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Fire Ecology

ORIGINAL RESEARCH

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Response of vulnerable karst forest ecosystems under different fire severities in the Northern Dinaric Karst mountains (Slovenia)

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Abstract

Background This study deals with wildfires in marginal areas of the Mediterranean climatic and biogeographical regions (Northern Mediterranean) where fires were not common. The aim of the research was to determine the differences in floristic composition and traits at different intensities of fire damage and to analyze the changes in forest ecosystems during the wildfires that took place in the summer of 2022. The study included both the zonal forests and non-native black pine (*Pinus nigra*) forests. Remote sensing techniques linked to the vegetation data sampled in the field during the 2023 vegetation season, the very first season after the fires, were also used in the fire assessment.

Results The study confirmed that satellite data analysis, orthophoto interpretation, and on-site vegetation sampling provide equivalent information on fire severity, opening up the possibility of transferring knowledge to similar post-fire sites without field sampling in the future. TWINSPAN classification analysis divided the sampled plots into clusters based on tree species prevalence and fire severity. The diagnostic species of the clusters were calculated using a fidelity measure. Ordination revealed that the first axis on the detrended correspondence analysis (DCA) correlated with wildfire severity. Ecological conditions and strategies, life forms, chorotypes, seed dispersal classes, and regeneration traits were analyzed along this gradient. We found that post-fire sites became warmer, drier, and lighter, which favored the growth of ruderal, theropytic, cosmopolitan, anemochorous and post-fire emergent species. After the fire, a "wave" of annual ruderal species was observed.

Conclusions The results indicate that post-fire recovery can be left to natural processes without human intervention, except in the case of non-native pine stands where planting or seeding may be necessary. Otherwise, it is essential to control the possible occurrence of invasive species. Isolated adaptations of species to fire have also been observed, such as heat-stimulated germination. Such adaptations could develop in regions exposed to frequent fires and where fires act as an evolutionary factor.

Keywords Ecology, Forest, Gradient, Ordination, Plant, Remote sensing, Succession, Trait, Vegetation classification, Wildfire

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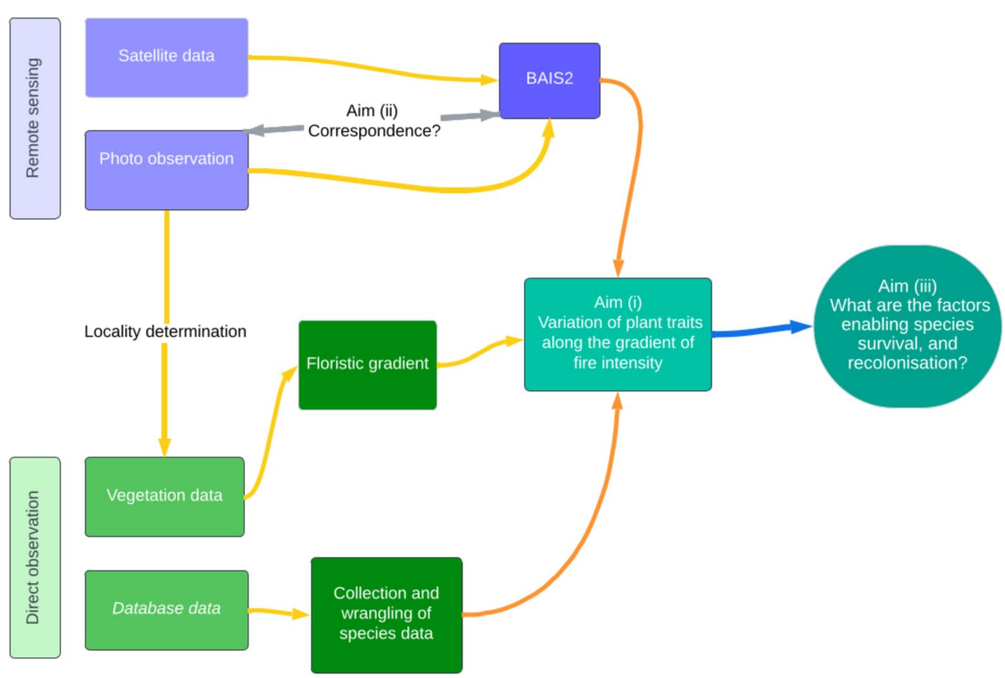
Resumen

Antecedentes Este estudio se enfoca a los incendios forestales en áreas marginales de regiones biogeográficas y climáticas del tipo mediterráneas donde los incendios no son comunes. El objetivo de la investigación fue determinar la diferencia en composición y características de diferentes intensidades de daño por fuegos y analizar los cambios en los ecosistemas forestales durante los incendios forestales que ocurrieron en el verano de 2022. El estudio incluye tanto la zona de bosques boreales y bosques no nativos de pino negro (Pins nigra). Técnicas de sensores remotos ligadas a datos de vegetación muestreados a campo durante la estación de crecimiento de 2023, la verdadera estación luego de los fuegos, fueron también usadas en la determinación de los incendios.

Resultados El estudio confirma que tanto el análisis de los datos del satélite, la interpretación de ortofotos y los muestreos de vegetación in situ, proveen de información equivalente sobre la severidad de los incendios, abriendo una oportunidad para transferir el conocimiento del post-fuego en sitios similares, y no tener que realizar los muestreos de campo en el futuro. El análisis de la clasificación por TWINSPAN divide las parcelas de muestreo en clústeres basado la prevalencia de especies de árboles y la severidad del fuego. Las especies diagnóstico fueron calculadas usando la medida de fidelidad. La ordenación reveló que el primer eje del análisis de las fluctuaciones sin tendencia (DFA) se correlacionó con la severidad del fuego. Las condiciones ecológicas y estrategias, las formas de vida, cariotipos, las clases de dispersión de semillas y las características de la regeneración, fueron analizadas a través de ese gradiente. Encontramos que los sitios post-fuego se trasformaban en más cálidos, secos, y livianos, lo que favoreció el crecimiento de especies ruderales, pteróftas, cosmopolitas, anemócoras y otras especies emergentes en el post-fuego. Luego del incendio, fue observada una "ola" de especies anuales ruderales.

Conclusiones Los resultados indican que la recuperación post-fuego puede ser lograda mediante procesos naturales sin intervención humana, exceptuando el caso de especies de rodales de pino no nativos en los cuales la siembra o plantación serían necesarias. De todos modos, es esencial el control sobre la posible aparición de especies invasoras. Las adaptaciones aisladas de especies al fuego también han sido observadas, como la germinación estimulada por el calor. Tales adaptaciones pueden desarrollarse en regiones expuestas a fuegos frecuentes y donde los fuegos actúan como un factor evolutivo.

Graphical Abstract



Introduction

Wildfires significantly affect the natural environment and human lives and they are a common phenomenon in the central Mediterranean region (Pausas et al. 1999, 2008) and throughout the world. Due to climate change, their intensity is increasing, resulting in serious economic losses and ecological destruction (Castelli et al. 2015). The ability to accurately predict areas that may be involved in a wildfire and the directions and reasons for its spread can help in fire management planning (Bot and Borges 2022). It is also important to know how resistant vegetation is to fires and what factors slow down the spread of fire. This information is important for the management of areas at the increased risk for fires, including the research area at the borders of the Mediterranean region.

Monitoring vegetation and its changes is an important part of botanical research in a world of rapid changes and biodiversity loss. Biodiversity loss caused by human activity, such as removal and homogenization of vegetation, inappropriate or insufficient management, as well as changes due to climate change (e.g., long periods of rain, drought, increase in the number of windy days) are a threat to humanity, sustainability of the environment, preservation of native species, and entire ecosystems.

Fire is often considered a primary disturbance agent because of its enormous importance in many ecosystems (Thonicke et al. 2001). In the context of climate change, periods of long-term drought and wind are becoming more frequent, and the frequency of wildfires is constantly increasing (Sathishkumar et al. 2023). In 2022, after a long and significant dry period, the Kras Plateau of southwestern Slovenia and northeastern Italy experienced conditions that favored the ignition of major fires (available online: https://www.Landsaf.ipma.pt, accessed 8 August 2023) that broke out in mid-July 2022 and lasted until early August 2022 (Košiček et al. 2023).

Severe fires cause significant changes in ecosystems, mainly due to the removal of vegetation (Key 2006) and changes in soil properties (Fernández-García et al. 2019). Repeated fires have led many species to adapt to the fire regime (Balao et al. 2018; Rundel et al. 2018), and Mediterranean vegetation is thus often considered very resistant to wildfires (Calvo et al. 2013). Many species in such a regime use the ability to regenerate vegetatively (resprouters), a regenerative trait that could facilitate vegetation regeneration in a regime of high fire severity and recurrence (Fernández-García et al. 2020). Fire recovery can be supported by heat-stimulated germination of dormant seeds that are resistant to high temperatures (seeders) (Lamont et al. 2019). Due to these adaptive properties and the fact that frequent fires in the same location also affect the succession of the community, thereby preventing the vegetation from progressing to more mature stages (Santana et al. 2010), shrub vegetation tends to regenerate quickly after a fire (Minor et al. 2017) and forest vegetation, which is usually less resistant to strong fires, is therefore replaced by shrub communities over time (Stevens-Rumann and Morgan 2019).

Our research included a comparison of two remote sensing techniques for detection of wildfire intensity, i.e., using satellite images and orthophoto interpretation, and an analysis of the effect fire intensity on the structure and function of forests.

Remote sensing is one of the most important tools in ecology and conservation for effective monitoring of ecosystems in space and time (Rocchini et al. 2018). It is also one of the most important tools for monitoring natural disasters and their consequences (e.g., fires, floods). Rapid information for accurate and rapid mapping of burned areas is essential to support fire management, address environmental damage, and monitor and manage vegetation recovery (Filipponi 2018). RS tools have proven useful for accurately estimating fire-affected areas and burn intensity, aiding wildfire prevention, and assessment and monitoring at global, regional, and local scales (Chuvieco 2009).

Fire severity is often estimated by visual control or measured in situ using field observations of several ecological parameters (Navarro et al. 2017). At the same time, a number of methods have been developed for mapping areas affected by fires after a fire using multitemporal or individual satellite images (Boschetti et al. 2010; Filipponi 2018). Recent studies have evaluated the severity of burn using Sentinel-2 data for pre-fire to post-fire comparisons (Navarro et al. 2017; Mallinis et al. 2018; Quintano et al. 2018). Our research was unique in combining field vegetation surveys with the use of RS techniques. To provide rapid information on fire-damaged areas, various indices (e.g., burned area index (BAI), normalized burn ratio (NBR), and their relative versions) have been used in the past to map burned areas. We used the BAIS2 index (Filipponi 2018), based on a combination of Sentinel-2 spectral bands, which was successfully tested in various case studies in Italy for the summer 2017 fires.

The aim of the research was to determine the drivers of changes in forest ecosystems under wildfires in the areas situated at the margin of the Mediterranean region not subjected to frequent fires until recently.

We set three main objectives:

i) We tried to compare the evaluation of the intensity of wildfires by data from satellite images and orthophoto interpretation, and to link the results to vegetation data.
ii) We aimed to detect differences in the floristic composition of forests and analyze the gradient of various traits along different intensities of fire.
iii) We analyzed the influence of fires on the structure and function of forests and we tried to determine which traits allow species to survive or reappear on burned areas and whether fire contributes to the spread of Mediterranean vegetation and invasive species under anthropogenic climate change.

Materials and methods

Study area

The research was conducted on the Kras Plateau, a limestone karst plateau situated above the Bay of Trieste in the northernmost part of the Adriatic Sea at an elevation of 200–500 m (Fig. 1). The climate is

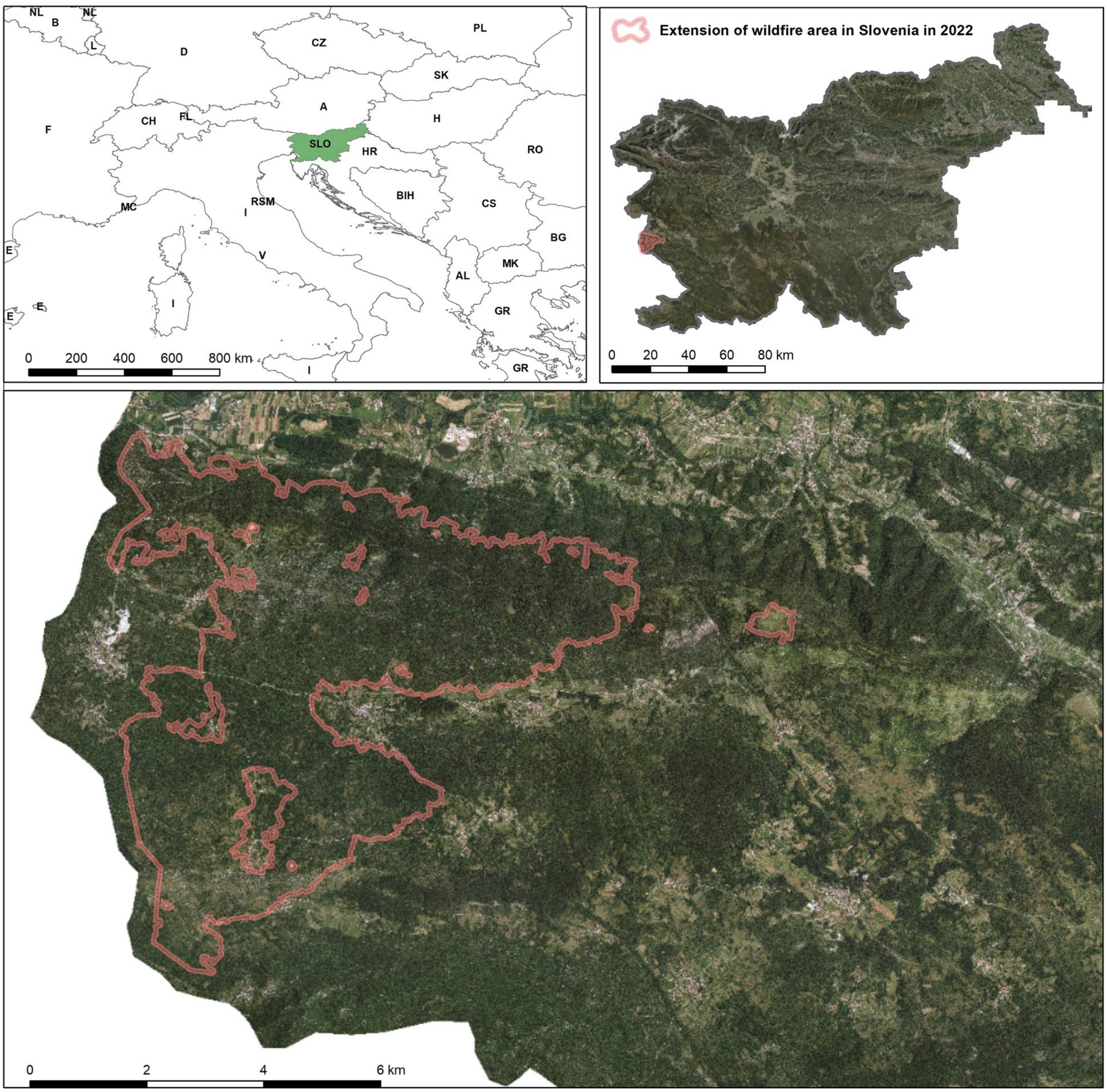


Fig. 1 Position of study area and extension of wildfire area of the Kras Plateau (southwestern Slovenia) and in the wider region

transitional between Mediterranean and continental (sub-Mediterranean), with rainy, cool winters and hot summers. Precipitation is about 1400 mm, and the average annual temperature is about 11 °C. The Kras Plateau is composed of karstified Mesozoic limestone, covered mainly by rendzinas and cambisols. The zonal forests are dominated by pubescent oak (*Quercus pubescens*), hop hornbeam (*Ostrya carpinifolia*), and flowering ash (*Fraxinus ornus*). The area has been partially reforested with non-native black pine (*Pinus nigra*), which forms dense communities and spreads subspontaneously. The study area is located at the margin of the Mediterranean biome (Mihevc et al. 2010; Dinerstein et al. 2017; Čarni 2019; 2022; Cervellini et al. 2020; Barčić et al. 2022).

The study area is part of the Kras Plateau. We focused on the burned part of the plateau and its immediate surroundings. The total burned area is 37 km^2.

Selection of plots and vegetation sampling

A total of 50 plots for field vegetation survey were selected within the burned area of the Kras Plateau. The plots were recorded in June 2023. This was the first growing season after the fire, at the time of optimal development of vegetation. When selecting the plots, we focused on forested areas exposed to wildfires of varying intensity, where either zonal forests or stands of black pine dominated before the fire. In order to maintain the same/similar geomorphological and ecological conditions, plots were selected on the flat parts of the Karst Plateau and outside of dolines (Čarni et al. 2022; Jakob et al. 2022). Plots with unburned vegetation were selected in close proximity to the burned areas. The Kras Plateau is very diverse in terms of both vegetation and structure, and the area of sample plots meeting our conditions (forest vegetation on the flatter plateau) was limited, which was reflected in the number of plots sampled.

Other factors limiting the number of plots were sampling effort and a narrow window of time. To ensure comparability of the plots, they had to be sampled in the same frame window to ensure approximately the same phenological development of vegetation. The plots were surveyed on the area of 10 m × 10 m (Kavgacı et al. 2010). All vascular flora was recorded for three vegetation layers (herb, shrub, and tree) according to the height of plants (up to 0.5 m for the herb layer, shrub between 0.5 and 5 m and tree layer higher). Tree and shrub species were recorded as two pseudospecies for burned and dead individuals and for burned surviving and undamaged individuals. Plant coverage was visually estimated in accordance with the 7-degree cover scale of the standard Central European method. We estimated the cover of all vegetation layers and of bare rock (Braun-Blanquet 1964; Dengler et al. 2008).

In the field, we attributed each sampled plot the intensity of wildfire, inferred from a physical map, prepared from data made by the Slovenia Forest Service (Košiček et al. 2023). The data from Košiček et al. (2023) was prepared on the basis of photo interpretation and field observations. Forests in the area were divided into four categories ranging from 1–ground fire up to 10% damage; 2b–between ground and crown fire, damage up to 50%, tree will survive; 2a–between ground and crown fire, damage between 50 and 90%, tree will die; to 3–crown fire, damage over 90% (Košiček et al. 2023). We established the fifth category for the purposes of our study for plots in unburned forests, category 0, no fire (Fig. 2).

Acquiring and processing of remote sensing data

Satellite data from Sentinel-2 (Drusch et al. 2012) were acquired and processed in Google Earth Engine (Gorelick et al. 2017). Sentinel-2 is a pair of antipodal satellites of the European space agencies' Copernicus program. The satellites have a polar orbit, synchronized with the Sun, so that every image of a point on Earth's surface is taken at the same hour each visit. Each point is revisited every 2–5 days.

The Google Earth engine is a cloud platform for processing and analysis of geospatial data. It is proprietary software of Google, which leases it for academic purposes free of charge (Gorelick et al. 2017).

An image from 2022-08-01 was used, the first available image after the fire was under control. To evaluate vegetation burnout, we calculated the Burned Area Index for Sentinel-2 (BAIS2) (Filipponi 2018).

BAIS2 combines data from five spectral bands acquired by the Sentinel-2 satellite (Vegetation red edge bands B06, B07, B8A, bands B4 - Red, and B12 - SWIR). Values of BAIS2 were attributed to our plots in ArcGis Pro. The spatial resolution of the BAIS2 raster is 10 m × 10 m, the same size as our plots. Where more than one raster pixel overlapped with our plots, a surface coverage weighted average was calculated.

Preparation of vegetation and remote sensing data

Vegetation data were stored in the TURBOVEG database (Hennekens and Schaminée 2001) and transferred to the JUICE 7.1 program for analysis and processing (Tichý 2002). We excluded burned (dead) shrub and tree species from the analyses, as well as from the calculations of plant traits. Burned species do not grow and therefore do not enter into mutual relationships with abiotic and biotic factors; they therefore do not participate in the formation of communities. We collected EIV (bioindicator values) from Pignatti et al. (2005) and functional trait values for

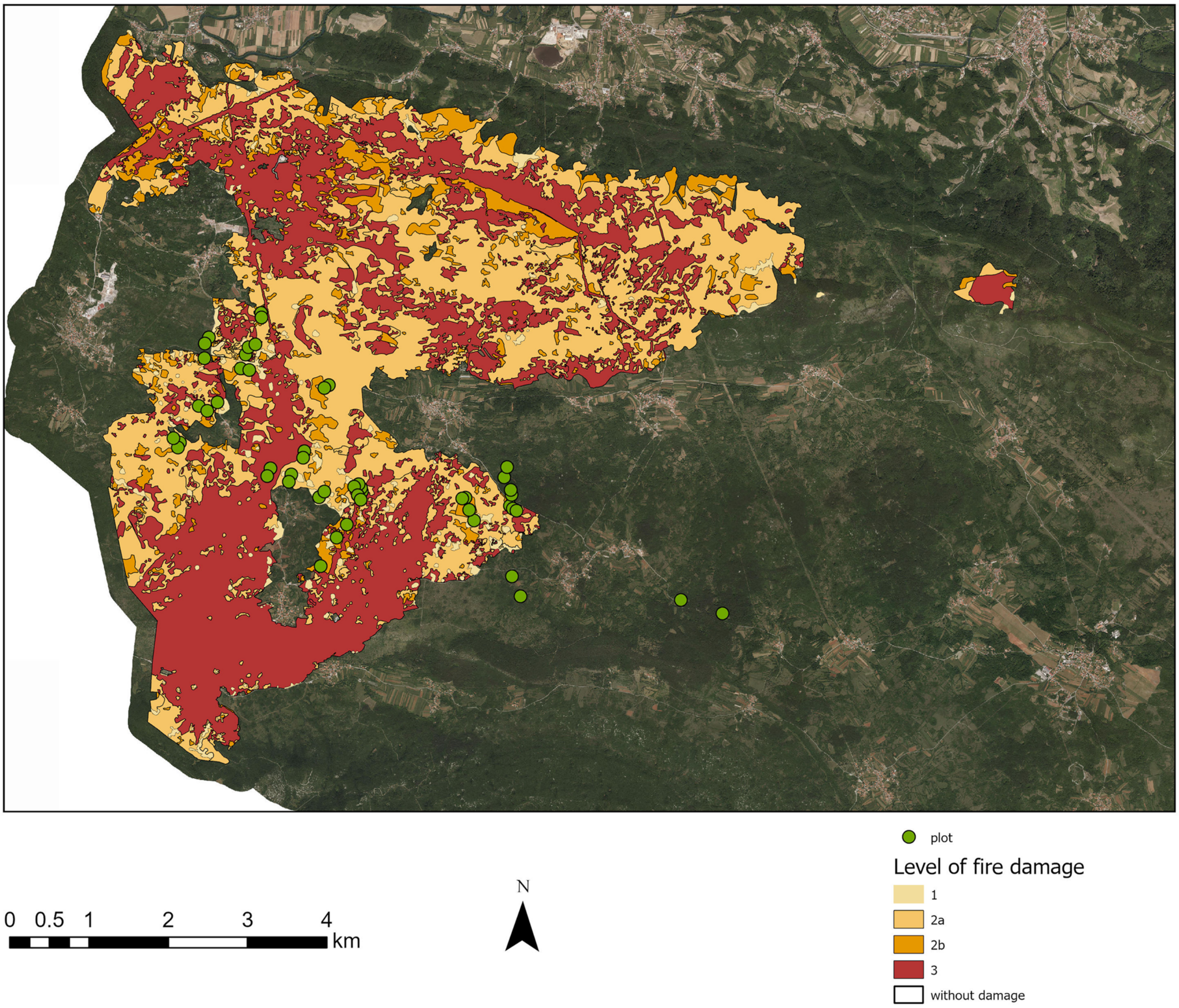


Fig. 2 Study area with visualization of fire damage localities (with localities of sampled vegetation plots in green) according to data made by the Slovenia Forest Service (Košiček et al. 2023) prepared on the basis of photo interpretation and field observations. Forests in the area are divided into four categories ranging from 1–ground fire up to 10% damage; 2b–between ground and crown fire, damage up to 50%, tree will survive; 2a–between ground and crown fire, damage between 50 and 90%, tree will die; to 3–crown fire, damage over 90%. Other parts are without damage

the species in our dataset from existing databases (Klotz et al. 2002; Tavşanoğlu and Pausas 2018).

We performed an unsupervised classification of the dataset using Two-Way Indicator Species Analysis (TWINSPAN) (Hill 1979). We settled 5 cut levels for species cover transformation (0 3 5 15 25) as proposed by Tichý (Tichý et al. 2020) and limited the minimum size of individual clusters to 5 plots in order to obtain sufficiently large and homogeneous clusters.

We reviewed the geolocations of our sampled plots in ArcGis Pro and investigated whether we had correctly determined fire intensity in the field, according to Košiček et al. (2023), and adjusted the fire intensity assessments of our plots accordingly.

BAIS2 values were attributed to sampled plots. Box-Whiskers diagrams were prepared for each group of plots, grouped by the reference fire intensity (Košiček et al. 2023) and TWINSPAN. The significance of differences was compared using the Tukey post hoc test. Normality was checked using the Lilliefors test. Analysis was performed with Statistica software (StatSoft 2011).

Analysis of vegetation data

Diagnostic species

A synoptic table to present the diagnostic species for groups of plots was prepared. Diagnostic species were defined by calculating the fidelity of each species to each plot group using the ϕ-coefficient as the fidelity measure (Chytrý et al. 2002), where species with a ϕ value above 0.40 were considered to be diagnostic. The ϕ coefficient was calculated for an equalized size of clusters. Species whose occurrence concentration in the plots of a particular group was not significant at $p < 0.05$ (Fisher's exact test) were excluded from the set of diagnostic species (Tichý and Chytrý 2006).

Ecological conditions

Pignatti bioindicator values reflecting ecological conditions in the sample plots were established for each species according to Pignatti (Pignatti et al. 2005). Before calculating the bioindicator values for plots, layers were merged (one species was taken only once) and burned species were excluded from the matrix. The same procedure was also applied to calculating the ecological strategies, frequency of classes of dispersal, chorotypes, and survival strategies.

Ordination and determination of the main floristic gradient

Ordination of vegetation plots was performed in the R environment, utilizing vegan package (Oksanen et al. 2022). DCA (detrended correspondence analysis) was chosen to accommodate the dispersal of our unimodal data. Plant coverage was translated into median percentages and normalized by square root transformation. The first axis of the DCA was accepted as the main floristic gradient.

Correlations

We calculated the correlation between the fire intensity category and the BAIS2 index for the entire burned area and its vicinity. The correlation was calculated via a heterogeneous correlation matrix consisting of polyserial correlation between BAIS2 and fire categories. We tested differences in mean BAIS2 value of fire categories with Tukey contrasts. Both tests were done in the R environment using packages polycorp and multcomp (Hothorn et al. 2016). In these analyses we only included forested areas.

We calculated the correlation of scores of the sample plots along the main floristic gradient represented by the first DCA axis and BIAS2, the structural properties of the sample plots (number of species, cover of vegetation layers (tree, shrub, herb) and bare rocks) by Spearman correlation in the Statistica program. The Spearman correlation between the first axis of the DCA and bioindicator values was calculated using the function envfit.iv in the JUICE program (Tichý 2002; Zelený and Schaffers 2012). Due to the circularity of the bioindicator values, a modified permutation test was applied. We calculated the parametric, in which an assumption of normal distribution of data was foreseen, permutation, in which we hypothesized that there was no relation between bioindicator values and scores on axis 1 and modified permutation, whereby this relation was considered by randomizing bioindicator values among species (Zelený and Chytrý 2007; Zelený and Schaffers 2012; Zelený 2018).

Ecological strategies

We investigated the CSR strategies of plant communities, developed 1 year after the fire (Grime 2001). The basis of this model is the ability of plants or plant communities to cope with stress and disturbance. There are three main strategies-competitors, stress tolerators, and ruderals (CSR)-and their combinations. Strategies of plant species were extracted from existing databases (Klotz et al. 2002). For the plant communities inhabiting our sampled plots, proportions of CSR strategies were calculated as community weighted means of strategies of the plant species present in the plot. The CSR ternate plot was used to visualize the relative positions of plant species and communities in the CSR strategy space. The community gets a functional signature (Pierce et al. 2017). When constructing the CSR triangle, only species with available information on ecological strategies were considered (193 out of 232 species).

Regression of plant traits

We tested the relationships between the first DCA axis and ecological strategies, life forms, seed dispersal classes (Lososová et al. 2023), chorotypes (Fattorini 2015; Pignatti et al. 2005), and regeneration traits (Tavşanoğlu and Pausas 2018), by linear regression (Lang and Ewald 2014; Bricca et al. 2023) using the lm function in the R software, where plot scores of plots on the first DCA axis were independent variables, and explanatory variables (ecological strategies, life forms, seed dispersal classes, chorotypes, regeneration traits) were dependent variables.

The nomenclature of plant species follows the Euro + Med Plantbase (available online: https://www.emplantbase.org, accessed 20 August 2023).

Results

Congruence between satellite images and orthophoto interpretation

Average BAIS2 index differed significantly between all categories of fire intensity by Košiček et al. 2023 ($p \cong 0.00$)

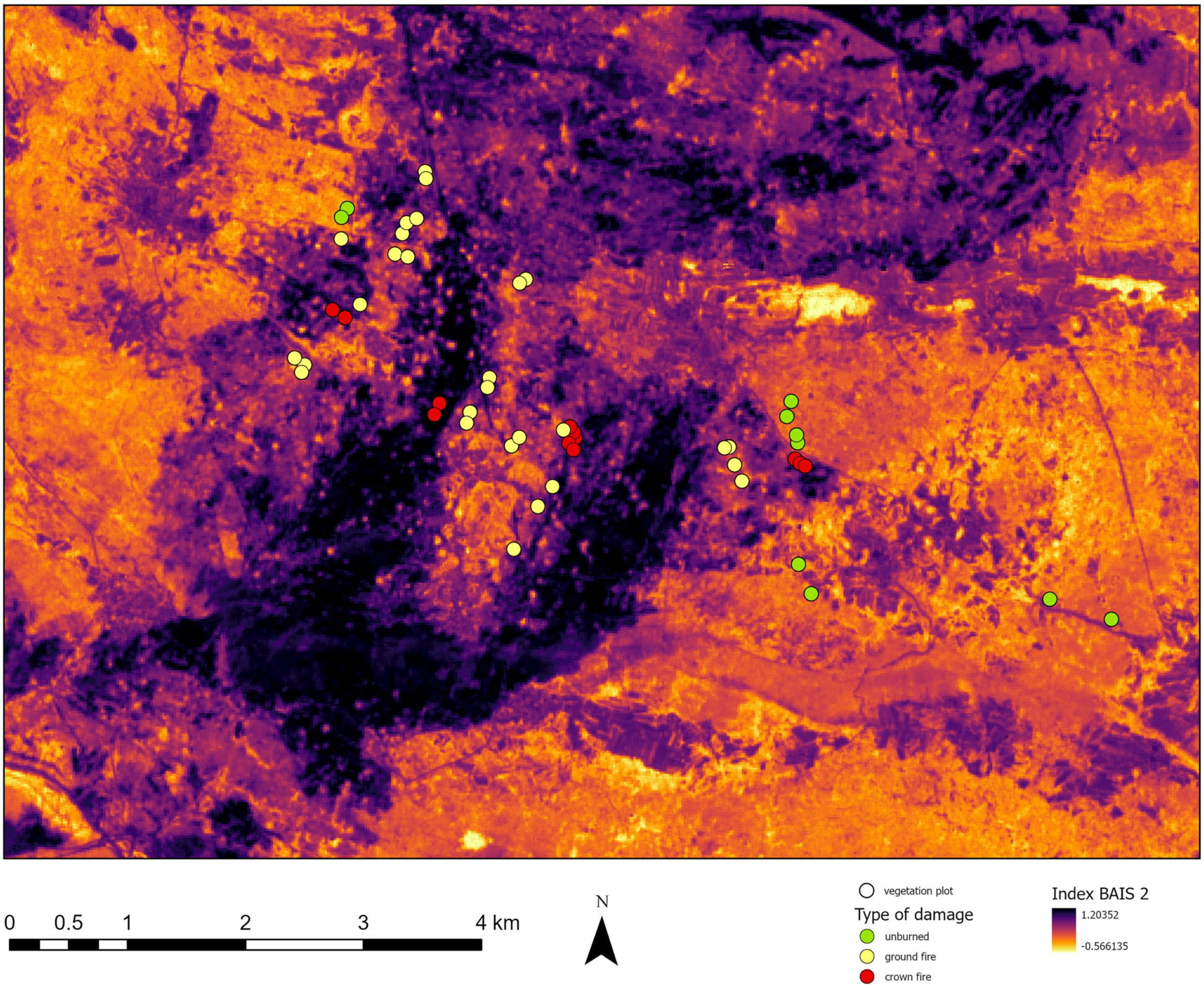


Fig. 3 Study area showing BAIS2 burn severity. Information from the field survey on the intensity of fire damage was assigned to the locations of the sampled vegetation plots (transparent circle). Where green plots were unburned (category C in Fig. 4; Table 1), plots with ground fire are yellow (B) and plots with crown fire are red (A). The highest values of the BAIS2 index (black) represent the greatest intensity of fire damage and the lowest values (yellow) represent the area without fire damage

over the whole area. The correlation between BAIS2 and intensity categories is moderately high ($\rho = -0.6248$). Further information can be found in the supplementary materials (Appendix S1 and Appendix S2). The BAIS2 index and fire intensity category were assigned to the sampled vegetation plots (Fig. 3).

The identification of fire severity in the field according to (Košiček 2023) was satisfactory. It was difficult to distinguish categories 2a and 2b in the field, and the identifications were corrected by joining reference points of our plots to fire intensity polygons by Košiček. Twinspan categorizations were largely congruent with field identifications of fire severity (Fig. 4, 5).

Floristic gradients and plant traits

Sampled plots were arranged in a table with a matrix of 232 species × 50 samples. The classification revealed six clusters, corresponding to the dominant tree species, as well as to the intensity of the wildfire (Fig. 5).

Plots in clusters 1 and 2 were affected by crown fire (also marked as category A), plots in clusters 3–5 were burned by a transition between crown and ground fires (further treated as ground fire) (B), and plots in cluster 6 remained unburned (C). It can be deduced that pine forests (with *Pinus nigra* trees) were more prone to severe fires and to escalation of fires from the ground to the crown. Native oak forests (with *Quercus pubescens*) were the least

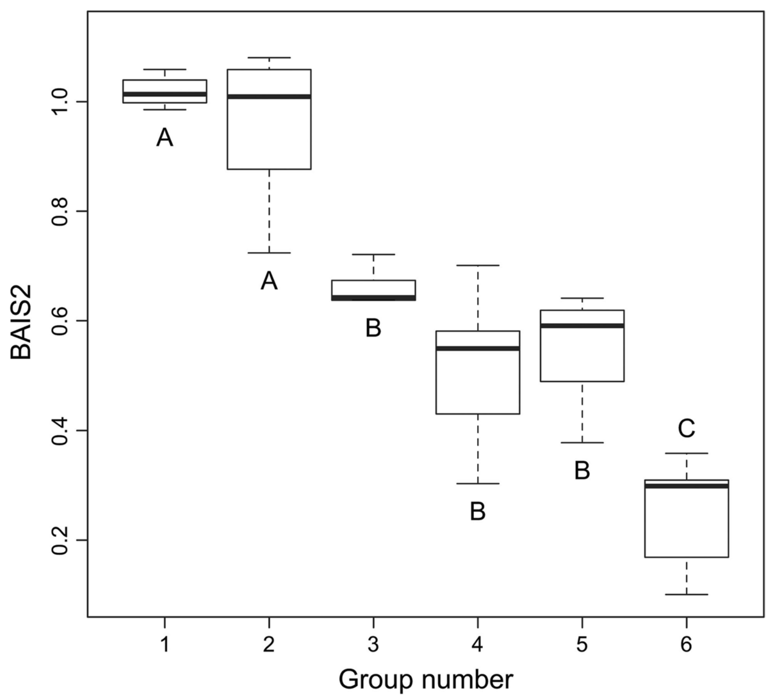


Fig. 4 Box-Whisker's diagram of plots grouped according to the TWINSPAN classification. There are three statistically significantly different groups: groups 1–2 affected by crown fire (marked as category A; see also Table 1.), 3–5 ground fire (B), and 6 unburned forests (C)

susceptible to fires. During the fieldwork, we detected groves of downy oaks, surrounded by completely burned pines; however, the oaks survived and were resprouting during recording season. Only where the fires were most severe did the oaks succumb to the fires.

Fraxinus ornus trees were fatally burned by the lower intensity of fire (ground fire) but can settle on burned surfaces more easily than other tree species; many small samples and resprouting rootstock could already be found in burned plots (Table 1). Some species adapted to such site conditions can be found in plots burned by crown fire, such as *Fumana procumberns* (in the seed bank, fire tolerant), *Lathyrus setifolius* (in the seed bank), and *Crocus variegatus* (surviving as a corm below ground). Some opportunistic plant species occured in all burned areas, such as *Erigeron annuus* and *Sonchus asper*. Species that can only survive a certain degree of fire appear in plots burned by ground fire and in unburned plots (but disappear with crown fires), such as *Hedera helix* and *Carex montana*. Some species

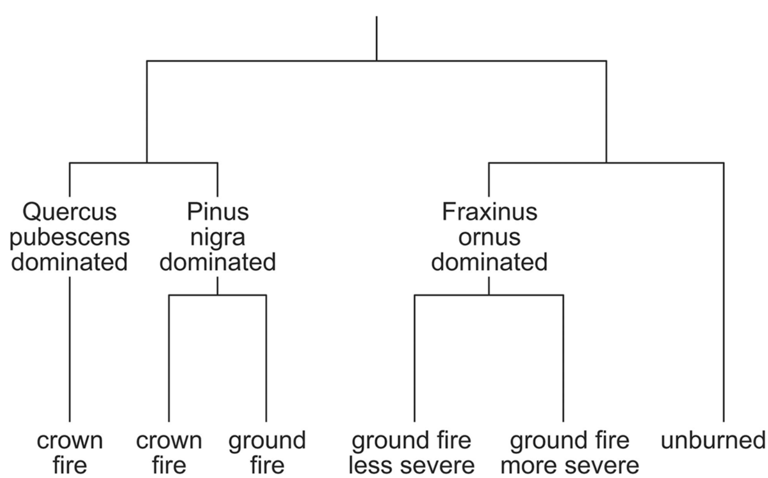


Fig. 5 Schematic dendrogram of the TWINSPAN classification with indication of type of wildfire and dominant tree species

Table 1. Synoptic table of elaborated sampled plots. We arranged groups according to TWINSPAN analysis and marked them by (solid and dashed) separators. Solid ones also distinguish various damage: crown (A), ground (B) and not burned (C). The header provides information about damage according to photo interpretation (0 no fire to 3 crown fire)

Type of fire		A A A A A A A	A A A A A	B B B B B B B B B	B B B B B B B B B B B	B B B B B B B B	C C C C C C C C C C
Intensity of fire (categories)		2 3 3 3 3 3 3	3 3 2 3 2	2 2 2 0 2 2 2 2 2	2 2 2 1 2 2 2 2 2 1 2	2 2 2 2 2 2 2 3	0 0 0 0 0 0 0 0 0 0
		a	a a	a b a ? a a a b a	b b b b b b b a b	a a a b a a b	
	layer						
***Quercus pubescens* burned**	1	. 1 2 . 2 4 2	. . . . .	. . . .	. . . . + ...	. 1 . . . . 1 .	. . . .
***Pinus nigra* burned**	1	. . . .	4 3 3 4 4	. . 1 1 . 1 2 3 .	. . . .	. . . .	. + ...
***Fraxinus ornus* burned**	1	3 3 3 4 3 2 3	2 + 3 1 3	1 2 3 3 1 2 + 2 +	2 1 3 2 2 2 . 1 1 1 1	1 1 1 1 2 2 + .	. . . .
***Fraxinus ornus* burned**	4	. . . .	. . . . .	. 1 1 . 2 + . 2 1	2 1 2 1 1 2 . 2 . + .	1 . 1 2 1 . + .	. . . .
***Ostrya carpinifolia* burned**	1	. . . 1 + . .	. . . . +	. . . .	. 2 3 . . 2 . . 2 . 1	. 1	. . . .
***Ostrya carpinifolia* burned**	4	. . . .	. + . . .	. . . .	. . . .	. . . .	. . . .
Quercus pubescens	1	3 . 1 . . 1 .	. . . . .	. + . . 1 . + 2 2	3 2 2 . 3 . 4 . . + +	. . 4 3 . 3 3 5	2 3 3 3 2 2 3 3 . .
Quercus pubescens	4	. + . . 1 1 .	. . . . .	. . . . +	1 . + ...	. . . .	. + + . + + + . 1 +
Quercus pubescens	6	. . . . . . +	. . . . .	. . + . + + . + .	+ + + . . + + + . + .	+ . + + . . + +	+ . + + + + + + . .
Pinus nigra	1	. . . .	. . . . +	1 4 3 3 3 4 . . .	. . . 2 . 2 1	. . . .	. 1 . . . . . . 4 4
Pinus nigra	6	. . . .	. . . . .	. + + + + + . + .	. . . + . . + ...	. . . .	. . . .
Fraxinus ornus	1	. . . .	. . . . .	3 2 . + 2 . 3 + 2	2 2 1 3 3 3 2 4 3 2 2	2 2 3 1 3 2 2 1	2 2 2 3 3 2 3 3 4 4
Fraxinus ornus	4	2 1 2 2 3 2 2	1 2 + + 1	2 2 2 2 2 2 2 1 1	2 1 1 1 2 2 + 2 1 2 3	2 + 1 + 2 2 1 .	1 2 + 1 2 1 2 2 3 3
Fraxinus ornus	6	. . + ...	. . + + +	+ 1 + + + + + + +	2 1 2 2 1 1 + 1 + + .	+ + + + + + + .	+ + + + + + + + + .
Ostrya carpinifolia	1	. . . .	. . . . .	. . . .	. 3 2 2 1 2 . 2 . 5 4	4 2 1	4 3 . . 3 3 2 2 . 2
Ostrya carpinifolia	4	. . . + + . .	. + . . .	. . . .	. . . . +	. . . .	+ + . + 1 1 + + 1 +
Ostrya carpinifolia	6	. . . .	. . . . +	. . . + . . . 1 +	1 1 1 2 + 1 + + + 1 .	1 1 1 + . . . +	+ + . . + . + + . .
Fumana procumbens	6	. . . + + + +	. . . . .	. . . . + .	. . . .	. . . .	. . . .
Lathyrus setifolius	6	. + . . + + .	. . . . .	. . . .	. . . .	. . . .	. . . .
Crocus variegatus	6	+ . + + + + .	+	+ . . . . . 1 . .	. . . . + + ...	. . . .	. + . + ...
Carex halleriana	6	. + . + 1 + .	. . . . .	. . . .	. . . . + ...	. + ...	. . . .
Argylobium zanonii	6	. . . + 1 1 .	1 . . + .	. . . . + + + . .	. . . .	. + . . . + . .	. . . .
***Cotinus coggygria* burned**	4	. 1 2 . . 1 .	. . 1 . 2	3 1 3 3 4 2 4 3 3	2 3 + . 4 3 2 2 2 + 2	3 3 3 2 3 2 2 2	. . . .
Erigeron annuus	6	+ + + + + + +	+ + . . +	+ + + + + + . 1 .	1 + + + + 1 . . + + +	+ + . + + + . .	. . . .
Sonchus a.* ssp. *glaucescens	6	+ + . . + + .	+	+ + + + + + + + +	+ + + . + 1 . . + + +	+ + + 1 1 + + +	. . . .
Robinia pseudacacia	6	1 1 1 + + + +	+ + . . .	. + + . + + + 1 .	2 + + 1 1 . + + . 1 +	. + 1 . . . + +	. . . .
Euonymus europaeus	6	+ + + . . . +	. . + . .	+ 1 + + . . + . +	. + . + . . . + + 1 .	+ 1 . + + + . .	. . . .
Dorycnium germanicum	6	+ . + + 1 1 .	. . . . .	. + + + + . + + +	+ + + + . + + ...	. + . + ...	. . . .
Lactuca serriola	6	. + + + + . +	+ 1 + + +	+ . + + + + + 1 .	. + . . + 1 + . + . +	+ . . + . + . .	. . . .
Viola alba	6	. 1 . + + 1 +	+ + . . .	. + . + ... +	. . . . + +	. + . + + . . +	. . . .
Taraxacum erythrospermum	6	+ + . . . + +	. . . . .	+ + + + + . . + +	. . + + + + + . + + 1	+ + + + . + . .	. + ... + . . .
Senecio vulgaris	6	+ . + . . . +	. . . . .	+ 1 . . + + . + .	+ . + + ... + +	. + . + ...	. . . .
Euphorbia cyparissias	6	. 1 + + + 1 +	+ . . . +	+ + . + + + + + +	+ + . . . + . . . + +	. . . . . + . .	. . . . . . + . . .
Crepis setosa	6	. + ...	. . . + .	. + + . + + . . +	. . . + + . . . + + .	+ + ...	. . . .
Celtis australis	6	+ 1 + + . + .	+ . . + .	. . + + . + + . .	. . + . + + + ...	. + + + . + . +	. . . . + . .
Lactuca perennis	6	. . + ...	+	+ . + . + . + + +	. + . . + . . . + . .	. . . . + . . .	. . . .
Vicia cordata	6	+ + + ...	. . + . +	+ . . . + ...	. . . .	. + + + 1 . + .	. . . .
Hedera helix	6	+	. . . . +	+ + + + + . + + +	+ + . 1 + + + + . + +	1 + + + . . 1 +	+ + 1 1 1 1 1 1 3 1
Carex montana	6	. . . . . + .	. . . . .	2 + . + . + . 1 2	1 + 1 1 1 1 1 . . 1 +	. + 2 . . + . 1	+ 1 1 + 1 1 2 . + +
Bromus erectus	6	. . . . + . .	. . . . .	1 . . . 1 . . + 1	2 + 2 . + . . + + . +	2 1 2 1 2 2 2 +	+ . . + . 1 2 + . .
Vincetoxicum hirundinaria	6	. . . .	. . . . .	. . . . +	1 . 1 . . . + . 1 . .	+ + . + . 1 + 1	+ . + + + + + 1 . .
Viola hirta	6	1 . 1	. . + + +	+ + + 1 + + + + +	1 + + 1 . + + + + + .	+ + + + . + . +	+ + + + + + 1 + + +
Carex flacca	6	. . . .	. . . . .	. . . .	1 2 3 . . . . 1 + . .	. + ... +	+ 1 . + + 3 + + + .
Cornus mas	6	. . . .	. . . . +	+ . . + + ...	. . . . 1 + + . + + .	. + + + + + 1 +	. . + + . . + + . .
Thalictrum minus	6	. . . .	. . . . .	. . . . + .	+ + + + . 1 . + . + .	. . . . . + . +	+ . . . + . . + . .
Polygonatum odoratum	6	. . . .	. . . . .	. . . . +	. . . . + + .	+ + ... 1	+ + . . + + + 1 . .
Viola riviniana	6	. . . .	. . . . .	. + . + ... +	+ + + . . . + ...	. . . .	+ . . . . + . + + +
Ruscus aculeatus	4	. . . .	. . . . .	+ . . + ...	. . . 1 . . . . . 1 .	+ 1 + 3 . . 2 .	. . + + ... +
Euonymus europaeus	4	+	. . . . .	+ . + . + ...	. . . . . . + + . . .	. . + + . . + +	+ + + 1 . + + + . +
Melittis melissophyllum	6	. . . .	. . . . .	. . . .	+ + ... 1	1 + . 1 . + 1 2	. . . . . 1 . . . .
Mercurialis ovata	6	. . . .	. . . . .	. . . .	1 1 + ...	+ . + ... +	. . . . 1 + 1 + . .
Cotinus coggygria	1	. . . .	. . . . .	1	. . . . 1 . .	. 1 2 1 . . 1 +	. . 2 3 1 . . . . .
***Juniperus communis* burned**	4	. . . .	. . . . .	. . + ... 2 2	. + + + . 1 . 1 . . +	. . . . . + . .	. . . .
Asparagus acutifolius	4	1 . + ...	. . . . .	. + . + ...	. . . + + + + ...	1 1 . 2 . + + +	+ + + . . . + + + +
Crataegus monogyna	4	. + + . . + .	. . . . .	+ + . + ... +	. . . + + + . . + + +	. + + + . . + .	+ + + 1 . + + . + +
Lathyrus cicera	6	. . . .	. . . . .	. . . .	. . . .	. . . . + . . .	. . . .
Cotinus coggygria	4	2 2 3 3 3 3 2	2 1 1 + 2	2 2 3 2 2 2 3 3 4	2 2 3 3 3 3 3 2 3 2 3	3 3 3 2 2 2 3 2	3 4 4 3 3 2 + 2 + +
Sesleria autumnalis	6	1 1 1 . + 1 .	+ 1 + + 1	. 1 + + 1 2 . 1 1	4 3 3 1 4 + 3 4 3 3 4	3 2 3 3 3 2 3 3	5 + 2 4 3 5 4 5 1 2
Brachypodium rupestre	6	+ 2 2 2 2 2 .	+ + . . .	+ + . . 1 1 1 + 2	3 2 4 . 2 . + 1 2 3 2	3 3 3 3 2 3 4 2	1 1 1 3 4 3 + 2 + .

1——(upper) tree layer, 2——lower tree layer, 4——shrub layer, 6——herb layer. In the table, there are dominant tree species (burned/in red/and living/in green/) as well as diagnostic species for crown fire plots /in violet/, diagnostic species for all burned plots (crown and ground fire)/in blue/, diagnostic species that support a certain degree of fire (appearing in unburned and in plots damaged by ground fire) /in yellow/, and the most common species in the whole dataset /in black/

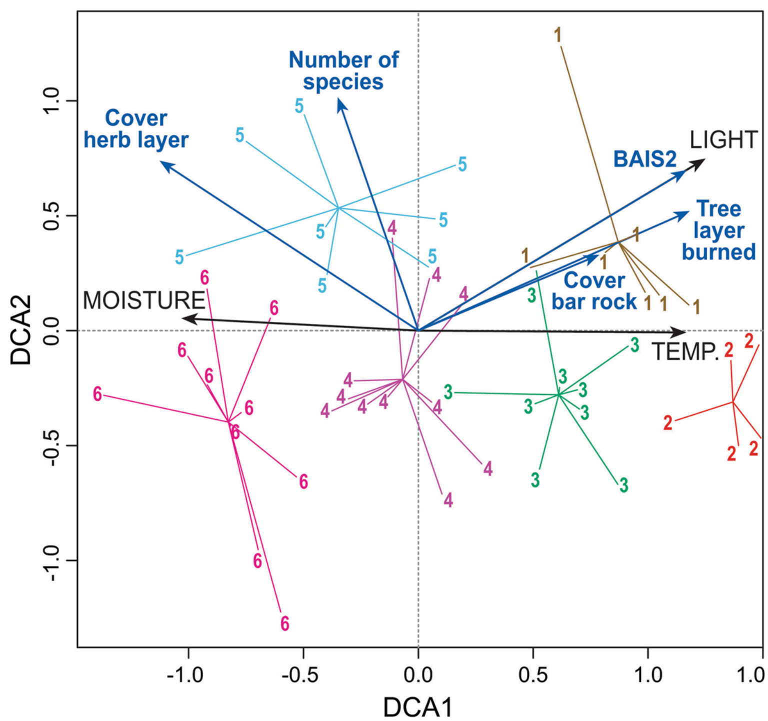


Fig. 6 Diagram of detrended correspondence analysis (DCA). Plots are marked by the TWINSPAN cluster numbers, as in Fig. 4. BAIS2, percentage cover of burned trees, herb layer, bare rocks, and number of species, as well as bioindicators for temperature, moisture and light, are passively projected on the diagram plane. Eigenvalues of the first two axes are 0.3247 and 0.2189, respectively

can be identified in all plots, such as *Cotinus coggygria* and *Sesleria autumnalis*. The ordination prepared by detrended correspondence analysis (DCA) revealed the most important floristic gradient (Fig. 6). In the left part of the ordination plane are the unburned plots, and in the right part are the plots subjected to the crown fire. The passively projected parameters suggest that axis 1 reflects the intensity of fire, with indicators such as BAIS2, cover of burnt trees, and ecological conditions in stands becoming drier, warmer, and lighter towards the right side of the *x* axis.

The correlation between the first axis of the DCA and the BAIS2, the structural characteristics of the sampled plots and the bioindicator values were calculated and tested (Table 2). We found that the BIAS2 correlated positively and strongly with the floristic gradient of axis 1, as did the cover of burned trees and the cover of bare rocks, while the number of plant species and the cover of the herb layer decreased. Among the ecological conditions estimated by the bioindicator values, only temperature EIV changed significantly along axis 1 in the most rigorous analysis.

Table 2 Spearman correlation of the first DCA axis with BIAS, structural properties of plots (number of species, cover of layers and bare rock) and bioindicator values. We used a permutation test, with which we treated bioindicator values

Variable	Axis 1	*p*	Bioindicator	Axis 1	P.par	P.perm	P.modif
BIAS2	0.815	***	Light	0.601	***	**	-
Number of species	− 0.325	*	Temperature	0.629	***	**	*
Cover tree layer	− 0.166	-	Moisture	− 0.48	***	**	-
Cover tree layer burned	0.835	***	Reaction	− 0.088	-	-	-
Cover bare rock	− 0.135	-	Nutrients	0.089	-	-	-
Cover shrub layer burned	0.09	-					
Cover herb layer	− 0.809	***					
Cover bare rock	0.636	***					

P, calculated probability in interval; ***0.001; **0.01; *0.05, as *P.par*, P parametric; *P.perm.*, permutation test; *P.modif*, modified permutation test

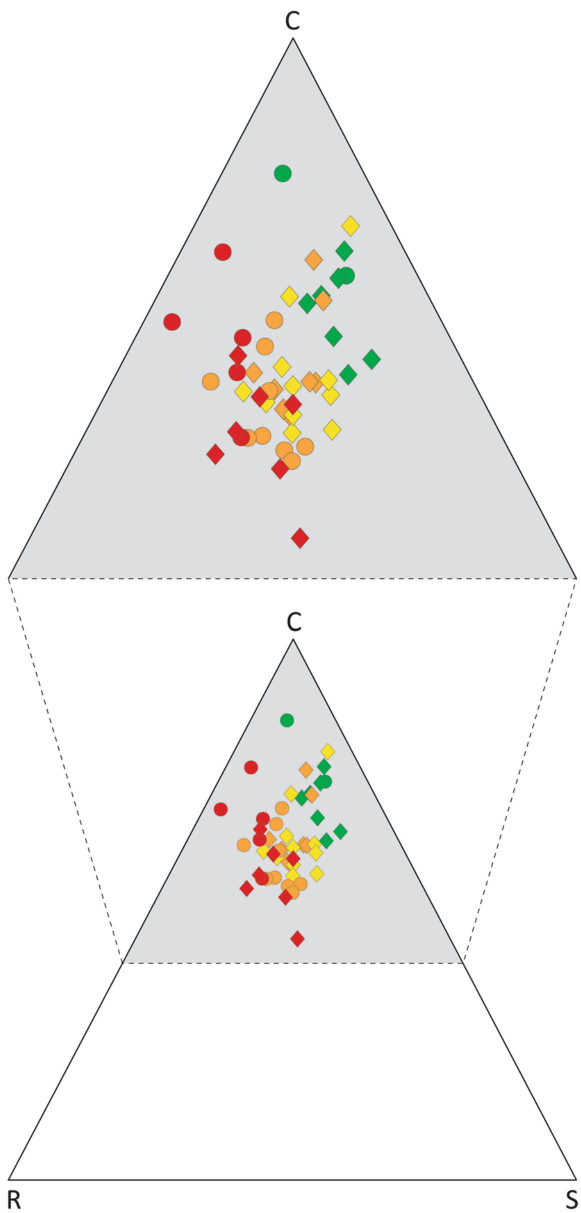


Fig. 7 Ecological strategy competitor (C) and to a minor degree also stress-tolerator (S) change towards a ruderal strategy (R) in burned plots. Red plots are subject to crown fire and orange and yellow to different intensities of ground fire and green unburned forests. Diamonds represent zonal and circles pine forests

Impact of fires on the structure and functions of forests
Ecological strategies (Fig. 7) change significantly under wildfire from the competitor/stress-tolerator strategies in unburned forests to a ruderal strategy in burned ones.

Linear regression (Table 3) showed that the *ecological strategies* describe the changes well. A decrease in competitors and stress tolerators can be observed and an increase in ruderal plants in the burned plots. *Life forms* did not exhibit significant changes along the gradient, except for therophytes, which increased in burned plots. Concerning *chorotypes*, widely distributed (cosmopolitic) species and species of Mediterranean origin are more prevalent in burned plots, while more Eurasian and boreal species are more abundant in unburned plots and in plots burned by less severe ground fire. We observed greater numbers of species in *dispersal class* 1, which exhibited very limited dispersal capability, and class 5, which displayed quite considerable dispersal capability in burned plots. The latter species are anemochorous herbs or dwarf shrubs and are dispersed by pappus or dusty seeds. Class 6 plants were more abundant in less burned and unburned plots. These species are zoochorous; they also spread over long distances. Analysis of the *reproduction traits* showed that resprouting capacity did not change along the gradient, but post-fire seeders emergence increased in burned plots. Many of these are in fact post-fire colonizers.

Discussion
Fires, once rare in our study area, have increased, probably due to climate change and land use changes (Fernandez-Anez et al. 2021; Košiček et al. 2023). In fire-prone areas, such as the Karst plateau, black pine afforestations face problems caused by wildfires, leading to efforts to convert stands into deciduous forests (Gajšek et al. 2015; Diaci et al. 2019). *Pinus nigra*, although thriving in its native southern European range, faces problems in non-native areas due to its inability to regenerate after fires (Tavşanoğlu and Pausas 2018). On the other hand, Pausas et al. (2008) not only highlights the resilience of some Mediterranean ecosystems but also points to the vulnerability of fire-sensitive forests, especially those of human origin.

Congruence between satellite images and orthophoto interpretation
Part of our research involved comparing data on wildfire intensity detected in the field with data obtained through remote sensing (RS), which utilizes satellite imagery and orthophoto interpretation. Similar to Chuvieco (Chuvieco 2009), we found that RS tools are effective in providing precise fire-affected area estimations and burn intensity information. To generate rapid information on fire-affected areas, previous studies have used several metric indices, such as NBR (normalized burn ratio) and BAIS2 (Filipponi 2018). In preliminary studies, we found NBR also correlated reasonably well (Pearson $p = 0.65$), but BAIS2 correlated significantly more, as was already shown in Filipponi (2018). We found that BAIS2

Table 3 Linear regression, in which the independent variable is the position of sample plots' scores along the first DCA axis and dependent variables are plant traits (ecological strategies, life forms, chorotypes, dispersal classes and regeneration strategies) appearing in individual plot

	t value	*F*	Adj*R2*	*p*	Significance
Ecological strategies					
Competitors	− 3,153	9.94	0.154	0.00279	**
Stress-tolerators	− 2,643	6.99	0.109	0.011	*
Ruderals	8,301	68.9	0.581	7.76E−11	***
Life forms					
Chamaephytes	− 0.21	0.044	− 0.0199	0.834	-
Geophytes	− 1.93	5.85	0.055	0.554	-
Hemikriptophytes	0.359	0.129	− 0.0181	0.721	-
Phanerophytes	− 1.94	3.77	0.0534	0.0581	-
Therophytes	5.33	28.46	0.359	2.56E−06	***
Chorotypes					
Mediterranean	2.35	5.53	0.0845	0.0229	*
Eurasian	− 3863	14.93	0.221	3.35E−04	***
Boreal	− 2884	8.31	0.1299	0.005861	**
Cosmopolitic	5699	32.48	0.391	7.19E−07	***
Dispersal classes					
Class 1	4061	16.49	0.2402	1.80E−04	***
Class 2	0.0407	3.08	0.0407	0.0856	-
Class 3	− 1,467	2152	0.02297	0.149	-
Class 4	1,421	2019	0.0204	0.162	-
Class 5	6392	40.86	0.448	6.30E−08	***
Class 6	− 3.72	13.84	0.207	0.000521	***
Regenerations traits					
Resprouting capacity after fire	0.151	0.0229	− 0.0203	0.88	-
Post-fire seedling emergence	7956	63.31	0.56	2.56E−07	***

F, statistics of the test; *AdjR2*, adjusted R2; significance of *p* value in the interval: ***0.001, **0.01, *0.05

correlates well with the fire intensity classifications from photo interpretation and might provide a cost effective and fast solution for monitoring at reasonable resolution and accuracy.

Floristic gradients and plant traits

In the context of the present study, we found differences in vegetation changes under wildfire as in the central part of the Mediterranean Basin (Pausas et al. 2004; Pausas and Keeley 2014). Therefore, a more comprehensive treatment of plant and community responses after fires is therefore needed to understand these environments and address fires (Prior and Bowman 2020).

These habitats are dominated by annuals, which are highly competitive, particularly when winters are relatively wet and summers are hot (Di Biase et al. 2021). On the other hand, it must also be considered that annual plants take advantage of opportunity, while perennials struggle to survive the first year (Thompson 2020). It should be noted that these are largely opportunistic annuals, whose occurrence was even favoured by the abundant precipitation in the subsequent year (van Blerk et al. 2021). However, only two species are known to have heat-stimulated germination (*Argyrolobium zanonii, Trifolium campestre*) (Reyes and Trabaud 2009; Tavşanoğlu and Pausas 2018). But we can find many post-fire colonizers, including *Robinia pseudoacacia* and *Ailanthus altissima*, which are invasive in the region (Čarni et al. 2017; Saulino et al. 2023).

Impact of fires on the structure and functions of forests

Fires cause plant mortality and changes in soil properties, drastically altering the *ecological conditions* of sites. After a fire, areas become drier, warmer, and lighter. These areas provide open habitats that accommodate thermo-xerophilous species (Pausas and Keeley 2019).

It is important to emphasise that in the first year after the fire, we found many anemochorous weeds (i.e., *Sonchus asper*, *Erigeron annuus*, *Lactuca serriola*, *Cirsium*, and *Carduus sp.*, *Senecio inaequidens*). Many of those are invasive species and archaeophytes. We also encountered invasive non-native trees *Ailanthus altissima* and *Robinia pseudoacacia*. Some seeders may have come from neighboring vegetation and belong to the group of post-fire colonizers (Prior and Bowman 2020). Fire acts as a selective agent by clearing space previously occupied by other species, paving the way for light-tolerant, disturbance-tolerant species such as ruderal and invasive species (Klinger and Brooks 2017; St. Clair and Bishop 2019; Stanton et al. 2023), while this open space in competition among species and increased resource availability also provides space for native shrubs and trees to germinate (Thom et al. 2017).

Many species (particularly woody species) regenerate as resprouters after fires and can be treated as obligate resprouters after fires. However, they also have seedling regenerations that are unrelated to the fire and regenerate under favorable conditions (open canopy, nutrients) (Vilagrosa et al. 2014).

These may indicate that the forests of the northern Kras are sensitive to invasions of alien species as well as more pyrophytic species from the Mediterranean regions, due to the lack of native, fire adapted herb species that would fill all the available niches after the fire.

However, there are also native species present, whose abundance was greatly increased by the fire (i.e., *Verbascum phoeniceum*, *Argyrolobium zanonii*, *Medicago sp.*). The adaptation of individual species to changes (climate and fire) is an essential factor (Saxe et al. 2001; Pulsford et al. 2016), and continuous monitoring will be needed to see how this ecosystem adapts to new ecological conditions and how sensitive it is to plant invasions, whether natural or human induced. The most common species on all plots include *Cotinus coggygria*, *Sesleria autumnalis*, and *Brachypodium rupestre*. The mentioned grass species have the ability to resprout and have dense leaf sheaths for protection and rapid recovery after fire (Pilon et al. 2021), which may be an adaptation for fire resistance, but also provide ample fuel for ground fires for the very same reason. Fires can act as a mechanism to maintain a particular habitat, e.g., fire can often maintain shrub and halt succession to forest in the Mediterranean fire prone ecosystems (Kavgacı et al. 2010).

Projections indicate an increasing fire risk in both southern Europe (Dupuy et al. 2020; Senande-Rivera et al. 2022) and the Mediterranean region. Summer temperatures and the severity and frequency of hydrological/ecological droughts are expected to increase, leading to an increase in the severity and frequency of fires caused by anthropogenic climate change (Cos et al. 2022; IPCC et al. 2023). It is important to monitor border regions such as our research area where previously rare fires are becoming more frequent, and we have to consider possible post-fire scenarios and management strategies.

Conclusion

The study confirmed that the analysis of satellite data, the interpretation of orthophotos, and on-site vegetation sampling provide equivalent information on the severity of fires. The results indicate opportunities for further research to develop the method and how all three methods can be optimally combined to obtain a comprehensive assessment of fire severity and determine fire prevention measures.

The analysis showed that many species were found in all sample plots along the gradient representing the fire intensity. This indicate that post-fire recovery may be an autosuccession without intermediate stages (shrub) (Kavgacı et al. 2016; Mantero et al. 2023). We can find a well-developed shrub layer dominated by *Fraxinus ornus* and *Cotinus coggygria* after 1 year, even in forests subjected to a crown fire. As young forests in the region are dominated by *Fraxinus ornus* and have a similar floristic composition (Zupančič and Žagar 2002), the results suggest that recovery could occur without intervention, i.e., no planting or seeding is required, except in pine stands, although the possible occurrence of invasive species (e.g., *Robina pseudoacacia, Ailanthus altissima*) needs to be controlled. However, isolated adaptations of species to fires have been observed (e.g., heat-stimulated germination). Such adaptations could develop in regions exposed to frequent fires and where fires act as an evolutionary factor (Pausas and Keeley 2023). A "wave" of annual, ruderal species can be observed, which will soon disappear if further fires do not reopen the landscape and provide them with suitable sites.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-024-00267-x.

Additional file 1: Table S1. Table of sampled plots.

Additional file 2: Table S2. Statistics of traits in clusters.

Additional file 3: Appendix S1. Correlation and significance test between category of damage and BAIS2 in the whole area.

Additional file 4: Appendix S2. Box-Whiskers diagrams of BAIS2 values grouped according to category of damage in the whole area.

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Authors' contributions

AČ, AJ, and MBV conceived the research idea; AČ, AJ, LČ, and MBV collected field data; AJ, LČ, and MBV prepared the GIS analysis, AČ and AJ prepared the numerical analysis, AČ, LČ, and AJ prepared the draft version of the manuscript and all authors contributed significantly to the editing.

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Availability of data and materials

Not applicable.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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