.9	5.4086	**0.027**
Seed number (for individual plant)	Residuals	29	107,990,777	3,723,820		
(f)	log(dNBR)	1	93,672,314	93,672,314	25.155	**< 0.001**

highest resilience, thanks to its high resprouting ability, an adaptation to the frequent surface fires occurring in its range. *Cotinus coggygria* ability to cope with fire events was already demonstrated (Pilon et al. 2021). Postfire seeding in our study was affected by increasing value of severity consistent with other studies (Crotteau

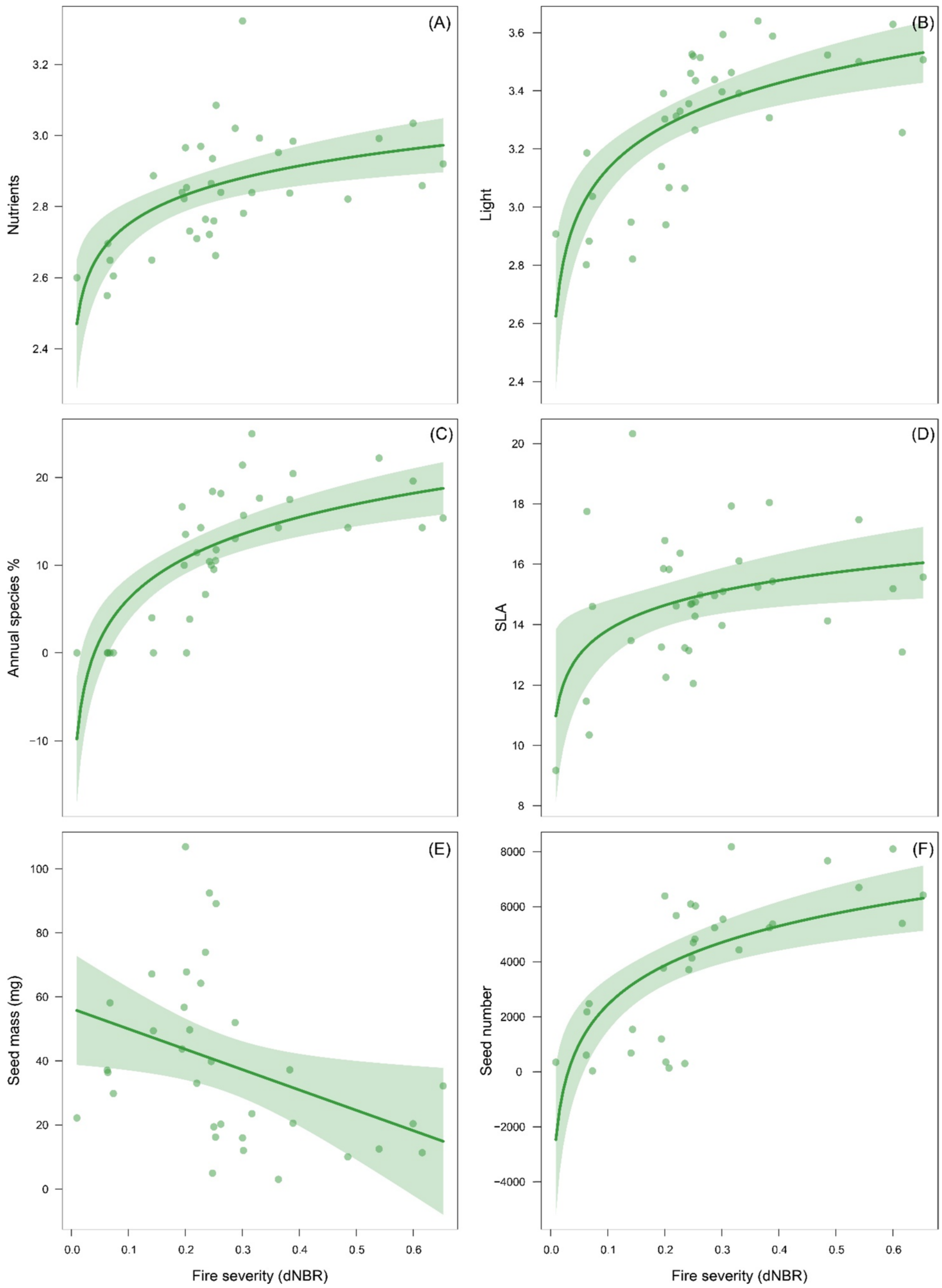

Fig. 5 Relationship between functional identity indices and dNBR. In particular, (**A**) relationship with Landolt's indicator values of nutrients, (**B**) Landolt's indicator values of light request, (**C**) percentage of annual species, (**D**) specific leaf area, (**E**) seed mass, and (**F**) seed number. All the parameters are the community-weighted mean values

et al. 2013). Interestingly, the species with the lowest number of seedling recruitment was *Quercus pubescens*, while *Ostrya carpinifolia* was not affected by fire severity showing a constant low number of seedlings in the sample areas. This can suggest a life history tradeoff for the species *Quercus pubescens*, investing more in resistance of the single tree instead of promoting resilience capability. Altogether, our data showed that the higher was the fire severity, the higher was the possibility to move the forest community towards initial development stages dominated by the shrub *Cotinus coggygria* and some scattered *Quercus pubescens* surviving the disturbance event. This novel community might slow down the succession of the Karst forest, limiting the growth of new *Quercus* sp. seedlings (Gavinet et al. 2019) mainly due to allelopathic substances released in the soil which affect the germination. The interplay between species in the tree germination is still a poorly understood mechanism, but our result, together with other findings in the literature, seems to confirm that *Cotinus coggygria* may take advantage in the germination process (Rey Benayas et al. 2005; Gavinet et al. 2016). Once the shrub layer is established, all the vegetation succession is delayed by the high amount of stem density created by the shrub layer. This layer limits the resources for the *Quercus sp.* seedlings to establish; therefore, more time is needed for the fully recover (Vesk et al. 2008). This appears a crucial aspect for ecosystem restoration after fire disturbance, especially in the face of an increasing number of extreme wildfire events in the Karst area following the ongoing climate change, which could favor an intermediate succession dominated by *Cotinus coggygria.*

As far as the herbaceous layer is concerned, fire severity increased the overall species richness, independent to their exotic status (i.e., not significant interaction). Indeed, high fire severity promote habitat heterogeneity when compared with the initial forest stage (Agee 1993; Perry et al. 2011), by increasing the number of available niches (Burkle et al. 2015). In particular, environmental heterogeneity promotes a scattered distributions of clustered populations of species that colonized the new available niches across habitats (Myers et al. 2015; Dawe et al. 2022; Trotta et al. 2023a). Among the colonizers, increasing fire severity appears to create the perfect condition for pioneer and ruderal species, most of them alien (e.g., *Erigeron canadensis*, *Erigeron sumatrensis*). Consistently with other studies, our results suggest that alien cover is enhanced by fire severity (Reilly et al. 2020; Trotta et al. 2023b), significantly shifting their relative abundance contribution to the whole understory community. This potential shift in abundance was also associated to a gradual species turnover induced by the fire severity. In particular, we showed fire severity is a significant gradient mimicking the departure from climax vegetation along a vegetation succession. Here, the disturbance intensity (fire severity) well represents the floristic distance of burned vegetation to the unburned forest, potentially triggering different pathways to the restoration of the original understory vegetation cover (Dawe et al. 2022). A mid-severity is partially replacing the original understory, favoring some characteristic species of open forest and Karst dry grassland. This intermediate disturbance level seems hence to promote biodiversity by creating new opportunities for light demanding species, consistently to what observed in other forest due to intensive coppice management (Della Longa et al. 2020). A more severe fire is, instead, able to trigger a dramatic change in the forest understory with a main forest species replacement in favor to ruderal and alien species. This is probably due to the higher light availability but also to the great availability of bare soil to colonize as well as to the immediate increase of nutrient supply generated by burned organic matter in the first year after the fire event (Fuentes-Ramirez et al. 2018). These speculations are indirectly supported by the CWM indicator values calculated for nutrients and light request. In particular, our analysis showed that plant community had a higher demand for nutrients and light in areas subjected to the most intense fire, probably due to the low canopy cover and the soil nutrient enrichment after the fire (Hobbs and Huenneke 1992). This confirms what found in literature where it was observed that nutrients increase during the early stage of forest recovery (i.e., 1 year after the fire) according to fire severity, while total nitrogen, total carbon, and soil organic matter exhibited a long-term nutrient depletion, especially in areas affected by high severity burning (Francos et al. 2018; Fuentes-Ramirez et al. 2018).

Consistently to previous studies, we found fire severity to affect changes in recovery and succession in plant communities via changes not only on species composition but also on functional trait community identity (Anderson-Teixeira et al. 2013; Poulos et al. 2020; Liang and Hurteau 2023). Our results on the functional identity of the newly formed herbaceous community (i.e., CWM of each considered trait) have given new insight on the traits that are promoted by wildfire severity. The new community was dominated by annual plants and by plants with higher SLA. Both these traits are generally associated with fast-growing species as they confer an advantage in environment with high supply of resources, allowing the plant to rapidly occupy the new niches available (Montesinos 2022). The functional trait filter induced by fire contributes to explain the high abundance (i.e., cover value) of alien and ruderal plants; plant guilds generally well adapted species to resource-rich environments (D'Antonio 1999). The reproductive strategy selected by fire severity underlines the changes in the functional identity of the understory. The new community exhibits plants that produce light seeds (small) but in large quantity. These two characteristics are often associated with a disturbed environment where, although seed mass is an important parameter in determining the establishment of seedlings (Howe et al. 1985; Kidson and Westoby 2000), the spread velocity (and then the colonization success) is higher by increasing the propagule pressure (Martínez-Ghersa and Ghersa 2006). We expect that the normal evolution of a forest affected by wildfire will be a gradual recolonization by forest specialist and at the end the full recovery of the forest community, with the disappearance of the ruderal and alien species given the right amount of time (Trotta et al. 2023a). In the future, we are planning to conduct a study aiming at elucidating the process through a chronosequence of wildfires in the Karst landscape.

Our study uniquely demonstrates how fire severity can strongly alter the initial response, diversity, and functional identity of the Karst ecosystems, therefore highlighting the need for conservation strategies aimed at limiting fire damages through prevention measures. Wildfires are common in the area: more than 190 fires have occurred within the Italian Karst since 1970. Fortunately, most of them were less than 1 ha in area probably thanks to an active land governance (Spadoni et al. 2023). A well-managed land use mosaic, where pastoral and forestry activities are supported and maintained, can reduce fuel load and continuity, thus helping to decrease the spread, intensity, and severity of fires (Moreira et al. 2011, 2020; Corona et al. 2015; Colonico et al. 2022). However, local or fragmented initiatives might result ineffective, especially in a scenario of increasing frequency of extreme fire events (Ascoli et al. 2023). In fact, integrated solutions which involve different sectoral policies (e.g., forestry, agriculture, nature conservation, energy, tourism) within a unified strategy for managing wildfire risk can mitigate more efficiently the effects of wildfires at landscape scale (Ascoli et al. 2023). Our results suggest that, from a management perspective, policies need to promote more resilient species in fire-prone areas, as these species can help improve ecosystem resilience. In addition, to limit the spread of alien species, it is essential to reduce the spread of fast-growing annual species, which tend to increase in the seed bank when there is fragmentation due to agricultural and urban environments or forest tracks (Boscutti et al. 2022).

Conclusions

We evidenced that remote sensing-derived fire severity was an effective tool to depict a fine-tuned picture of the gradual changes occurring in broadleaf forest after a fire event. Our results highlighted the vulnerability of temperate Karst forest to a high level of fire severity, as that forecasted following the ongoing change in climate, resulting in significant tree stem mortality and potential long-term changes in tree community structure and composition. The fire might promote a rapid transition to a shrub-dominated community (i.e., *Cotinus coggygria*) promoting a long-lasting shrub stand potentially affecting the future dynamic nature of post-fire succession. Furthermore, our study highlights the role of fire severity in shaping herbaceous community dynamics: high severity fires promote habitat heterogeneity and niche availability, leading to an increase in species richness and a change in functional identity. Such an increase is accompanied by a shift towards pioneer and ruderal species, many of which are alien, potentially threatening native biodiversity. Overall, our study highlights the complex interactions between wildfire severity, vegetation dynamics, and functional traits and emphasizes the need for conservation and management practices considering the effects of high severity fire on ecosystem resilience and biodiversity.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00330-7.

Supplementary Material 1: Table S1 and Table S2.

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Authors' contributions

GA, FB, LC, and GT conceived the ideas and designed methodology; LC, GT, SP, and GA collected all the data; GT and LC analyzed the data; GT and LC led the writing of the manuscript. GA coordinates the working group. All authors contributed critically to the drafts and gave final approval for publications.

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Availability of data and materials

All the data are available at the public repository Mendeley Data. https://doi.org/10.17632/t2cxrczh7h.1.

Declarations

Competing interests

The authors declare no competing interests.

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