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The footprint of large wildfires on the multifunctionality of fire-prone pine ecosystems is driven by the interaction of fire regime attributes

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Abstract

Background Mediterranean ecosystems dominated by *Pinus pinaster* Ait. (maritime pine) are subject to a shift from fuel-limited to drought-driven fire regimes, characterized by an increasing wildfire extent, recurrence, and severity. Previous studies have not addressed the interacting effects of fire recurrence and severity on the ecosystem multifunctionality (EMF) of maritime pine forests, although complex relationships between such fire regime attributes are expected. Here, we evaluated the medium-term effects of fire recurrence and severity on the EMF response of unmanaged, native pine ecosystems dominated by *Pinus pinaster* in the western Mediterranean Basin. We considered four key ecosystem functions computed from functional indicators (carbon regulation, decomposition, soil fertility, and plant production), which were pooled into an EMF construct. The fire regime effects on the trade-offs and synergies between the considered ecosystem functions were also analyzed.

Results Multiple ecosystem functions responded differentially to fire recurrence and severity. Fire recurrence had a strong effect on soil fertility, decomposition, and plant production functions. No significant effects of fire severity on any of the individual functions were detected. However, both fire regime attributes interacted to determine soil fertility and decomposition functions, suggesting that their performance is only impaired by fire severity when fire recurrence is low. The differing responses to the fire regime attributes among ecosystem functions fostered a significant EMF response to fire severity and its interaction with fire recurrence, indicating that the effect of fire severity on EMF was stronger under low fire recurrence scenarios, even when relationships between individual functions and fire severity were weak. Fire recurrence caused significant trade-offs between functions to emerge. However, these trade-offs were not strong enough to differ significantly from the intrinsic trade-offs (i.e., regardless of the fire regime) of maritime pine ecosystems.

Conclusions Our results indicated the need to use an integrative approach to assess the response of ecosystem functioning to the fire regime in maritime pine ecosystems. Adaptive management responses are necessary towards the minimization of repeated burnings and the reduction of the fuel load in unmanaged maritime pine stands of the western Mediterranean Basin with similar characteristics to those analyzed in this study.

Keywords Ecosystem multifunctionality, Fire recurrence, Fire severity, Maritime pine, *Pinus pinaster*, Ecosystem functions trade-offs

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Resumen

Antecedentes Los ecosistemas mediterráneos dominados por pino marítimo (Pinus pinaster Ait.) están sujetos a cambios en regímenes de fuego limitados por el combustible hacia regímenes conducidos por la sequía, y caracterizados por un incremento en la extensión, recurrencia y severidad de los incendios. Estudios previos no han abordado los efectos interactivos de la recurrencia y severidad del fuego en la multifuncionalidad de los ecosistemas (EMF) en bosques de pino marítimo, aunque cabe esperar relaciones complejas entre estos atributos del regimen de fuego. En este trabajo, evaluamos los efectos a medio plazo de la recurrencia y severidad en la respuesta de la multifuncionalidad de los ecosistemas (EMF) de bosques nativos dominados por pino marítimo no gestionados en la cuenca Mediterránea occidental. Consideramos cuatro funciones clave calculadas a partir de indicadores funcionales (regulación del carbono, descomposición, fertilidad del suelo, y producción egetal) los cuales fueron agrupados en un constructo EMF. Los efectos del régimen de fuego sobre las sinergias y contrapartidas entre las funciones ecosistémicas también fueron analizados.

Resultados Múltiples funciones ecosistémicas respondieron diferencialmente a la recurrencia y severidad. La recurrencia del fuego tuvo un efecto muy fuerte en la fertilidad del suelo, en la descomposición y en las funciones de producción. Ningún efecto significativo de la severidad del fuego fue detectado en ninguna de las funciones individuales. Sin embargo, los atributos de ambos regímenes de fuego interactuaron para determinar las funciones de fertilidad y descomposición, sugiriendo que su rendimiento es afectado por la severidad solo cuando la recurrencia del fuego es baja. Las diferentes respuestas a los atributos de los regímenes de fuego entre las funciones ecosistémicas promueven una respuesta significativa de la EMF a la severidad del fuego y su interacción con la recurrencia, indicando que el efecto de la severidad sobre la EMF fue más fuerte bajo escenarios de baja recurrencia, aun cuando las relaciones entre funciones individuales y la severidad fueran débiles. La recurrencia del fuego causó la aparición de ontrapartidas significativas entre funciones. Obviamente, estas contrapartidas no fueron lo suficientemente fuertes para diferir significativamente de aquellas intrínsecas (i.e., independientemente del régimen de fuego) en los ecosistemas de pino marítimo.

Conclusiones Nuestros resultados indican la necesidad de usar una aproximación integrada para determinar la respuesta del funcionamiento al régimen de fuego en ecosistemas de pino marítimo. Respuestas de manejo adaptativo son necesarias para la minimización de quemas repetidas y la reducción de la carga de combustible en rodales de pino marítimo no gestionados en la cuenca Mediterránea, con características similares a aquellos analizados en este estudio.

Background

Mediterranean forest ecosystems are distributed over ca. 100 Mha throughout the Mediterranean Basin (Lanly 1997) and have been subject to frequent wildfires for millennia (Keeley et al. 2012) as in other Mediterranean climate-type regions across the globe (Pausas and Keeley 2009; Xofis et al. 2020). Under natural fire disturbance regimes, wildfires are considered as an evolutionary force (Seidl et al. 2014) not only shaping species fire-adaptive traits of Mediterranean plant communities (Keeley et al. 2011) but also the historical landscape structure related to the patchiness of fire effects (i.e., pyrodiversity; Jones and Tingley 2022). However, altered fire disturbance regimes currently observed in Mediterranean forests have led to a heightened concern about their unprecedented consequences on ecosystem functions and processes (Lasslop et al. 2019), as well as on ecosystem services' provisioning to society for human wellbeing (Huerta et al. 2022).

The interaction between human-induced drivers of global change in fire-prone ecosystems of southern European countries is responsible for the switch from fuel-limited to drought-driven fire regimes (Fernandes et al. 2014), characterized by an increasing wildfire extent, recurrence, and severity (Vilà-Cabrera et al. 2018; Rodrigues et al. 2023). First, socioeconomic transitions involving rural abandonment over the last decades (Pausas and Keeley 2009) led to a concomitant cessation of forest wood gathering, traditional agriculture, and livestock farming practices (Fernandes 2013). These land-use changes, together with the lack of adaptive management strategies (Vilà-Cabrera et al. 2018), have exacerbated the simplification of the landscape mosaic (Pelorosso et al. 2011) and thus the load and connectivity of flammable fuels (Moreira et al. 2011). Second, extended periods of summer drought and elevated temperatures, attributable to anthropogenic climate change (Turner 2010), have intensified fuel dryness conditions conducive to extreme fire events (Ruffault et al. 2018).

Global change feedbacks are especially relevant in fire-prone ecosystems dominated by *Pinus pinaster* Ait. (maritime pine), one of the most widely distributed pine forests together with *Pinus halepensis* Mill. (Aleppo pine), in Mediterranean Basin lowlands and the Atlantic coast of Portugal (Tapias et al. 2004). Maritime pine forests are native to the western Mediterranean Basin (Tapias et al. 2004), but their distribution in this region has been expanded by plantation development in the mid-twentieth century for wood production and resin tapping (Proença et al. 2010; (Fernandes et al. 2016a). In addition, the species has been introduced in temperate regions of Australia, South Africa, or Chile, among other countries, due to its wide tolerance to soil types and climatic conditions (Tapias et al. 2004; Santamaría 2015). Maritime pine stands are intrinsically flammable because of the structure, physicochemical properties and accumulation rates of the litter (Fernandes and Rigolot 2007). Crowning potential is also elevated by the common presence of a well-developed understory, usually dominated by fine-fuel rich species (Fernández-García et al. 2019a), and ladder fuels that enhance vertical fuel continuity (Castedo-Dorado et al. 2012). As an adaption to frequent, stand-replacing crown fires in several provenance regions of the western Mediterranean Basin, *Pinus pinaster* populations feature early flowering (4–10 years) and are able to massively release seeds that are protected from fire in serotinous cones (Tapias et al. 2004; Calvo et al. 2008; (Fernández-García et al. 2019a). The opening of serotinous cones occurs progressively during a period of two to three days following the thermal shock, which leads to an effective seed dispersal after the fire has been extinguished (Fernandes and Rigolot 2007). Regardless of the fire-evader strategy of the species to attain successful post-fire recruitment, fuel management is a key element of maritime pine stands such that stand production and fire resistance objectives are simultaneously met (Fernandes and Rigolot 2007). In this context, the modification of the understory fuel load and structure through mechanical treatments or prescribed burning is considered essential to minimize surface fire intensity (Fernandes and Botelho 2004). Similarly, the removal of ladder fuels by pruning and stand thinning is mandatory to minimize crowing potential in the stand (Fernandes and Rigolot 2007; Jiménez et al. 2016). These treatments are anticipated to effectively reduce fire hazard while promoting stand production and wood quality (Chambonnet 2005). However, the implementation of active fuel management practices has been discontinued in many cases (Rodriguez-Vallejo and Navarro-Cerrillo 2019; Alegria et al. 2021) because of the low demand of forest resources in maritime pine ecosystems by rural populations (e.g., resin tapping; Torres et al. 2016). This situation is particularly aggravated in the transition area of Atlantic and Mediterranean climatic conditions in the westernmost part of the Mediterranean Basin, where high plant productivity and increased summer drought coexist (Fernandes and Rigolot 2007). Together with fuel build-up, the expansion of the wildland-urban interface to the vicinity of unmanaged maritime pine stands raised fire ignition probability and thus the recurrence of extreme wildfire events (Fernandes et al. 2014; Fuentes et al. 2018), with often catastrophic results in populated areas (Pausas and Keeley 2009).

The effects of recurrent and severe wildfires in the vegetation and soils of fire-prone pine ecosystems are well documented (e.g., Calvo et al. 2008; Calvo et al. 2016; Taboada et al. 2017; Fernández-García et al. 2019a, 2020a; Fernández-Guisuraga et al. 2022a). In these scenarios, seedling recruitment may be hampered due to immaturity risk of seeder species (Calvo et al. 2008), seed bank damage (Maia et al. 2012), and high seedling mortality in the early post-fire stages (Fernandes et al. 2008). Similarly, changes in the composition and structure of the woody understory community can undermine the establishment and growth of pine seedlings and saplings through facilitative or competitive interactions (Taboada et al. 2017; (Fernández-Guisuraga et al. 2022a). Resprouter species in the understory can easily recolonize the open spaces created by stand-replacing wildfires (Calvo et al. 2003). Additionally, shrubs that depend on fire-stimulated recruitment from existing seed banks (Taboada et al. 2017) or opportunistic species that rely on seed dispersal from unburned patches nearby (Arnan et al. 2013) could rapidly colonize recently burned areas. In addition to changes in the vegetation composition and structure, recurrent and severe wildfires may entail intense heat-induced effects on physicochemical (Mataix-Solera et al. 2011; Romeo et al. 2020) and biological (e.g., Rincón and Pueyo 2010; Fernández-García et al. 2020a>; Sáenz de Miera et al., 2020) soil attributes, particularly in the first soil centimeters (Badía et al. 2017). However, these shifts are highly variable as a function of (i) the considered post-fire time period (Muñoz-Rojas et al. 2016) due to the transient nature of heat-induced effects (Hart et al. 2005) and (ii) the relevance of biotic feedbacks exerted by above and belowground communities (Adkins et al. 2020). For example, previous research evidenced that frequent wildfires may induce soil organic matter and nutrient depletion as a consequence of successive heating, low vegetation recovery, and subsequent soil erosion processes (Knicker 2007*and references therein*). However, increased fire recurrence has been also reported to promote the establishment of more productive, resprouter plant species (Nano and Clarke 2011; Pausas and Keeley 2014), thus increasing soil organic carbon (SOC) and nutrients concentration in the short-term after fire (Moghli et al. 2022).

Due to the anticipated contrasting effects of recurrent and severe wildfires on several ecosystem attributes or functional indicators (Moghli et al. 2022), the use of an integrative methodology to assess the impact of fire regimes on the response of fire prone ecosystems (e.g., ecosystem multifunctionality (EMF) evaluation) is considered more appropriate than the common use of single indicators to avoid biased perceptions (Lucas-Borja et al. 2021). Also, the use of single attributes is not consistent because ecosystems are valued for their capability of maintaining several functions simultaneously (Hector and Bagchi 2007; Hedo et al. 2015), and complex tradeoffs can emerge between multiple ecosystem attributes (Byrnes et al. 2014). Previous studies have seldom considered the effect of fire recurrence (Moghli et al. 2022) and severity (Huerta et al. 2022) on the EMF, nor the interacting effects of fire recurrence and severity, although we expect complex relationships between such fire regime attributes in the functioning of fire-prone pine ecosystems (Fernández-García et al. 2019a, 2020a). Also, to the best of our knowledge, there are no studies using an integrative EMF methodology to assess ecosystem response to fire in pine ecosystems dominated by maritime pine worldwide and particularly in the Mediterranean Basin. Altogether, these knowledge gaps limit our understanding about processes driving ecosystem resilience and multifunctionality dynamics in the current context of global change. We aimed to bridge these gaps by evaluating the medium-term (three years after wildfire) effects of fire recurrence and severity on the EMF response of a burned pine ecosystem dominated by *Pinus pinaster* in the western Mediterranean Basin. We considered four key ecosystem functions computed from functional indicators: (1) carbon (C) regulation, (2) decomposition, (3) soil fertility, and (4) plant production. The fire regime effects on the trade-offs and synergies between the considered ecosystem functions were also analyzed. We focused on medium-term effects because, at this time scale, abiotic and biotic feedbacks are expected to drive long-term ecosystem stability (Hart et al. 2005; Adkins et al. 2020).

Methods

Study site

The study site is located inside the perimeter of a stand-replacingwildfire that occurred in summer 2012 (19–21 August) on Sierra del Teleno mountain range (western Mediterranean Basin; Fig. 1). The wildfire burned 11,602 ha mostly covered by *Pinus pinaster* ecosystems native to the study site, which has been corroborated by paleobotanical studies covering the last 1000 years (Santamaría 2015). However, maritime pine forests have undergone an important expansion in the last two centuries in the site owing to an increasing concern for the conservation of the stands during their exploitation (Santamaría 2015). Fuel hazard reduction treatments of these stands ceased in the last decade of the twentieth century (Taboada et al. 2021). The Haines index (Haines 1988) reached its highest value during the initiation and spread of the wildfire, indicative of extreme fire weather conditions (García-Llamas et al. 2019). There were no substantial unburned islands within the fire scar.

The site lies at an altitude between 836 and 1499 m, in the limit of the Mediterranean climate region (Fernández-Guisuraga et al. 2022b). The mean annual temperature and the annual precipitation are 10 °C and 640 mm respectively, with less than 2 months of summer drought (Ninyerola et al. 2005). The dominant soil types at a spatial resolution of 1 km (Jones et al. 2005) are acidic and classified as Haplic Umbrisols and Dystric Regosols according to the Harmonized World Soil Database (Nachtergaele et al. 2010). Three years after the wildfire, the vegetation in the study site was mainly dominated by *Pinus pinaster* (obligate seeder) regeneration stands in seedling and sapling growth stages, with a well-developed shrub community dominated by the resprouters *Pterospartum tridentatum* (L.) Willk. and *Erica australis* L., as well as the obligate seeder *Halimium lasianthum* subsp. *alyssoides* (Lam.).

Fire regime characterization

We used a Landsat Thematic Mapper (TM) false color composite (R = band 5; G = band 4; B = band 1) to digitize the perimeter of a previous large wildfire occurred in 1998 (around 3000 ha) within the study site. Therefore, we defined two fire recurrence scenarios within the 2012 fire scar (Fig. 1): low recurrence (one wildfire in the last 15 years) and high recurrence (two wildfires in the last 15 years) (Fernández-Guisuraga et al. 2019), which is consistent with the fire return intervals over the last decades in the maritime pine stands in the region (Taboada et al. 2021). The two fire recurrence scenarios have similar mean altitude (low recurrence = 971 ± 99 m; high recurrence = 1,035 ± 91 m) and slope (low recurrence = 5.7 ± 4.4º; high recurrence = 7.2 ± 4.9º), and soil types are homogeneously distributed in them (field observation). Therefore, it can be assumed that the variability in abiotic conditions between fire recurrence scenarios is minimal. The areas affected by a single fire event (low recurrence) had a mean pine density of 906 individuals/ha in the pre-fire situation (stand age = 35–95 years old). The areas affected by two fire events (high recurrence) featured a pre-fire mean pine density of 13 individuals/ha (stand age = 12–14 years old) (Taboada et al. 2018). The cover of the understory community in

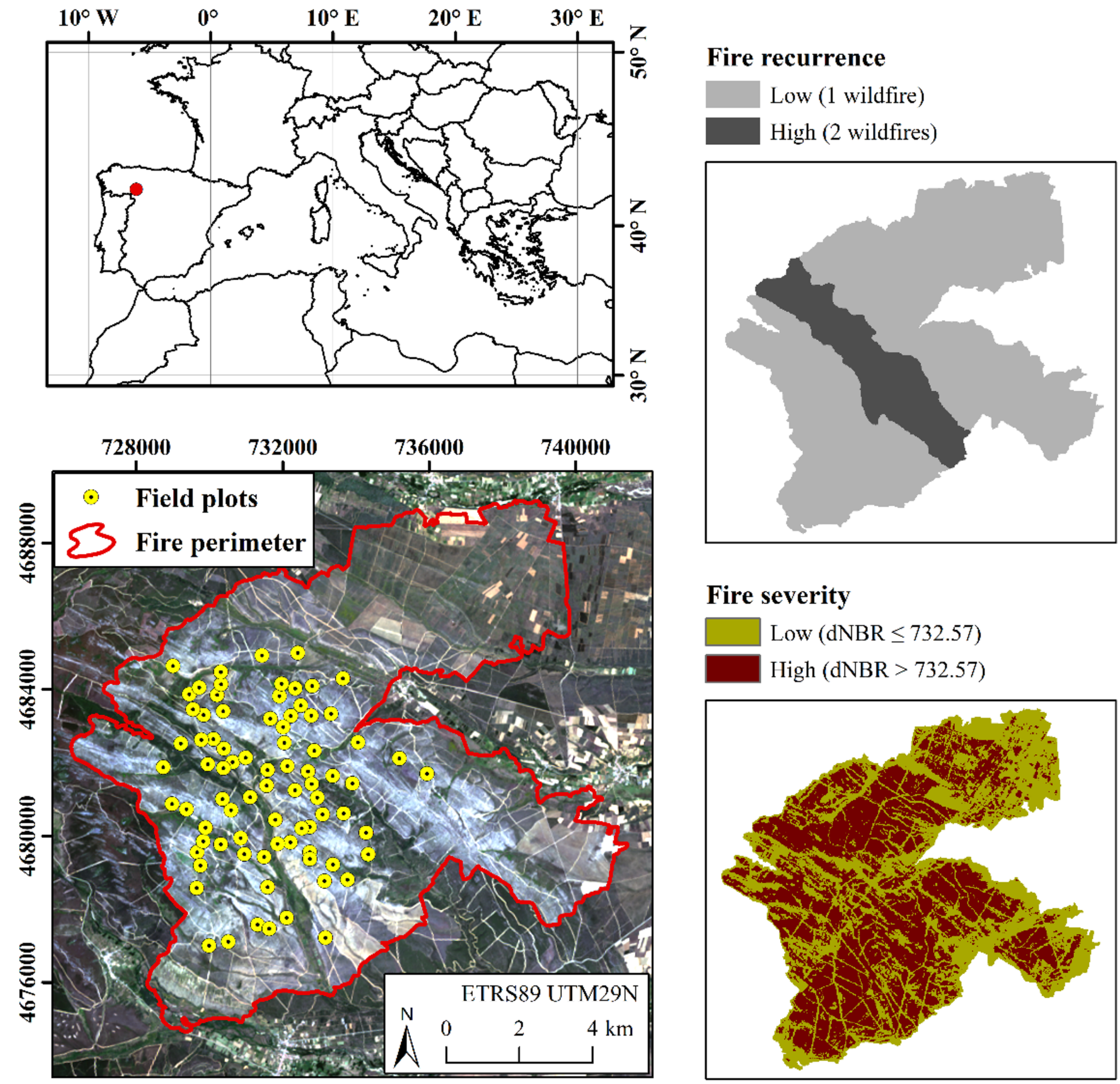

Fig. 1 Spatial patterns of fire recurrence and severity, as well as the location of the field plots within the fire scar of the wildfire occurred in summer 2012 in the Sierra del Teleno mountain range (western Mediterranean Basin)

the pre-fire situation was remarkably higher in the high fire recurrence scenarios than in areas burned only once (regional Forest Service of Castilla y León, personal communication). Subsequent to the 1998 and 2012 wildfires, high-intensity salvage logging of the burned *Pinus pinaster* stands was implemented by the regional Forest Service, with 70–80% of the merchantable burned wood (> 10 cm diameter) removed.

Fire severity, as a descriptor of aboveground biomass consumption (Morgan et al. 2014) of the 2012 wildfire in the study site, was estimated using the differenced Normalized Burn Ratio (dNBR; Key 2006). The dNBR was computed from bottom-of-atmosphere (BOA) reflectance data of bands 4 (near infrared) and 7 (short-wave infrared) of pre (September 20, 2011) and post-fire (September 6, 2012) Landsat 7 Enhanced Thematic Mapper Plus (ETM+) Collection 1 Level-1 scenes (Path 203/Row 31) downloaded from the USGS Earth Explorer data portal (http://earthexplorer.usgs.gov/). To obtain a Landsat 7 ETM + BOA product, we performed an atmospheric and topographic correction to the optical bands of pre and post-fire scenes using the ATCOR algorithm (Richter and Schläpfer 2018), which was parametrized following the methodology of Fernández-Guisuraga et al. (2021). The dNBR was computed following the Eq. 1 and Eq. 2.

$$NBR_{ETM+} = (Band4 - Band7)/(Band4 + Band7) \quad (1)$$

$$dNBR = 1000\left(NBR_{pre} - NBR_{post}\right) - offset \quad (2)$$

The offset term in Eq. 2 is calculated as the mean dNBR value from pixels in unchanged areas between pre- and post-fire scenes outside the wildfire perimeter (Parks et al. 2014). We chose the dNBR index because it is used operationally as the primary spectral index within the European Forest Fire Information System (EFFIS) and in the Monitoring Trends in Burn Severity (MTBS) program in the USA, together with the Relative dNBR (RdNBR; Miller et al. 2009). Also, the dNBR index is the methodological reference for the estimation of fire severity in initial assessments (Soverel et al. 2010) and previously offered a higher performance than the RdNBR in the study site (Fernández-García et al. 2018a). The dNBR fire severity retrieval was validated through the Composite Burn Index (Key and Benson 2005), a standard and integrative multi-strata approach to conduct initial assessments of fire severity in the field and validate remote sensing products (Holden et al. 2009). We measured the CBI in 54 field plots of 30 m × 30 m 3 months after the wildfire. The plots were established in the field using a random sampling design. The linear relationship between the dNBR and the CBI had a coefficient of determination (R^2) of 0.86. The equation of the linear model and CBI thresholds proposed in the literature (Quintano et al. 2017; (Fernández-García et al. 2018b) were used to establish two fire severity categories based on the dNBR (Fig. 1): low ($dNBR \leq 732.57$) and high ($dNBR > 732.57$).

We identified four recurrence-severity scenarios within the 2012 fire scar by overlaying the fire recurrence and severity classes (low recurrence-low severity, low recurrence-high severity, high recurrence-low severity and high recurrence-high severity). Three years after the 2012 wildfire, resprouter shrub species dominated over obligate seeder shrubs in the high fire recurrence scenarios, the opposite pattern being observed in areas burned with low fire recurrence, characterized by a higher cover of obligate seeders shrubs and pine seedlings/saplings (Fernández-Guisuraga et al. 2020). Fire severity was inversely related to the recovery of *Pinus pinaster* in both fire recurrence scenarios, but no clear effect of fire severity on the shrub community recovery emerged (Fernández-Guisuraga et al. 2019).

Field sampling and laboratory analyses

In summer 2015 (3 years after the last wildfire), we established 80 field plots of 2 m × 2 m for vegetation and soil sampling following an equally stratified random design, using the fire recurrence and severity scenarios as strata (Fig. 1). The field plots were located in burned maritime pine ecosystems within the fire perimeter using as reference the Spanish Forest Map and ensuring a minimum distance of 500 m from the fire perimeter. We used a GPS receiver in real time kinematics mode ($RMSE_{X,Y}$ < 3 cm) to locate the plots in the field. First, the vascular plants in each plot were assigned to a growth form according to plant habit and height (Vashistha et al. 2011): (1) trees, (2) shrubs and subshrubs, and (3) forbs and grasses. Then, we measured vegetation cover by growth forms in steps of 5% through a visual estimation method (Calvo et al. 2008).

A composite soil sample made of four subsamples of the uppermost 3 cm was collected from the cardinal points of each plot. Prior to sample collection, we removed litter and charred woody debris. The samples were sieved in the field with a 2-mm mesh size and then were separated into two fractions. One fraction was air-dried for 1 week in the laboratory before analyzing soil chemical properties. The other fraction was stored at 4 ºC in the field and delivered to the laboratory, where they were frozen at − 20 ºC until soil enzyme analyses.

Six soil functional indicators were determined as proxies of several ecosystem functions and EMF, together with vegetation cover by growth forms (Table 1). SOC was determined by the Walkley-Black dichromate oxidation method (Nelson and Sommers 1982). Available phosphorous (P) was analyzed on a UV Mini 1240 spectrophotometer at a wavelength of 882 nm after digestion with $HClO_4$ following the method of Olsen et al. (1954). Total nitrogen (N) was determined by a distillation method using an automatic micro-Kjeldahl analyzer (Bremner and Mulvaney, 1982). Acid phosphatase (phosphate-monoester phosphohydrolase) and β-glucosidase (β-D-glucoside glucohydrolase) enzyme activities were determined using the procedure of Tabatabai (1994), and urease (urea amidohydrolase) activity using a PharmaSpec 1700 spectrophotometer following the method of Kandeler and Gerber (1988).

Ecosystem multifunctionality calculation and data analyses

The ecosystem functional indicators measured in the field plots (SOC, enzyme activities, total N, available P, and vegetation cover by growth forms) were assigned to one of the four ecosystem functions considered in this

Table 1 Functional indicators considered as proxies of ecosystem functions and ecosystem multifunctionality (EMF)

Ecosystem function	Functional indicator	Unit
Carbon regulation	Soil organic carbon (SOC)	%
Decomposition	β-Glucosidase activity	μmol_{p-NP} $hour^{-1}$ g^{-1} soil
	Urease activity	μmol_{N-NH4+} $hour^{-1}$ g^{-1} soil
	Acid phosphatase activity	μmol_{p-NP} $hour^{-1}$ g^{-1} soil
Soil fertility	Total nitrogen (N)	%
	Available phosphorous (P)	mg kg^{-1}
Plant production	Cover of trees	%
	Cover of shrubs and subshrubs	%
	Cover of forbs and grasses	%

study: C regulation, decomposition, soil fertility, and plant production (Table 1). SOC pool is the largest carbon reservoir in the short and medium-term after fire in fire-prone Mediterranean ecosystems (Kaye et al. 2010; Fonseca et al. 2022). Fire-induced changes in SOC have direct and indirect effects on soil organic matter turnover (Maslov et al. 2020), ecosystem productivity (Fernández et al. 1999), and, ultimately, on the global C cycle and the climate system (Novara et al. 2011). Therefore, SOC was used as a proxy for C regulation function. Decomposition function was estimated from soil enzyme activities (β-glucosidase, acid phosphatase, and urease) because of their essential role in catalyzing biochemical reactions related to soil organic matter degradation and nutrient turnover (Sinsabaugh et al. 2008; Kotroczó et al. 2014). Total N and available P content in the soil were used as a proxy for soil fertility function. Besides controlling many biogeochemical reactions in terrestrial ecosystems (Maestre et al. 2012), these nutrients sustain a wide variety of physicochemical processes in organisms and strongly limit primary production in most ecosystems worldwide (Elser et al. 2007; Fatemi et al. 2016). Finally, plant production function was assessed from vegetation cover by growth forms, which is considered as a strong proxy for aboveground biomass distributed across the plant community strata, and thus for ecosystem productivity in many biomes (Maestre et al. 2012; Brun et al. 2019*and references therein*), including Mediterranean ecosystems (Madrigal-González et al. 2022).

According to Maestre et al. (2012), we assumed that higher values of each functional indicator corresponded to higher performance of the underlying ecosystem function. The average of the top-functioning 5% plots for each raw indicator were used to standardize them into a percentage of maximum performance (Delgado-Baquerizo et al. 2016). The standardized functional indicators were pooled into the four considered ecosystem functions. EMF was computed through the averaging approach of the individual functions (Maestre et al. 2012). The standardization by the top-functioning plots and the averaging approach are among the most widely implemented in the literature because of the straightforward interpretation of the ecosystem capability to sustain multiple functions (Maestre et al. 2012; Byrnes et al. 2014; Huerta et al. 2022; Fernández-Guisuraga et al. 2023).

The multivariate associations between the pool of ecosystem functions (i.e., C regulation, decomposition, soil fertility, plant production) and fire recurrence, fire severity, and their interaction, were explored through a permutational multivariate analysis of variance (PERMANOVA) implemented with 1000 random permutations. Then, we fitted ordinary least square (OLS) models (two-way analysis of variance (ANOVA)) to assess whether the fire regime had a significant effect on each ecosystem function and EMF. Therefore, the dependent variables in OLS models were as follows: (i) C regulation, (ii) decomposition, (iii) soil fertility, (iv) plant production, and (v) EMF. The predictors were the fire recurrence, severity, and their interaction. Finally, the trade-offs and synergies between ecosystem functions in the different fire recurrence and severity scenarios were unraveled through Pearson correlation heatmaps. Following the method of Moghli et al. (2022) and Felipe-Lucia et al. (2018), we first estimated intrinsic synergies and trade-offs between functions, regardless of the fire regime, by computing Pearson correlations between OLS model residuals for each function using fire recurrence and severity as predictors. Second, we removed the influence of shared responses to fire severity through the calculation of Pearson correlations between OLS model residuals for each function using fire severity alone as predictor. Third, we removed the effect of shared responses to fire recurrence in the same way, but using fire recurrence as the only predictor in OLS models for each function. Significant differences between the correlations of each pair of functions among the three correlation matrices were tested using the Zou's confidence interval (Zou 2007).

Statistical significance was considered at 5% level (*p-values* lower than 0.05) for all analyses, which were performed in R 4.2.2 (R Core Team, 2022) using *vegan* (Oksanen et al., 2020), *corrplot* (Wie and Simko 2021) and *cocor* (Diedenhofen and Musch 2015) packages.

Results

The analysis of the behavior of individual ecosystem functions in the medium-term after fire (Table 2; Fig. 2A–D) showed that fire recurrence had a strong effect (*p-values* < 0.01) on soil fertility, decomposition, and plant production functions. No significant effects of fire severity on any of the functions were detected (*p-values* > 0.05). However, both fire regime attributes interacted (*p-values* < 0.01) to determine soil fertility and decomposition functions. Specifically, the C regulation function did not show a significant response (*p-values* > 0.05) to changes in fire recurrence and severity (Table 2; Fig. 2C). The soil fertility function significantly declined (*p-value* < 0.001) with fire recurrence (Table 2; Fig. 2A), the decomposition function following the opposite pattern (Table 2; Fig. 2B). The significant interaction between fire recurrence and severity evidenced in soil fertility and decomposition functions (*p-values* < 0.01) indicates that the performance of both functions was only impaired by fire severity when fire recurrence is low (*p-values* < 0.05). The response of plant production function was only affected by fire recurrence (Table 2; Fig. 2D), showing a significant increase (*p-value* < 0.01) in scenarios of high fire recurrence.

The differential responses of the individual ecosystem functions to the fire regime attributes translated into a significant EMF response to fire severity (*p-value* < 0.05) and its interaction with fire recurrence (*p-value* < 0.01), but the isolated effect of fire recurrence was not significant (*p-value* > 0.05) (Table 2; Fig. 2E). The interaction between fire recurrence and severity indicates that high fire severity had a negative effect on EMF only under low fire recurrence scenarios (*p-value* < 0.01).

These results are consistent with the PERMANOVA fitted to the pool of individual ecosystem functions, which were not significantly associated with fire recurrence (*pseudo-F* = 0.254; *p-value* = 0.636), but with fire severity (*pseudo-F* = 6.025; *p-value* = 0.013) and the interaction between both fire regime attributes (*pseudo-F* = 9.757; *p-value* = 0.003).

There were no significant intrinsic trade-offs between ecosystem functions/EMF, i.e., without the influence of the fire regime (Fig. 3A). The same pattern was observed when considering the environmental filter exerted by fire severity (Fig. 3C). We evidenced that fire recurrence caused two significant trade-offs to emerge: between soil fertility and both decomposition and plant production functions (Fig. 3B). However, there were no significant differences in the Pearson correlation coefficients of each pair of functions between the three correlation matrices

Table 2 Effect of fire recurrence (R) and severity (S), as well as their interaction (R×S), on the individual ecosystem functions and ecosystem multifunctionality (EMF). The significance of ordinary least square (OLS) model parameters is represented by ***(*p-value* < 0.001), **(*p-value* < 0.01), *(*p-value* < 0.05), and ns (*p-value* > 0.05)

Response variable	df	Parameter	Sum of squares	*F*-value	*p*-value	
C regulation	1	R	0.034	1.473	0.228	ns
	1	S	0.002	0.104	0.748	ns
	1	R×S	0.087	3.824	0.054	ns
Decomposition	1	R	0.416	24.269	< 0.001	***
	1	S	0.031	1.790	0.185	ns
	1	R×S	0.139	8.120	0.006	**
Soil fertility	1	R	0.697	42.070	< 0.001	***
	1	S	0.060	3.628	0.060	ns
	1	R×S	0.168	10.129	0.002	**
Plant production	1	R	0.242	6.964	0.009	**
	1	S	0.119	3.340	0.071	ns
	1	R×S	0.000	0.000	0.984	ns
EMF	1	R	0.001	0.124	0.726	ns
	1	S	0.041	5.813	0.018	*
	1	R×S	0.072	10.142	0.002	**

df, degrees of freedom

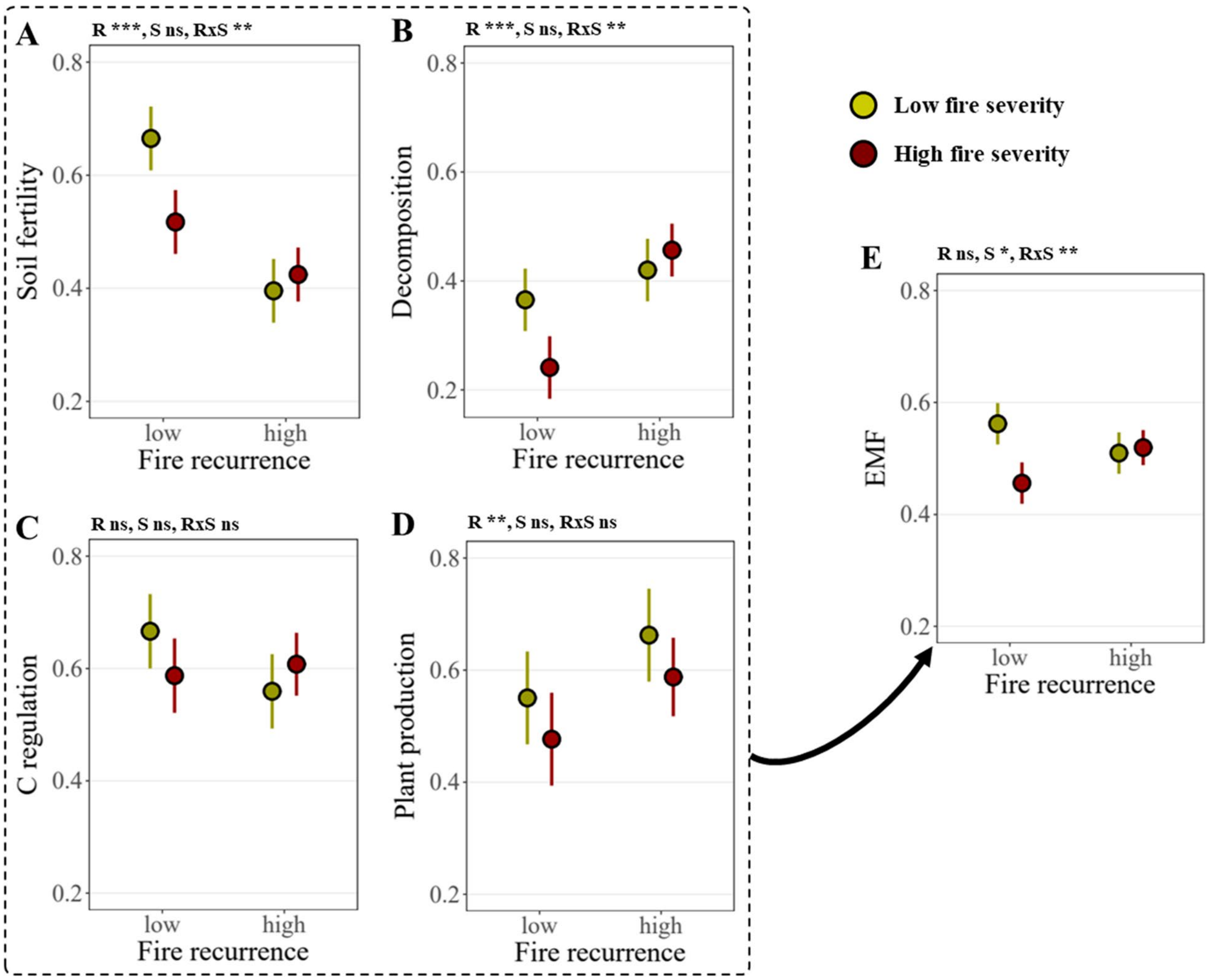

Fig. 2 Predicted effects (mean ± 95% confidence intervals) of fire recurrence (R) and severity (S), as well as their interaction (R×S), on soil fertility (**A**), decomposition (**B**), C regulation (**C**), and plant production (**D**) functions, as well as on ecosystem multifunctionality (EMF) (**E**). The significance of ordinary least square (OLS) model parameters is represented by ***(*p-value* < 0.001), **(*p-value* < 0.01), *(*p-value* < 0.05), and ns (*p-value* > 0.05)

or scenarios (intrinsic synergies/trade-offs, driven by fire recurrence and driven by fire severity) (Table 3).

Discussion

The understanding of how fire regime attributes shape ecosystem functions and processes threatened by land-use changes and anthropogenic climate warming is of utmost importance for predicting ecosystem responses to future global change scenarios (Bowman et al. 2014; Archibald et al. 2018). This will also provide integrated insights on management strategies tailored to secure the provision of multiple functions and ecosystem services in the context of global change (Fernandes et al. 2016b; Taboada et al. 2021). This study represents a first attempt to shed light into the response of pine ecosystems' functioning as modulated by the interacting effects of fire recurrence and severity using an integrative ecosystem multifunctionality approach. This is particularly relevant in the current context of projected increases in wildfire frequency (Turco et al. 2014) and severity (van Mantgem et al. 2013) in Mediterranean-type ecosystems worldwide. A key finding of our study is that fire recurrence and severity attributes interacted strongly to modulate the response of the pool of ecosystem functions (i.e., EMF) in burned maritime pine ecosystems in the medium-term after fire. Our study also highlights the need to use an integrative methodology to assess the response of ecosystem functioning to fire, since multiple ecosystem functions responded differentially to both attributes of the fire regime, as evidenced in previous research (e.g., Fernández-García et al. 2020a; Huerta et al. 2022; Moghli et al. 2022). In this sense, most of the individual functions showed a strong response to changes in fire recurrence, and some of them to the interaction

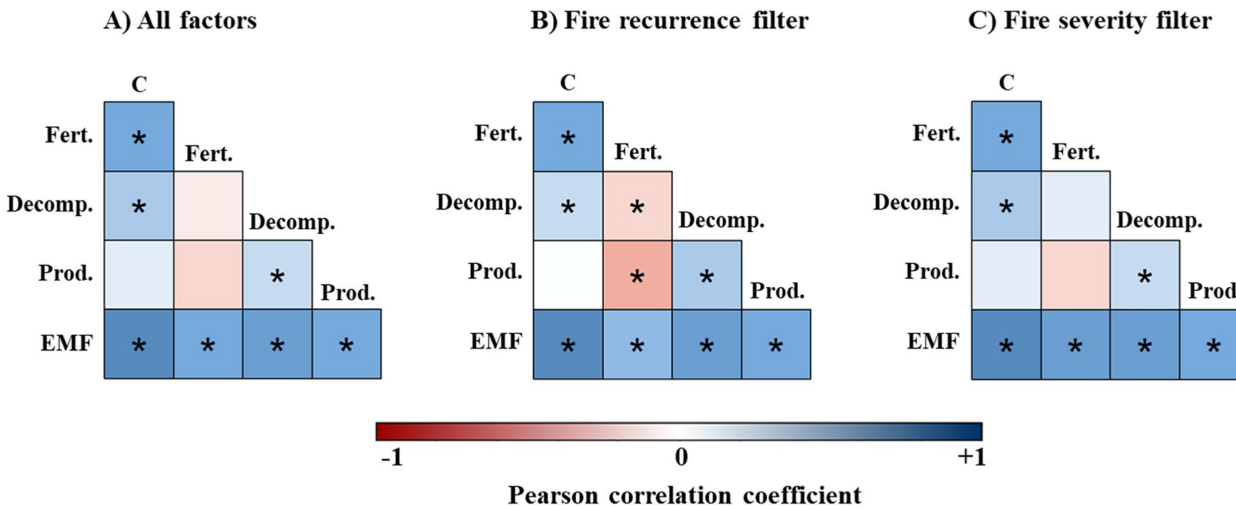

Fig. 3 Intrinsic synergies and trade-offs between standardized ecosystem functions (**A**), synergies and trade-offs driven by fire recurrence (**B**), and synergies and trade-offs driven by fire severity (**C**). Asterisks denote significant Pearson correlations between each pair of ecosystem functions within each scenario (**A**–**C**).

Table 3 Test for significant differences between the Pearson correlations of each pair of functions/EMF among the three correlation matrices using the Zou's confidence interval. The three correlation matrices correspond to intrinsic synergies and trade-offs (I), synergies and trade-offs driven by fire recurrence (R), and synergies and trade-offs driven by fire severity (S). If the Zou's confidence interval (lower confidence interval (LCI) and upper confidence interval (UCI) does not include zero, the two correlations are significantly different

Pearson correlations	I vs. R		I vs. S		R vs. S	
	LCI	UCI	LCI	UCI	LCI	UCI
C ~ Fert.	− 0.23	0.21	− 0.25	0.19	− 0.23	0.19
C ~ Decomp.	− 0.22	0.33	− 0.31	0.23	− 0.37	0.17
C ~ Prod.	− 0.21	0.37	− 0.27	0.31	− 0.22	0.37
C ~ EMF	− 0.11	0.13	− 0.12	0.12	− 0.11	0.13
Fert. ~ Decomp.	− 0.12	0.45	− 0.41	0.18	− 0.01	0.57
Fert. ~ Prod.	− 0.10	0.45	− 0.32	0.27	− 0.05	0.51
Fert. ~ EMF	− 0.15	0.33	− 0.29	0.15	− 0.07	0.39
Decomp. ~ Prod.	− 0.39	0.17	− 0.26	0.30	− 0.38	0.16
Decomp. ~ EMF	− 0.21	0.19	− 0.24	0.14	− 0.15	0.23
Prod. ~ EMF	− 0.17	0.26	− 0.20	0.25	− 0.18	0.26

between fire recurrence and fire severity, whereas no individual function was sensitive to the isolated effect of fire severity.

The absence of a clear effect of fire recurrence and severity on the C regulation function may be related with the high net primary production of secondary succession in burned areas and the associated organic matter inputs to the soil from litterfall and root litter decomposition (Knicker et al. 2005; Heath et al. 2015). Indeed, the recovery of resprouter shrub species was very high three years after fire in the study site, particularly in the most disturbed scenarios (Fernández-García et al. 2020b). Also, the recruitment of pine seedlings and obligate seeder shrubs was noticeable in scenarios of low fire recurrence because of the higher replenishment of canopy and soil seed banks under longer fire-free periods (time since last fire of 15 years) (Fernández-García et al. 2019a), and the more favorable microclimatic conditions on the forest floor for seedling establishment (Taboada et al. 2017). In addition, soil organic carbon release from decaying burnt wood, particularly in the first 2 years after fire (Marañón-Jiménez and Castro 2013), may help to buffer the effects of fire recurrence and severity on soils (Knicker 2007). The fast reestablishment of resprouter species may also be accountable for the strong increase of plant production function in scenarios of high fire recurrence. First, post-fire resprouting capacity has a key role in plant species fitness since bud-forming tissues of resprouter species enable a rapid recovery of aboveground biomass shortly after the fire (Keeley et al. 2011; Pausas and Keeley 2014). Second, resprouter species have competitive advantages over seeder species with increased resource availability (Keeley et al. 2016). Accordingly, decreases in maritime pine cover with fire recurrence may cause spatio-temporal changes in resource allocation and contribute to higher production and diversity of the understory community (Tessler et al. 2016; (Fernández-Guisuraga et al. 2022a).

Previous studies also evidenced that recurrent fires can reduce nutrient pools of the soil in fire-prone Mediterranean ecosystems (e.g., Caon et al. 2014*and references therein*). Nutrient volatilization, surface runoff, and erosion processes may be associated with nutrient depletion in frequently burned areas if cumulative soil losses in the medium term after fire could not be offset by nitrogen fixation or soil organic matter mineralization (Mayor et al. 2016a; Hinojosa et al. 2021). The opposite trend followed by the decomposition function in high recurrence scenarios (increase with fire recurrence) can be explained by the close relationship between soil nutrients and extracellular enzyme activity (Fernández-García et al. 2019b), since these enzymes originate from living organisms to catalyze important reactions in the cycling of soil nutrients (Miesel et al. 2011; (Mayor et al. 2016b). In this sense, several authors evidenced that high nutrient availability inhibits the production of these substrate-dependent enzymes because of the involved energy costs (Bünemann 2008). Also, the dominance of resprouter species may be responsible for the increased decomposition function in high fire recurrence scenarios. According to previous studies (López-Poma and Bautista 2014; (Mayor et al. 2016b), resprouter species are very likely to survive the fire and regain their above-ground biomass in the same location, with the root system being mostly unaffected. Thus, the resilience of rhizosphere hotspots, with enhanced microbial activity, is greater when associated to resprouter rather than to seeder species. Remarkably, the soil fertility and decomposition feedbacks were modulated by fire severity only when fire recurrence was low, as evidenced by the significant interaction between both fire regime attributes. This result may be attributable to the high pre-fire load of the surface fuel complex in unmanaged maritime pine stands of low fire recurrence scenarios in the site (Fernández-Guisuraga et al. 2022b) owing to the high rates of flammable litter accumulation and the well-developed understory. In this context, the high fuel load close to the ground would have contributed to an extreme fire behavior and a strong fire heat-induced impact on soil biochemical properties (Pausas et al. 2002), whose legacy would even persist in the medium-term after the wildfire.

The divergent responses among functions fostered a significant EMF response to fire severity and its interaction with fire recurrence, indicating that the negative effect of high fire severity on EMF was stronger under low fire recurrence scenarios, even when relationships between individual functions and fire severity were weak. This suggests that ignoring the interplay among functions can lead to biased assumptions about fire disturbance responses when ecosystem functioning is analyzed as a whole (Lefcheck et al. 2015; Moghli et al. 2022). Indeed, EMF is considered an ecosystem-level outcome in its own right rather than a substitute for or an indicator of patterns in individual functions (Byrnes et al. 2014; Grman et al. 2018). Our results suggest that, when considering the functioning of the maritime pine ecosystem as a whole, management efforts should be targeted at reducing fire risk in order to ensure sufficiently long fire-free intervals (Fernández-García et al. 2019a) and reducing the fuel load in the surface fuel complex to minimize surface fire intensity and crown fire hazard (Fernández-Guisuraga et al. 2022b). However, we recognize that specific management goals would require the consideration of individual functions and the associated ecosystem services to keep their performance at high levels.

The environmental filter exerted by fire recurrence caused two significant trade-offs to emerge, involving soil fertility, decomposition, and plant production functions. This is consistent with the lower soil fertility function and higher decomposition and plant production functions evidenced in the high fire recurrence scenarios as compared to the low recurrence scenarios (Fig. 2). Despite this trend, we found no significant differences between intrinsic synergies and trade-offs in our study site and those driven by fire recurrence and severity. This suggests that the filter exerted by the fire regime is not strong enough to cause substantial changes in the intrinsic relationships between functions in Mediterranean ecosystems, as found by Moghli et al. (2022) in burned *Pinus halepensis* forests of eastern Spain. However, projected global change scenarios in Mediterranean ecosystems can turn the trends observed here into significant trade-offs.

We acknowledge that our study is based on a single fire event with limited fire recurrence, and thus the replicability of the EMF methodological approach should be further tested in other unmanaged maritime pine stands of the western Mediterranean Basin with similar characteristics to those analyzed here. Future research should also focus on testing our approach in maritime pine ecosystems with different fire history and at different time scales after fire, as well as in managed stands to evaluate the effectiveness of fuel hazard reduction treatments in preserving ecosystem functioning.

Conclusions

In this study, we analyzed for the first time the interacting effects of recurrence and severity attributes of the fire regime on the ecosystem functioning of pine forests dominated by *Pinus pinaster* in the western Mediterranean Basin using an integrative ecosystem multifunctionality approach. Our results indicated that multiple ecosystem functions showed divergent responses to both attributes of the fire regime, and thus, the use of an integrative approach to assess the response of ecosystem functioning to fire is deemed necessary. In this context, we found that fire recurrence and severity interacted strongly to modulate the response of ecosystem multifunctionality over the medium-term after fire, indicating a stronger impact of fire severity on ecosystem functioning under low fire recurrence scenarios than in more frequently burned areas. Therefore, our results suggest that adaptive management responses are necessary towards the minimization of repeated burnings and the reduction of the fuel load in unmanaged maritime pine ecosystems of the western Mediterranean Basin.

Abbreviations

ANOVA	Analysis of variance
BOA	Bottom-of-atmosphere
C	Carbon
CBI	Composite Burn Index
dNBR	Differenced Normalized Burn Ratio
EFFIS	European Forest Fire Information System
EMF	Ecosystem multifunctionality
ETM+	Enhanced Thematic Mapper Plus
MBC	Microbial biomass carbon
MTBS	Monitoring Trends in Burn Severity
N	Total nitrogen
OLS	Ordinary least square
P	Available phosphorous
PERMANOVA	Permutational multivariate analysis of variance
RdNBR	Relative differenced Normalized Burn Ratio
SOC	Soil organic carbon
TM	Landsat Thematic Mapper

Authors' contributions

J.M.F.G., E.M., and L.C. conceived and designed the experiment. J.M.F.G., E.M., and L.C. collected field data. J.M.F.G. analyzed the data. J.M.F.G. wrote the manuscript. E.M. and L.C. revised the manuscript. E.M. and L.C. coordinated the study. The authors read and approved the final manuscript.

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Availability of data and materials

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

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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