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RECEIVED 01 March 2023

ACCEPTED 26 April 2023

PUBLISHED 10 May 2023

CITATION

Saulino L, Rita A, Stinca A, Liuzzi G, Silvestro R,
Rossi S and Saracino A (2023) Wildfire
promotes the invasion of *Robinia
pseudoacacia* in the unmanaged
Mediterranean *Castanea sativa* coppice
forests.
Front. For. Glob. Change 6:1177551.
doi: 10.3389/ffgc.2023.1177551

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Wildfire promotes the invasion of *Robinia pseudoacacia* in the unmanaged Mediterranean *Castanea sativa* coppice forests

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In the Mediterranean region of southern Europe, *Castanea sativa* Mill. (*Castanea*) coppice stands are being invaded by non-native pioneer tree species due to recurrent coppicing and wildfire disturbances. There is a need to control the spread of non-native tree species in *Castanea* coppices due to their pivotal socio-economic role, however, to facilitate this, further research into invasive strategies and their interactions with disturbances is required. The non-native *Robinia pseudoacacia* L. (*Robinia*) has widely colonized the overaged and unmanaged *Castanea* coppice forests in Vesuvius National Park, which were disturbed by the low-severity fires in the summer of 2017. Here, we aimed to assess the functional traits conferring a competitive advantage to the *Robinia* over *Castanea* and the changes in spatial stand patterns driven by wildfire disturbance. To achieve this we assessed the spatial stem patterns, regeneration strategies, and conducted field-assessments and remote sensing of the spring leaf phenology of both *Castanea* and *Robinia* in five 300–600 m² plots. After the 2017 wildfire, root suckers constituted 72% (± 12) of the *Robinia* vegetative living sprouts and occurred up to a distance of 10 m from the adult parent trees under the canopy of the *Castanea* trees. NDVI-based estimates at the start of the growing season (*sos*) in *Castanea* occurred over a 7 day period, from DOY 118–124, increasing at a rate (*rsp*) of 0.10–0.16, in agreement with the field-based assessment of spring leaf phenology. In *Robinia*, the *sos* estimated at DOY 109 from the NDVI seasonal trajectory disagreed with the field-based observations, which started later than *Castanea*, after approximately DOY 133. Here, the high percentage cover (~90%) of the understory species influenced NDVI-based estimates of *Robinia* leaf spring phenology. The results suggest that low-severity wildfires increased the invasiveness of *Robinia*, and that vegetative regeneration strategies, rather than earlier spring phenology, conferred a competitive advantage in the fire-disturbed *Castanea* coppice stands.

The results thus suggest that appropriate management of invasive *Robinia* trees to conserve the continuous canopy cover of *Castanea* stands should guide nature-based solutions to control the spread of non-native tree species.

KEYWORDS

chestnut coppice, invasive plant traits, vegetative regeneration, spring leaf phenology, remote sensing, root suckers

1. Introduction

The anthropogenic migration of species beyond their native ranges has substantially increased in the last century, and there does not appear to be any signs of global saturation (Seebens et al., 2017). In the Mediterranean Basin, the ecological and socioeconomic impacts of exotic species invasions has drastically increased in recent decades (Kourantidou et al., 2021), and this frequently has detrimental effects on ecosystem services and human well-being (Stoett et al., 2019). Biological invasions and climate change are considered the key drivers threatening the conservation of native flora in protected areas around the world, and this is jeopardizing efforts to halt biodiversity loss (Gallardo et al., 2017). The impacts are particularly dramatic in the protected areas of southern Europe around the Mediterranean, where losses of biodiversity occur more frequently as a consequence of the wide and diffuse socioeconomic activities, coupled with the ongoing issues regarding climate and land use changes (Nadal-Sala et al., 2019; Fois et al., 2020).

Conservation and restoration of disturbed native habitats and plant communities requires an understanding of the mechanisms and patterns by which invasive species outperform native species. The spread of invasive plants is mainly linked to their functional traits (e.g., growth rate, early leaf onset, and resprouting ability) (Van Kleunen et al., 2010) and to key processes (biotic and abiotic filters) of ecosystems at local and landscape scales that promote colonization and establishment (e.g., disturbances, resource availability, empty niches) (Theoharides and Dukes, 2007). Among the strategies for tree invasion, vegetative regeneration is one of the major drivers of tree species colonization (Nunez-Mir et al., 2019). A large proportion of invasive trees spread and persist outside their native range via vegetative regeneration strategies such as resprouting (i.e., from root fragments and basal stems), layering, and suckering (Reichard and Hamilton, 1997).

Concurrently, plant traits related to phenology also contribute significantly to the spread of non-native species (Fridley, 2012), emphasizing their invasiveness (Chuine and Beaubien, 2001) and inequality between non-native and native invasive species (Wolkovich and Cleland, 2014). Early leaf growth can enable non-native species to take advantage of light availability and carbon assimilation while native species remain leafless, explaining their persistence in non-native habitats (Harrington et al., 1989; Wolkovich and Cleland, 2011). Despite efforts to identify the common traits of invasive plants, knowledge of the key functional traits for invasive non-native tree species is still lacking (Nunez-Mir et al., 2019). Understanding the traits conferring invasiveness allows for the proper management of established non-native tree species (Mathakutha et al., 2019) and can help to predict whether

and how non-native species will potentially become invasive when introduced into a new ecosystem. Therefore, assessing the key functional traits that enable non-native tree species to become invasive is crucial for implementing appropriate management programs in invaded local vegetation communities (Gallagher et al., 2015), especially in forest areas where environmental resources can be deliberately manipulated (Funk et al., 2016).

In European Mediterranean landscapes, *Castanea sativa* Mill. (hereafter *Castanea*) stands are the most frequent human-made forest type, replacing native deciduous forests in the lowland mountain belt (Allevato et al., 2012). Currently, in Europe, *Castanea* forests cover approximately two million hectares, and 40% of this growth is in Italy, from plain to hilly topographies (INFC, 2005). *Castanea* stands are prone to invasion from *Robinia pseudoacacia* L. (hereafter *Robinia*), and this is exacerbated by natural and anthropogenic disturbances, especially coppicing, as it spreads easily in both managed and unmanaged coppice stands (Radtke et al., 2013; Marcolin et al., 2020). *Robinia* is a North American, nitrogen-fixing, and light-demanding pioneer tree species that frequently occurs in forest and non-forest sites in Europe (Cierjacks et al., 2013). In Mediterranean mountainous forests, its past spread has been encouraged mainly by extensive planting for afforestation, wood provisioning, and to prevent and control erosion along mountain slopes (Vítková et al., 2017, 2020), which highlights its potential role in regulating ecosystem services (Castro-Díez et al., 2019).

Outside its native range, *Robinia* is considered an invasive tree species that colonizes and persists in new environmental habitats (Richardson and Pyšek, 2006). Its spread has been recognized in many protected areas from riparian to hilly landscapes (Motta et al., 2009), often replacing native forest vegetation and impacting mostly on the plant-soil biotic community traits analyzed (Lazzaro et al., 2018; De Marco et al., 2023). Due to its invasiveness, *Robinia* is currently listed as a dangerous invasive tree and has been targeted for controlled management in European and Asian countries (Lazzaro et al., 2020). In southern Switzerland and northern Italy, *Robinia* has replaced entire valleys of European *Castanea* coppice forests (Sabo, 2000; Sitzia et al., 2012) and further *Castanea* forests in Italy are expected to be invaded (Benespero et al., 2012). Its capability to spread beyond places of introduction and to establish forest habitats with conservation objectives requires active management to counteract its invasiveness (Kleinbauer et al., 2010). Understanding how to effectively counteract the invasiveness of *Robinia*, especially in protected forest areas, requires useful insights into its autecology, ecophysiological traits, and the site features of colonized forest community types.

The evolutionary dynamics of *Castanea* coppice forests along the Italian peninsula are affected by various human-mediated disturbances. In this context, *Castanea* coppices represent an opportunity to shed light on the invasive strategies displayed by the non-native *Robinia* species and on the management options required to cope with its spread in fire-disturbed stands. Past eruption episodes repeatedly destroyed the native vegetation on the slopes of the Somma-Vesuvius stratovolcano, the last of which occurred in 1944 (De Vivo et al., 2019). However, charcoal and archeological analyses attested to the presence of *Castanea* before the Roman Period (Di Pasquale et al., 2010). In the last century, the bare slopes of the Somma-Vesuvius volcano has been prone to soil erosion and has thus been reforested with a number of species, including *Robinia* and shrub *Genista etnensis* (Raf.) DC. (Stinca et al., 2015) to mitigate the hydrogeological hazards of andic soil. Since its plantation in the southeastern and northeastern flanks of Mount Somma, *Robinia* has spread in broadleaved forests, especially in *Castanea* coppice stands. Moreover, recurrent wildfires have disturbed the forests of Vesuvius National Park, especially in the summer of 2017, as approximately 88% of the total forested area was burned, causing serious damage to the existing biodiversity and ecosystem services supply (Silvestro et al., 2021; Cervelli et al., 2022). In the summer of 2017, low-severity wildfires experienced by *Castanea* coppice forests on the northern slopes (Saulino et al., 2020) increased *Robinia*'s invasiveness, posing relevant issues for post-fire management. Considering the recent increase in the number and severity of wildfires observed in the Mediterranean basin (San-Miguel-Ayanz et al., 2021), we believe that assessing the role of fire disturbances on the spread of invasive tree species (Keeley, 2006) could provide useful insights into the post-fire management of Mediterranean *Castanea* coppice stands.

In an overaged and unmanaged Mediterranean *Castanea* coppice stand of the Vesuvius National Park affected by the 2017 summer wildfires, we assessed (i) the functional traits conferring competitive advantages to invasive *Robinia* over *Castanea* trees, and (ii) the changes in stem spatial patterns driven by fire disturbances. We hypothesized that the early spring phenology and root sprouting would be identified as functional traits that confer a competitive advantage to *Robinia* in the colonization of *Castanea* coppice stands. Mediterranean chestnut coppice forests offer a useful and yet unexplored system for examining the role of species-specific functional traits which allow invasive *Robinia* to exploit empty niches following wildfire disturbances.

2. Materials and methods

2.1. Study site

Vesuvius National Park is a geo-site in southern Italy, covering 8,250 ha, including the Somma-Vesuvius volcanic complex, which is still active in mainland Europe (De Vivo et al., 2019). The slopes of the volcano are covered by mixed broadleaved, monospecific, and mixed Mediterranean coniferous and shrubland forests. On the northern slope of Mt. Somma, the *Castanea* forest covers 646 ha, distributed from a minimum elevation of 350 m a.s.l. to a maximum of 1,120 m a.s.l. (Figure 1). According to the European forest type classification EFTs (Barbati et al., 2014), the Mt. Somma *Castanea*

forest belong to the type level “8.7 Chestnut forest” in the category level “8. Thermophilous deciduous forest.”

In the last century, most of *Castanea* stands have been managed as coppices with standards for timber production to obtain small- to medium-sized pole assortments. Since the establishment of the National Park (1995), *Castanea* coppices have been unmanaged and frequently colonized by *Robinia* tree sprouts. Other native tree species include *Acer opalus* Mill. subsp. *obtusatum* (Waldst. & Kit. ex Willd.) Gams, *Fraxinus ornus* L. subsp. *ornus*, *Quercus ilex* L. subsp. *ilex* occurs sporadically and mainly in the understory layer of *Castanea* coppice stands. Native shrub species are common in coppice stands, particularly *Rubus ulmifolius* Schott and *Rubus hirtus* Waldst. & Kit. groups, *Cytisus scoparius* (L.) Link subsp. *scoparius*, *Sambucus nigra* L., *Hedera helix* subsp. *helix*, and *Emerus major* Mill. subsp. *emeroides* (Boiss & Spruner), Soldano & F. Conti (Supplementary Material 1). However, on the northeastern slope of Mt. Somma (<600 m a.s.l.), *Castanea* orchards are managed for fruit production, with a limited surface area of 72 ha.

The area has a Mediterranean climate with a cold winter and a relatively hot and dry summer (Stinca et al., 2015). In the summer, the average monthly temperature is 21.6°C whereas in the winter it is 5.7°C. The average annual rainfall is 1100 mm and this is asymmetrically distributed with 73 % occurring during the autumn-winter season and 27% in the spring-summer season.

2.2. Stem spatial pattern, size attributes, and plant diversity sampling

In the winter-spring 2022, synchronic sampling approach was applied to investigate *Castanea* stands invaded by the non-native species *Robinia* across multiple sites burned at same points in time, in the summer 2017. Such sampled plots were retrospectively organized to construct a *Robinia* invasion gradient. Synchronic approach is commonly used to compare and investigate non-native species invasion strategies in forest communities (Walker and Smith, 1997), especially when the bi-temporal - before-after disturbance approach (or diachronic sampling) - cannot be applied (Pino et al., 2009).

The spatial positions of stems and their size attributes were collected in five permanent plots ranging from 300 to 600 m² (Figures 2A–E). Here, the variability of plot size is imposed by the topography constraints of volcanic slope. The plots were positioned on the north face of the Somma-Vesuvius mountain, from 680 to 780 m a.s.l., with slope ranging from 25 to 30° (Figure 1A). In all plots, the forest soil developed on falls of ash and lapilli, and belongs to Molli-Vitric Andosols class according to the world reference base classification system (IUSS Working Group WRB, 2022), with a variable depth ranging from 100 to 150 cm.

In each plot, the relative spatial coordinates of all standing (live and dead) stem sprouts of *Castanea*, *Robinia*, and the other native tree species were recorded. For each stem, the X_i and Y_i Cartesian coordinates (m) were measured using a Vertex ultrasound hypsometer (Haglöf® Vertex Laser VL400). The diameter at breast height (DbH, cm) 1.30 m above-ground was measured for each stem sprout using a caliper. Total height (TH, m) and crown base height (CBH, m) were measured in standing

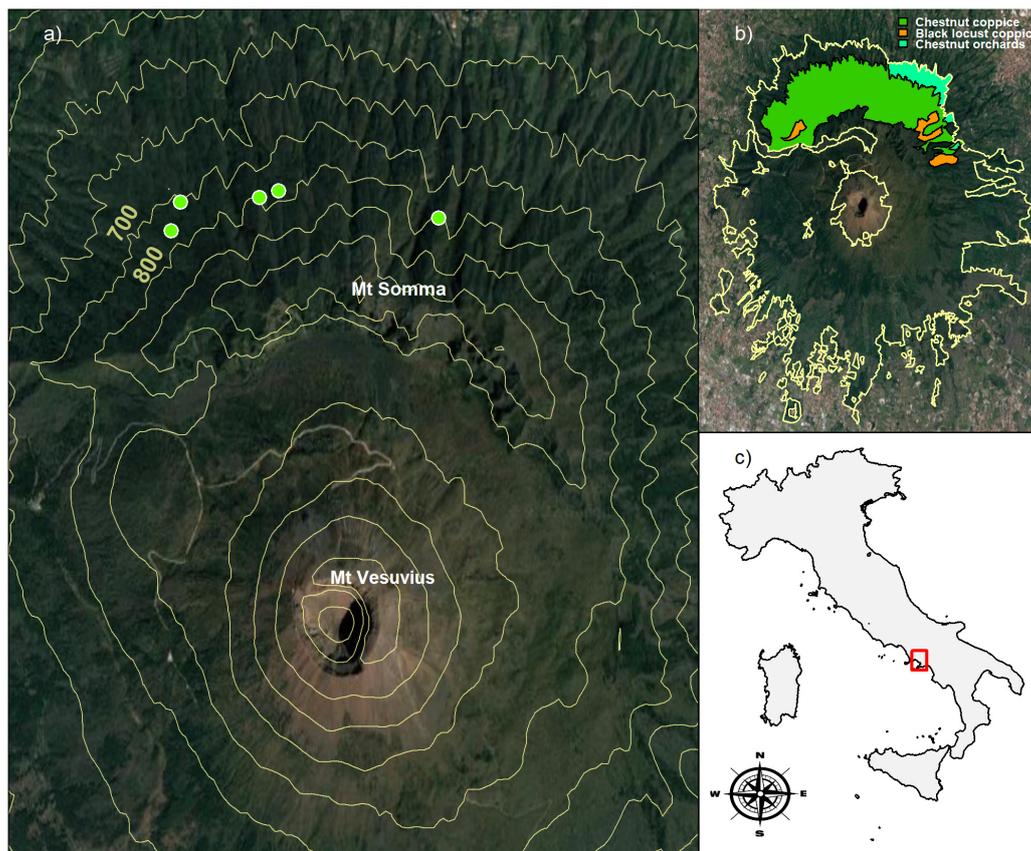


FIGURE 1

Location of the study sites in Vesuvius National Park, Southern Italy. (a) The green circular markers indicate the geospatial position of permanent plots, while the solid yellow contour lines represent 100 m elevation intervals; (b) the yellow boundary line represents the forest perimeter of Vesuvius National Park, while colored polygons indicate the forest types on Mt. Somma: chestnut coppice (green), chestnut orchards (light-green) and black locust coppice (orange). (c) The red square identifies the geographic position of the Vesuvius National Park. Aerial images were obtained from Google Maps Platform APIs service.

trees belonging to the dominant and intermediate positions using a Vertex ultrasound hypsometer.

In the winter-spring 2022, the diversity of the plant communities was assessed in terms of coverage of the different layers and all individual plant species. Vascular species cover was visually assessed according to the Braun-Blanquet scale [i.e., (r) rare; (+) <1%; (1) 1–5%; (2a) 6–15%; (2b) 16–25%; (3) 26–50%; (4) 51–75%; and (5) 76–100%] and transformed into an ordinal scale according to Van der Maarel (1979). Nomenclature and taxon delimitation followed recent checklists of Italian vascular flora (Bartolucci et al., 2018; Galasso et al., 2018). The taxonomic identification of the species is provided in [Supplementary Material 1](#).

2.3. Standing stems classification and post-fire scars assessment

The stems were classified as (i) basal sprouts for both *Castanea* and *Robinia* and (ii) root-suckerings only in *Robinia*, according to the definition provided by Del Tredici (2001). The root-suckerings of *Robinia* were classified based on their distance from the adult parent tree. However, root suckerings were manually dug in

doubtful cases to exclude their seed origin. Leeward fire scars on the basal portions of the stem sprouts were assessed by the scorched height (Gutsell and Johnson, 1996), about 5 years after the 2017 wildfires. Therefore, pre-fire stand structure was built excluding basal stem sprouts and root-suckerings having basal stem diameter ≤ 4 cm, corresponding in turn to an age ≤ 5 years. Age was determinate by visual counting of tree rings stem cross-section on six *Castanea* and six *Robinia* sprouts randomly sampled. Standing stem basal or root-suckerings sprouts were categorized as live not-scorched, dead not-scorched, live-scorched, and dead-scorched. The category dead-not scorched includes standing *Castanea* stem basal sprouts died for the spread of *Cryphonectria parasitica*, and exacerbated by the leaf area reduction of *Dryocosmus kuriphilus*, while *Robinia* root-suckerings died for self-thinning.

2.4. Spatial patterns and structural analysis

The spatial aggregation pattern of the standing trees and their stem diameter differentiations were assessed using two second-order spatially explicit procedures: (i) the normalized mark differentiation function $\tau(r)$ (Stoyan and Stoyan, 1994;

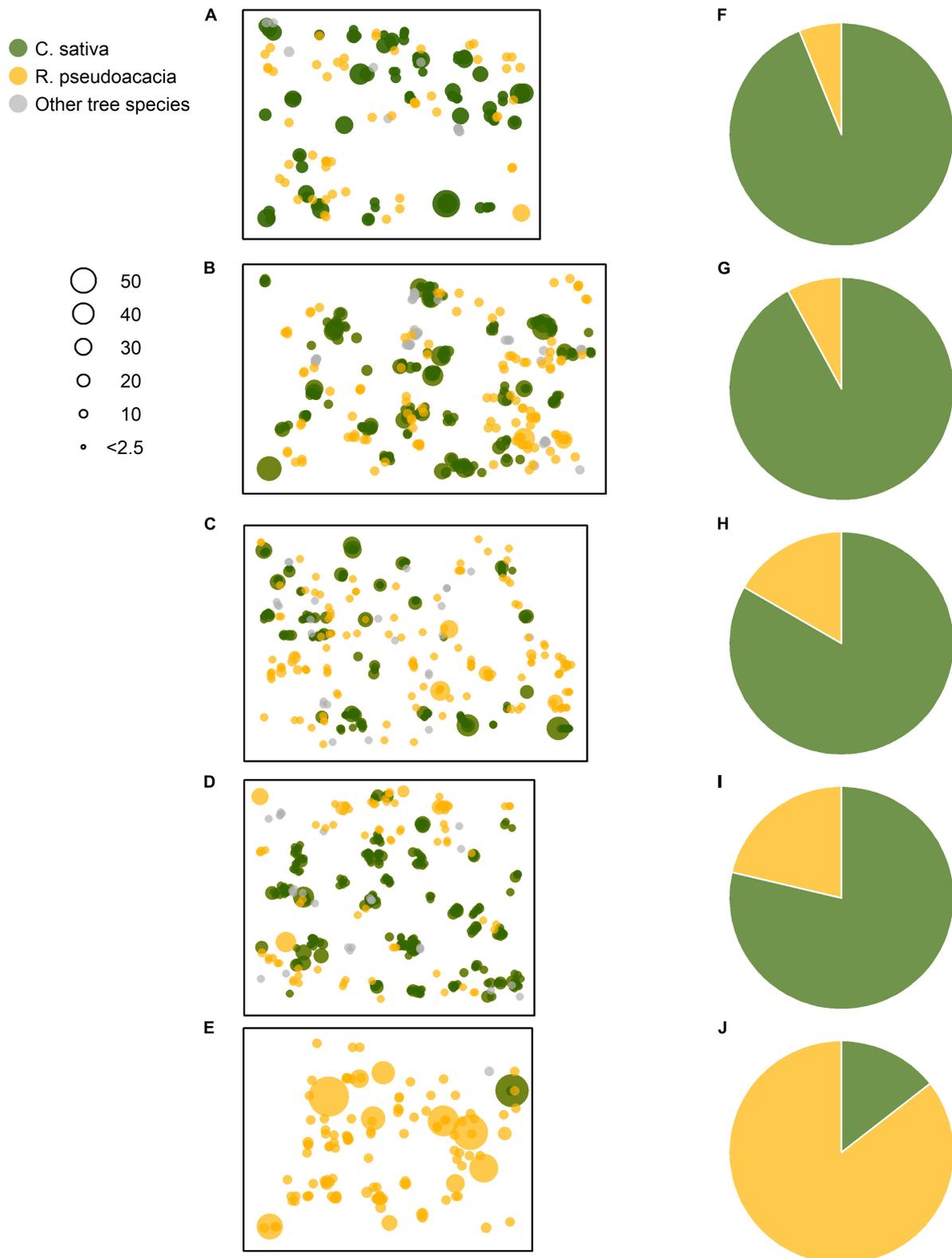


FIGURE 2

Spatial distributions of the sprouted stems and their sizes for the *Castanea*, *Robinia*, and other Mediterranean tree species. (A–E) The plots were ordered by decreasing basal area values of the standing *Castanea* sprouts belonging to the overstory layer. (F–J) Represent the basal area percentage (%) for the *Castanea* and *Robinia* sprouts belonging to the overstory layer. Point sizes are proportional to diameter at breast height (DbH, cm). (A–E) Correspond to the plots C1–R5 of [Table 1](#).

Hui and Pommerening, 2014) and (ii) the nearest neighbor distance distribution function $G(r)$ (Cressie, 2015). In the function $\tau(r)$, the diameter at breast height (DbH, cm) was used as a quantitative marker. The Epanechnikov kernel method (Pommerening and Grabarnik, 2019) was employed to estimate the mark differentiation function $\tau(r)$, applying a bandwidth value of 0.8 m and implementing the translation edge correction method to minimize bias. Bandwidth was estimated according to the formula developed by Illian et al. (2008) for planar Poisson processes. In the estimation of the function $G(r)$, the spatial Kaplan-Meier correction method was implemented to reduce the bias associated with the edge effect (Baddeley and Gill, 1997). Management and analysis of the spatial point patterns was performed in R using the “spatstat” package (Baddeley et al., 2015).

2.5. Remote sensed NDVI data

We used the recently improved Landsat Collection 2 products (USGS, 2021) available from the Google Earth Engine (GEE) open cloud-platform database (Gorelick et al., 2017). We selected Landsat 7 ETM+ (LE07) and 8 OLI/TIRS (LC08) Surface Reflectance Collection 2, Tier 1, Level 2 datasets (C02/T1_L2), spanning from January 4, 2005, to August 31, 2022, for Landsat 7 ETM+, and from April 24, 2013, to August 31, 2022, for Landsat 8 OLI/TIRS. The collection C02/T1_L2 includes data that are radiometrically and geometrically corrected and inter-calibrated across different Landsat instruments.¹ Before using the C02/T1_L2 data, the surface reflectance bands were scaled by applying a scale factor of 0.0000275 and an additional offset of -0.2 per pixel.²

The quality assessment mask to exclude pixels with clouds, shadow, water, and snow was produced by applying a multi-pass algorithm called “CFMask” (Foga et al., 2017) and employing the Landsat quality assessment band (QA_PIXEL) (Supplementary Material 2).³

For each plot (see below), the aforementioned Landsat datasets (C02/T1_L2) were used to assess the normalized difference vegetation index (NDVI) (Zhang et al., 2018). NDVI values were calculated per pixel across the stack of valid pixels (e.g., cloud and snow-free pixels). Prior to computing the NDVI, a filter that selected Landsat images with a sun elevation of $> 10^\circ$ was applied. Near-infrared and red surface reflectance bands from both Landsat sensors were used in the computation of the NDVI: B4 and B3 reflectance bands from Landsat LE07, B5, and B4 for Landsat LC08.

2.6. Satellite- and field based assessment of phenology

A double logistic function developed by Beck et al. (2006) was applied to model the annual NDVI trends. The function models

the NDVI as a function of time (t) using six parameters: the winter NDVI (mn) and the maximum NDVI of the growing season (mx), two inflection points at the start of the growing season (sos) and the end of the growing season (eos), and two slopes, the spring increasing rate (rsp) and the autumn decreasing rate (rau).

$$NDVI = mn + (mx - mn) \cdot$$

$$\left(\frac{1}{1 + e^{(-rsp \cdot (t - sos))}} + \frac{1}{1 + e^{(rau \cdot (t - eos))}} - 1 \right)$$

Prior to fitting the Beck function, the NDVI data were pre-processed using a two-step filtering procedure, consisting of the removal of (i) the altered observation related to the multiple wildfires that occurred in the summer of 2017 (i.e., from July 2, 2017, to December 31, 2017) (Supplementary Figure 1 in Supplementary Material 3) and (ii) incongruous/anomalous observations with the time of acquisition and expected phenological stage, especially low and high NDVI recordings that occurred later during the growing period or early in the dormant season. In the second step, we applied a stand-specific filtering procedure for each plot, pre-fitting the NDVI data, and computing the absolute residues for each NDVI value and the timing of the observations. All NDVI recordings with absolute residues (i.e., $|NDVI_{\text{predicted}} - NDVI_{\text{recorded}}|$) higher than 0.2 were discarded (Supplementary Figure 2 in Supplementary Material 3). After pre-processing, for each plot, a double logistic curve was fitted to the filtered NDVI recordings.

In the spring of 2022, the vegetative phenology of *Castanea* and *Robinia* stem sprouts growing in the understory and overstory layers was visually assessed using a digital camera. The gradual vegetative process from bud burst to leaf unfolding was assessed using the BBCH phenological scale (Meier, 1997).

The parameters of the model function were estimated using the iterative nonlinear least square method (Bates and Watts, 1988), employing the Levenberg-Marquardt optimization algorithm. Statistical differences among the estimated parameters were tested by applying the Wald test procedure using the *Bonferroni* multiplicity adjustment method, followed by Tukey’s multiple comparison test (Bretz et al., 2011). Management and analysis of the NDVI data were performed in R using “minpack.lm” (Elzhov et al., 2022) and “aomisc” (Onofri, 2020) packages. All data analysis were performed at significance level $p = 0.05$.

3. Results

3.1. Coppice stand structures and spatial sprout patterns

In all five plots, *Castanea* and *Robinia* stems grew in spatially restricted aggregations (Figures 2A–E). *Castanea* was the dominant tree species in the stands, with the basal area of these living trees accounting for 78–94% of the overstory layer (Figures 2F–I). In contrast, *Robinia* contributed much less to the overstory layer, with a basal area ranging from 6 to 22% (Figures 2F–I). In the coppice stand, where *Robinia* was the dominant tree species accounting for 87% of the basal area, *Castanea* contributed just 13% of the basal area (Figure 2J).

1 <https://www.usgs.gov/landsat-missions/landsat-collection-2-level-2-science-products>

2 <https://www.usgs.gov/faqs/how-do-i-use-scale-factor-landsat-level-2-science-products>

3 <https://code.earthengine.google.com/67d924911e9e2526e56d981ee064dadf>

TABLE 1 Post-fire stand structure attributes split by tree species (*Castanea* and *Robinia*) and plots.

Species ^a	Plot ^b	SD (n ha ⁻¹)	LBSS (n stool ⁻¹)	LBSD (n ha ⁻¹)	LRSD (n ha ⁻¹)	LSBA (m ² ha ⁻¹)	DSD (n ha ⁻¹)	DSBA (m ² ha ⁻¹)	QMD (cm)	AHD (m)
<i>Castanea</i>	C1	767	4 (±3)	3,133		37.7	1,034	1.2	27.0	17.3 (±0.8)
	C2	747	5 (±2)	3,787		31.1	1,386	3.7	26.5	15.0 (±1.2)
	C3	450	8 (±2)	3,517		34.3	1,416	3.8	28.1	15.7 (±1.7)
	C4	680	6 (±3)	3,980		31.6	1,180	7.9	25.9	16.2 (±2.1)
	R5	33	2 ^c	67		4.9	0	0.0	43.0 ^d	17.8 (±2.5)
<i>Robinia</i>	C1	67	2 (±1)	134	1,599	1.9	134	0.1	25.0	17.0 (±1.0)
	C2	293	2 (±1)	586	2,054	2.5	453	1.5	30.0	16.2 (±3.2)
	C3	250	3 (±2)	750	1,250	6.5	433	2.1	30.9	17.5 (±1.8)
	C4	340	3 (±1)	520	860	6.3	220	1.6	29.0	16.6 (±1.1)
	R5	600	2 (±1)	1,200	2,300	34.5	600	7.7	36.9	17.7 (±1.5)

SD, stool density (n ha⁻¹); LBSS, number of living basal sprouts per stool (n stool⁻¹); LBSD, living basal sprouts density (n ha⁻¹); LRSD, living root suckers density (n ha⁻¹); LSBA, living stem basal area (m² ha⁻¹); DSD, dead stem density (n ha⁻¹); DSBA, dead stem basal area (m² ha⁻¹); QMD, quadratic mean diameter of dominant living stem (cm); AHD, average height of dominant living stem (m).

^aOther Mediterranean woody species occur exclusively in the understory layer with a basal area <0.1 m² ha⁻¹.

^bPlot surface area (m²) and side sizes (m × m): C1 – 300 (20 × 15), C2 – 375 (25 × 15), C3 – 600 (30 × 20), C4 – 500 (25 × 20), R5 – 300 (20 × 15).

^cOnly one *Castanea* stool occurs in plot R5.

^dOnly one *Castanea* basal sprout belongs to the overstory layer in plot R5.

Where *Castanea* dominates the overstory layer, its stool density ranges from 450 to 767 stools ha⁻¹ (Table 1). The average number of live basal sprouts ranged from 4 (±3) to 8 (±2) per stool sample. However, there was a minimum value of 33 stools ha⁻¹ for *Castanea*, containing only two living basal sprouts, which were observed in the coppice stand dominated by *Robinia*. Stool density and the number of living basal sprouts per stool with the *Robinia* was lower when compared with the *Castanea*, ranging from 67 to 340 stools ha⁻¹ and from 2 (±1) to 3 (±2) sprouts per stool, respectively. A comparable value of 600 stools per hectare was observed in a coppice stand dominated by *Robinia*.

After the 2017 wildfire, in stands where *Castanea* was dominant in the overstory layer, living basal sprouts accounted for 74% (±2.6), ranging from 3,133 to 3,980 n ha⁻¹ (Table 1). Among them, the average basal sprouts with no fire scars accounted for 12% (±4.3) of the total sprouts for the species. Such basal sprouts are small, exhibiting an average stem diameter (DbH) of 3.9 (±1.2) cm. The basal area ranges from 31.1 to 37.7 m² ha⁻¹, accounting for an average of 89% (±7%) of the total *Castanea* basal area. The dead stem density varied from 1,034 to 1,416 n ha⁻¹, accounting for 11% (±7%) of the total *Castanea* stand basal area, ranging from 1.2 to 7.9 m² ha⁻¹. These dead stems exhibited an average DbH of 8.9 (±6.3) cm. The average number of dead sprouts with no basal fire scars accounted for only 4% (±1%) of the total dead basal sprouts.

Living root suckers of *Robinia* accounted for 72% (±12%), compared to 28% (±11%) of the basal sprouts in the total living vegetative sprouts (Table 1). Among them, the basal fire-scorched living root suckers accounted for 10% (±3%), exhibiting a DbH of 6.2 (±1.2) cm. In contrast, living root suckers with no fire scars accounted for 90% (±3%). Such root suckers had a small diameter at breast height (DbH < 4 cm) up to a distance of 10 m from the *Robinia* adult parent ramets (Figure 3 in the Supplementary Material 3). The basal area of the living vegetative sprouts ranged from 1.9 to 6.3 m² ha⁻¹ in *Castanea* dominated coppice stands, while in the *Robinia*-dominated coppice stands they accounted for

34.5 m² ha⁻¹. The remaining vegetative sprouts of the *Robinia* regenerated from the basal stems, and accounted for an average of 28% (±12%) of the total living vegetative sprouts. In *Robinia*, fire-scorched stems accounted for 100% of the dead vegetative sprouts, showing a basal area ranging from 0.1 to 7.7 m² ha⁻¹ (Table 1).

The average total height of the dominant *Castanea* sprouts range from 15.0 (±1.2) to 17.8 (±2.5) m, while in *Robinia* they ranged from 16.2 (±3.2) to 17.7 m (±1.5) (Table 1). In both tree species, the crown base of the overstory layer was 10.5 (±1.7) m above the ground.

In each plot where *Castanea* was dominant, the pre- and post-fire 2017 event nearest-neighbor NN cumulative distribution functions $G(r)$ indicated a clustered spatial pattern of the coppice stands (Figures 3A, C). However, the estimation of the NN cumulative distribution functions $G(r)$ was hampered in the plots where the occurrence of *Castanea* (plot R5) and *Robinia* (C1–C4) stems was low (Table 1). In the 2017 pre-fire stands, 70–90% of the *Castanea* stems exhibited a spatial aggregation pattern with inter-stem distance close to 2 m (Figure 3A). Five years after the wildfire event, 95% of the *Castanea* neighboring stems exhibited a clustered spatial assemblage with an inter-stem distance of up to 0.5 m (Figure 3C).

In contrast, in the 2017 pre-fire stand where *Robinia* was dominant, its stems showed random spatial patterns with inter-distances not different from those expected when using the hypothesis of complete spatial randomness (Figure 3B). Five years after the wildfire event, *Robinia* largely exhibited a clustered spatial pattern, with 65% of the stems having an inter-distance of <0.5 m and the remaining 35% with an inter-distance >0.5 m (Figure 3D). Above an inter-distance of 1 m, the stems showed random patterns that were not different from those expected under the hypothesis of complete spatial randomness (Figure 3D).

In post-fire stands, the estimated spatial distribution of the normalized stem diameter differentiation functions $\tau(r)$ indicates that clusters of different and similar-sized *Castanea* and *Robinia*

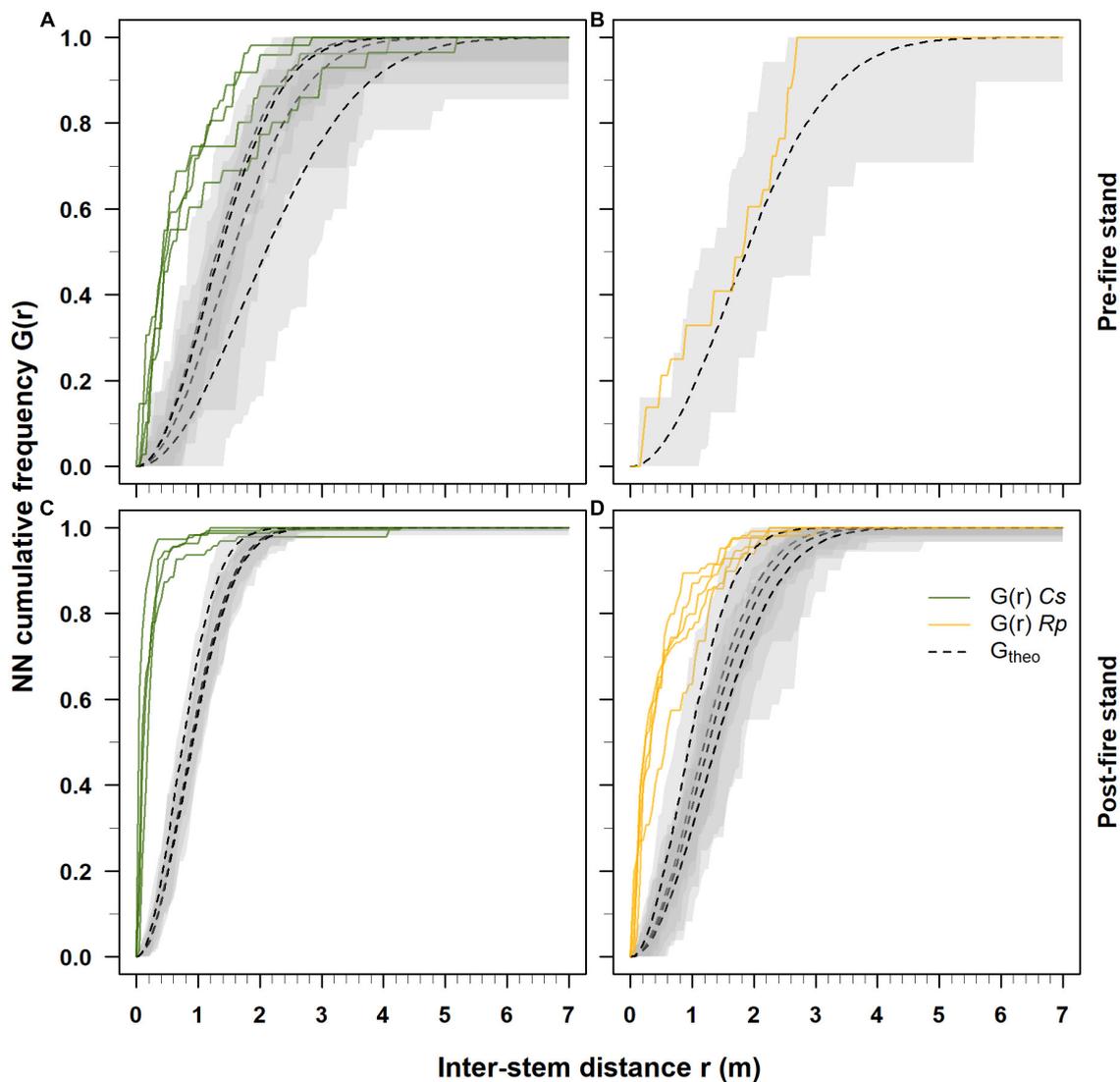


FIGURE 3

Cumulative frequency distribution of the nearest-neighbor (NN) distances estimated respectively for *Castanea* (Cs) and *Robinia* (Rp) in pre-2017 (A,B) and post-2017 fire event (C,D) coppice stands. Solid green and yellow lines indicate the estimated NN cumulative distribution functions $G(r)$ for *Castanea* and *Robinia*, respectively. Dotted black lines represent the cumulative NN distribution function G_{theo} with the CSR hypothesis, and gray bands are 95% envelope bands.

stems were spatially proximal and alternate in the coppice stands (Figures 4A–E).

The correlation range extended beyond 10 m for both the *Castanea* and *Robinia* stems. Up to an inter-distance of 2.1 m, and the stem size differentiation in *Castanea* was lower than expected for the uncorrelated stem diameters (Figures 4A–E). However, with >2 m, the inter-distance differentiation was substantially higher, with an irregular sequence of local minimum and maximum stem diameter differentiations among the neighboring stems (Figures 4A–E). In contrast, *Robinia* exhibited a more variable and complex spatial stem size differentiation than *Castanea* (Figures 4A–E). *Robinia* predominantly exhibited lower size differentiation (Figures 4A, C, D), although in a few cases it exhibited higher size differentiation $\tau(r)$ at variable inter-stem distance intervals ($1.8 \text{ m} < r < 6.0 \text{ m}$; $8.0 \text{ m} < r < 10.0 \text{ m}$) (Figures 4B, D) than expected under the hypothesis of uncorrelated

stem diameters. In the stand where *Robinia* was dominant, up to an inter-distance of 3.0 m, stem size differentiation among sprouts was lower than expected, while it was higher with an inter-distance $>3.0 \text{ m}$ (Figure 4E).

3.2. Curve-fitting and NDVI-based phenological parameters

The Beck double logistic function accurately modeled Landsat NDVI trajectories showing high pseudo R^2 values ranging from 0.88 to 0.91 (Figures 5A–E). All estimated NDVI-based phenological parameters were statistically significant at $p < 0.001$ (Supplementary Table 1 in Supplementary Material 3). Where *Castanea* was the dominant tree species in the overstory layer, the estimated spring phenological parameters (*sos* and *rsp*) differed

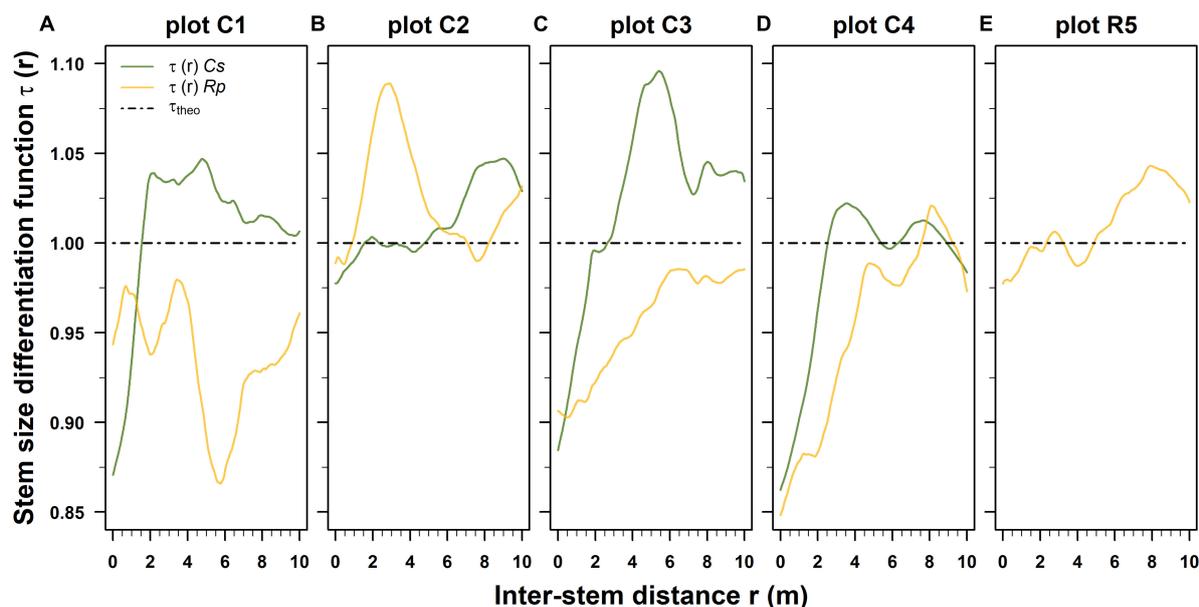


FIGURE 4

Post-fire normalized stem diameter differentiation function $\tau(r)$ estimated separately for *Castanea* (Cs) and *Robinia* (Rp) for each permanent plot, using the Epanechnikov kernel method and a bandwidth of 0.8 m. The dash-dotted black horizontal lines denote the condition of spatial uncorrelation among the stem diameters (τ_{theo}). Panels (A–E) were ordered by decreasing basal area values of standing *Castanea* tree sprouts belonging to the overstory layer. (A–E) Correspond to the plots C1–R5 of Table 1.

significantly ($p < 0.05$) from the parameters estimated for stands where *Robinia* dominated the overstory layer (Figures 6A, B). In the *Castanea* stand, the NDVI-based start of the growing season (sos) occurred in a time window of 7 days, from a minimum DOY of 118 (± 1) (28 April) to a maximum of 124 (± 1) (4 May) (Figure 6A). In contrast, in the stand where *Robinia* was dominant and the degree of cover by the understory species was approximately 90%, the estimated NDVI-based sos occurred on DOY 109 (± 3), 9–15 days early than the *Castanea* stand (Figures 5J, 6A). Additionally, significant differences were observed for the sos estimates of the *Castanea* in stands where the understory shrub species cover was higher than 20% (Figures 5F–I, 6A). The NDVI-based spring increasing rate parameter (rsp) estimated for *Castanea* was significantly lower than that estimated for *Robinia* (Figure 6B). A lower value of rsp account for 0.04 (± 0.001) in the *Robinia* coppice stand, in which the cover of the understory species was approximately 90% (Figures 5J, 6B). No significant differences were observed in the NDVI-based estimates for the rsp in stands dominated by the *Castanea*.

Field-based observations of the start of the growing season (sos) differed from the NDVI-based estimates in *Robinia*, while the results were accurate for the *Castanea* stands. On DOY 133 (May 13, 2022), on the northern slope of Mt. Somma, *Robinia* vegetative sprouts belonging to both the understory and overstory layers, exhibited a delay in leaf phenology when compared to *Castanea* (Supplementary Figure 4 in the Supplementary Material 3). Here, *Robinia* was mostly in the early stages of bud burst with buds slightly swollen and brown colored, while *Castanea* exhibited green leaves on >50% of their maximum laminar expansions (Supplementary Figure 4 in Supplementary Material 3).

4. Discussion

4.1. Stand spatial structures and vegetative regeneration strategies

Vegetative regeneration, rather than earlier spring phenology, confers a competitive advantage to *Robinia* over *Castanea* basal sprouts after a fire disturbance. The production of basal sprouts in both *Castanea* and *Robinia*, as well as root-suckers in *Robinia*, was found to be stimulated by fire disturbance, due to the presence of scorched stems that were <2 m in the study area and the documented occurrence of low-severity wildfires at the same site by Saulino et al. (2020). Hence, a double vegetative regeneration strategy enables *Robinia* to take advantage of wildfire disturbances by exploiting empty niches and thus persisting in *Castanea* coppice stands. Vegetative regeneration enables most tree species to cope with disturbances, such as wildfires or coppicing (Del Tredici, 2001). Furthermore, many root-suckering species have shallow horizontal roots that produce extensive clonal growth from endogenous uninjured buds and exogenous reparative buds after injury or senescence of the roots (Del Tredici, 2001). In this investigation the allocation of resources to the shallow horizontal roots allowed *Robinia* to spatially advance in the soil up to 10 m away from the parent plant in adjacent coppice stands, appearing as single root-suckers in the understory layer of the *Castanea* stands 5 years after the fire.

Under suppressed conditions, the aboveground root sucker portions of the plant exhibited a low stem size with only a few thin branches (personal observation). This latent stage is probably metabolically dependent on the adult parent trees, allowing *Robinia* to persist until the next disturbance in the overstory, which

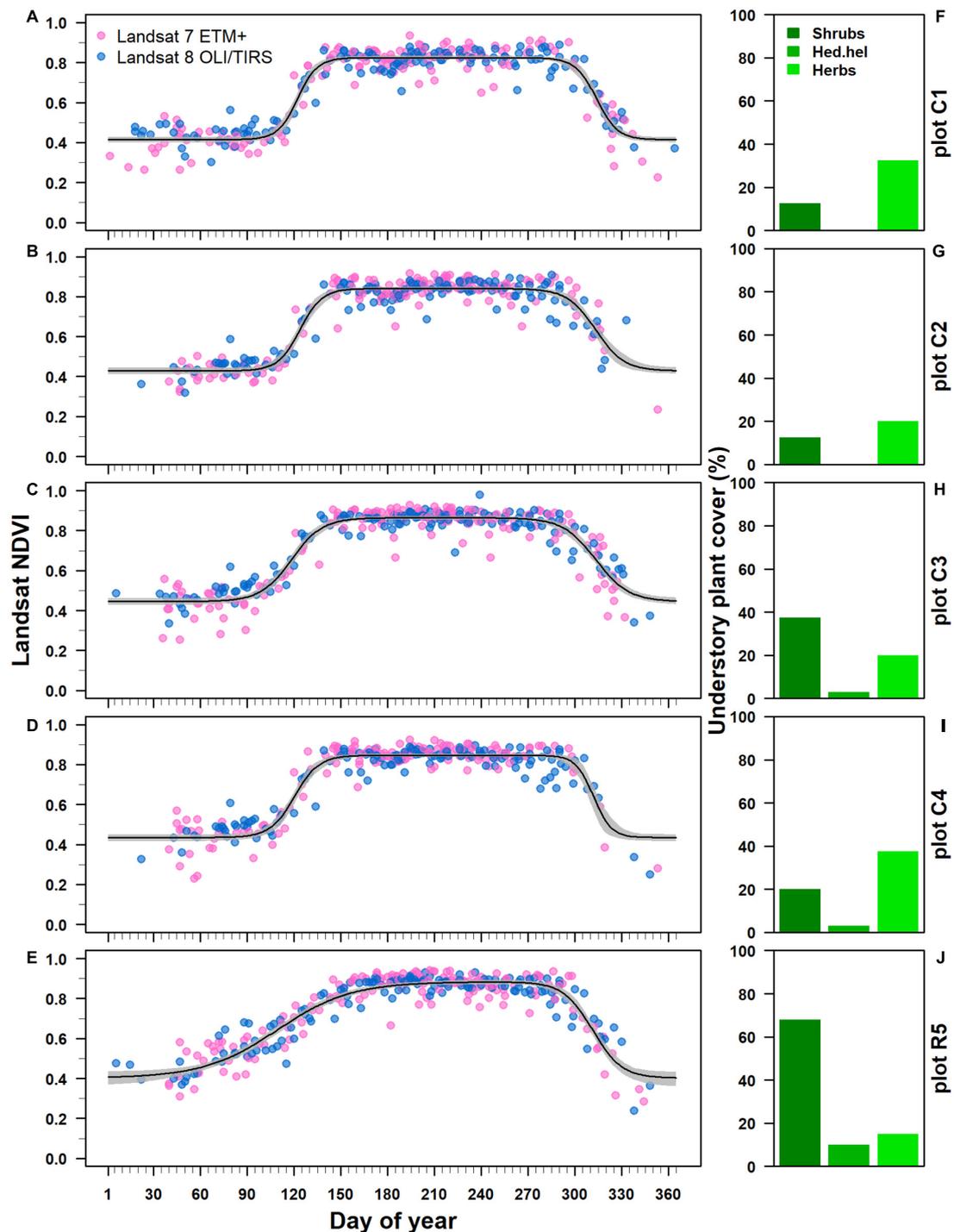


FIGURE 5

Pixel-based Landsat NDVI trajectory for *Castanea* and *Robinia* coppice forest stands. (A–E) The NDVI trajectories were ordered by decreasing basal area values for the standing *Castanea* tree sprouts belonging to the overstory layer. Each black line represents the Back double logistic function fitted to NDVI values derived from both Landsat 7 ETM+ (blue points) and Landsat 8 OLI/TIRS (pink points) satellites. Gray bands represents 95% confidence intervals. (F–J) Show the percentage cover of understory species: shrub species (shrubs), *Hedera helix* subsp. *helix* (Hed.hel) and herbaceous species (Herbs).

modifies the near-ground light regime. Indeed, *Robinia* occurred as a cluster of stems spatially alternating with clusters of *Castanea* stems or as belts at the margins of the *Castanea* coppice stand, in canopy gaps generated by single trees dying, wildfires, wind throw, or uprooting, which consequently reduced the competition

for light resources (Cierjacks et al., 2013). However, the spatial patterns of the young *Robinia* suckers that sprout from sub-superficial roots could be related to physiological integration processes (Zhang et al., 2006). Jung et al. (2009) found that *Robinia* suckers are interconnected through shallow horizontal

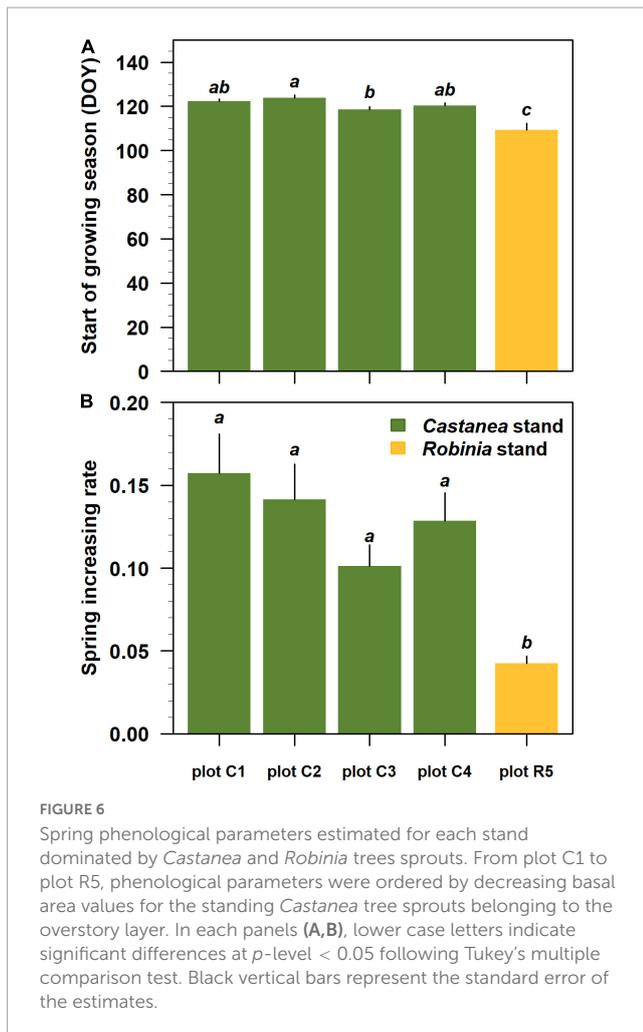


FIGURE 6
Spring phenological parameters estimated for each stand dominated by *Castanea* and *Robinia* trees sprouts. From plot C1 to plot R5, phenological parameters were ordered by decreasing basal area values for the standing *Castanea* tree sprouts belonging to the overstory layer. In each panels (A,B), lower case letters indicate significant differences at p -level < 0.05 following Tukey's multiple comparison test. Black vertical bars represent the standard error of the estimates.

roots to parent trees, highlighting their role in the allocation of photosynthates to the horizontal roots until they are capable of sprouting new suckers. The *Robinia* root suckers take advantage of the shared nutritive resources among the connected adult parent ramets, and this influences their survival and ecophysiological responses to changing environmental growth conditions (Zhang et al., 2006). Repeated human disturbances (e.g., wildfires and clear-cutting) favor spatially fixed basal sprouts and the ubiquitous and far-reaching root suckers of *Robinia*, amplify their invasiveness over *Castanea* basal sprouts, as was recently observed in similar *Castanea* coppice forests in northeastern Italy (Radtke et al., 2013; Marcolin et al., 2020).

Robinia seedlings were not observed under the fire-disturbed *Castanea* canopy cover. It is well known that light-demanding *Robinia* does not occur as seedling (Vítková et al., 2017), because its ripe seeds exhibit physical dormancy (Baskin and Baskin, 2014) which varies at the individual tree level and with the persistence of seedpods in the crown during the winter (Masaka and Yamada, 2009). This seed trait favors a persistent soil seed bank that lowers the germination rate in the absence of thermal or mechanical scarification (Giuliani et al., 2015). However, the lack of *Robinia* seedlings suggests that the heat flux in the soil during the low-intensity wildfire, as documented by the height of the scorched basal stems (<2 m), stimulated the basal stem and root bud banks, rather than the soil seed bank.

Additionally, *Robinia* takes advantage from a lower susceptibility to diseases and pests (Cierjacks et al., 2013) than the *Castanea* trees. In the unmanaged coppice forest, we observed mortality of *Castanea* stem basal sprouts related to *Cryphonectria parasitica* and exacerbated by leaf area reduction caused by *Dryocosmus kuriphilus* attacks in the last decades (Gehring et al., 2018). Therefore, the lower susceptibility to diseases and pests exhibited by *Robinia* could represent an advantageous trait, allowing it to invade and persist in *Castanea* coppice stands.

Disturbances such as fire and coppicing promote fluctuating and spatial heterogeneous light environmental conditions which stimulate both basal and root resprout of the light-demanding *Robinia*. In our protected context, like in other Mediterranean areas which shared similar disturbances, coppicing has been discontinuous for decades and has favored senescence of *Robinia* (Motta et al., 2009), while mixed-severity fires (Saulino et al., 2020) represent the main physical stimulus for the spatial advancement of *Robinia* by root-suckering. Consequently, all measures of fire suppression in chestnut stands with and without *Robinia* in the canopy layer or colonized only by its root-suckering in the suppressed layer, are effective against the invasion of *Robinia* in canopy gaps after the dominant trees of both species are killed by fire. Nature-based solutions (Gann et al., 2019) such as salvage logging restricted to areas with charred *Robinia* trees, burned wood chips and mulching in the influence area of roots could reduce light availability for root-suckering and may aid the recovery of *Castanea* resprouts. In undisturbed dense and close stands, incomplete girdling (see Nicolescu et al., 2020) and pollarding of dominant trees in the dormant season could be mechanical control techniques to be verified for their effectiveness. In our study site, stem and crown of dominant *Robinia* trees growing on the slope, carried the root-climbing liana *Hedera helix* more frequently compared to *Castanea*. The overload induces a reduction of leaf surface in the crown and mechanical instability with uprooting, suggesting a biological control technique which could favor colonization by bird disperser (mainly *Columba palumbus*, Snow and Snow, 1988), rather than eliminating this liana species. Finally, the evergreen native *Rubus* spp. shrub cover prevents the formation of root-suckering by reducing light on the ground (Warne, 2016) which, in the long run can be obtained also by planting under the canopy native already present shade-tolerant evergreen broadleaved tree and shrub species.

Although we investigated spring phenology and regeneration strategies of both *Robinia* and *Castanea* in small plots in a small Mediterranean chestnut forest, our results well clarify their different role played in spatial niche exploitation and in competitive interaction between non-native and native tree species, where vegetative regeneration from the roots rather than advanced spring phenology allows *Robinia* to take advantage of recurrent wildfire disturbances and spreads in to *Castanea* coppice forest.

4.2. Divergence in the spring leaf phenology

Relevant phenological attributes related to leaf phenology have been observed in invasive plants (Fridley, 2012). However, the advanced spring phenology is recognized as a trait that confers

a competitive advantage during the colonization of exotic species (Polgar et al., 2014). In our study, the start of the growing season for the exotic *Robinia* was found to differ from that of *Castanea* in both young and adult sprouts. In the field, we observed that the growing season occurred later in *Robinia* than in *Castanea*, suggesting that success in the colonization of *Castanea* stands by *Robinia* is unrelated to the competitive advantage of an advanced spring phenology. Spring phenology and its close interaction with climate and genotype are well-recognized in the literature (Murray et al., 1989; Silvestro et al., 2019). However, the combination of a winter chilling, photoperiod, and spring warming (forcing) is strongly involved in the triggering of bud-break and leaf-out in tree species (Polgar and Primack, 2011; Rossi and Isabel, 2017). Nevertheless, winter chilling has been identified as a necessary requirement for leaf spring phenology in most invasive species (Laube et al., 2014; Polgar et al., 2014). The late spring phenology observed in *Robinia* suggests that it probably requires a higher level of winter chilling to achieve leaf out in the spring season (Laube et al., 2014; Fu et al., 2015) when compared with *Castanea*. However, a high chilling requirement in winter can significantly reduce the probability that invasive species such as *Robinia* will gain an additional competitive advantage under ongoing climate warming. Nevertheless, in *Robinia*, later leaf-out could be interpreted as an adaptive trait useful for maximizing the length of the growing season and avoiding the occurrence of leaf damage due to late spring frost events (Allevato et al., 2019).

This species-specific phenological pattern provides interesting insights into the interpretation of satellite-derived spring phenological parameters. Indeed, the observed divergences between field and remote sensing assessments of the *Robinia* spring phenology were related to the degree of understory cover from the shrub [mainly *Rubus* spp. and *Cytisus scoparius* (L.) Link subsp. *scoparius*] and herbaceous [*Sesleria autumnalis* (Scop.) F.W.Schultz, *Luzula sylvatica* (Huds.) Gaudin s.l., *Dryochloa drymeja* (Mert. & W.D.J.Koch) Holub subsp. *exaltata* (C.Presl) Foggi & Signorini] species. In the low-elevation mountains in the southern Mediterranean, such understory species are characterized by an early and progressive bud break that starts approximately in the middle of February. Moreover, the winter green habitus of herbaceous understory species and of root-climbing liana (*Hedera helix* subsp. *helix*) contributed to maintaining the high winter NDVI (0.42 approximately), as was recently observed in other stratified Mediterranean forests (Helman et al., 2015; Helman, 2018). Therefore, in the spring, from the beginning of March to the middle of April, when *Robinia* exhibits dormant buds with no signs of vegetative activity, NDVI-based satellite assessment of its phenology is influenced by the cover and phenology of common understory vegetation assemblages under a continuous canopy dominated by *Robinia*. Once established, *Robinia* trees increase the soil nitrogen stock (Boring and Swank, 1984; De Marco et al., 2023), enhancing the eutrophication of understory community species by establishing nitrophytic, ruderal, and non-native plant species (Von Holle et al., 2013). Nevertheless, *Castanea* spring phenology was appropriately assessed from the NDVI-based satellite, without divergence between the field and remote assessments at the start of the growing season and the increasing rate in the spring. Indeed, in the coppice stand where *Castanea* is dominant in the overstory layer, understory vegetation cover consistently differs from that in the coppice

stand where *Robinia* dominates in the overstory layer. Differences in species composition suggest that ground recognition is an essential requirement in the validation of satellite-retrieved spring phenology, especially in forest stands where shrubs and herbaceous cover are both abundant. Indeed, in both evergreen and deciduous stratified forests, changes in understory species cover and composition within a pixel results in changes to the time series for the remote-sensed spectral signals because of the distinct phenology of the plant species involved (Ryu et al., 2014; Helman et al., 2015). These represent cases in which the changes in the NDVI signal could be misinterpreted as a spring phenological change, while it is actually related to changes in species composition and phenology within the pixel (Helman, 2018).

5. Conclusion

Robinia is progressively colonizing the ancient *Castanea* coppice forest in Vesuvius National Park using two vegetative regeneration strategies: basal stem sprouting and root suckering from endogenous uninjured buds and exogenous reparative buds after injury or senescence of the shallow horizontal roots. We found that vegetative regeneration rather than early spring phenology, allows *Robinia* to spatially advance, colonize, and persist in patches of coppice stands that have been disturbed by fire. The results of this study suggest that even with low severity wildfires, the invasiveness of *Robinia* will increase, as the fires will still stimulate the resprouting of suckers from roots. Although our study falls in a small area within the distribution of Mediterranean *Castanea* coppices, our results agree with the observed vegetative regeneration strategies adopted by *Robinia* in the invasion of chestnut forests. Furthermore, advanced spring phenology of exotic species conferring them a competitive advantage over native species, in *Robinia* plays, instead, a marginal role, suggesting that vegetative regeneration is more effective for the invasion of the Mediterranean *Castanea* forests. More broadly, although the strategies and patterns of spatial invasion of the alien species *Robinia* are site-specific, the methodology approach proposed in the present study is replicable in other sites where the disturbances (mainly fire and coppicing) threaten the existence of a culturally valuable Mediterranean landscape such as the *Castanea* coppice. From a management perspective, additional studies on root-sucker clonality in *Robinia* could provide further ecological and evolutionary insights into the ecophysiological relationship between parent trees and root suckers. An improved understanding of the functional traits that allow exotic trees to be invasive would help to provide reliable guidelines for the management of *Castanea* coppice stands under changing climatic and land use conditions. Our findings highlight that appropriate control methods are required for invasive *Robinia* tree sprouts in order to conserve the continuous canopy cover in *Castanea* stands. However, increasing insights into vegetative regeneration strategies based on species-specific phenological traits could support forest managers in developing appropriate nature-based solutions to control the spread of non-native tree species, especially in protected areas where chemical control methods are forbidden.

Data availability statement

The original contributions presented in this study are included in the article/**Supplementary material**, further inquiries can be directed to the corresponding author.

Author contributions

LS and AnS: conceptualization, methodology, and writing—original draft. LS, AdS, and GL: data curation. LS: formal analysis, software, and visualization. LS, AnS, GL, AdS, and AR: investigation. All authors contributed to writing—review and editing and approved the submitted version.

Funding

This work was supported by the Technical-Scientific Agreement between the National Park Cilento Vallo di Diano e Alburni and the Department of Agricultural Sciences of the University of Naples Federico II (CUP: E77G22000440005), granted to AnS.

Acknowledgments

We are grateful to E. S. Ziccardi and S. Somma for their valuable support in the field sampling. We thank the staff at Raggruppamento Carabinieri Biodiversità di Caserta for providing authorization to access the Riserva Forestale di Protezione Tirone Alto Vesuvio. This study was carried out within the Agritech National Research Center and received funding from the European Union Next-Generation EU (Piano Nazionale di

Ripresa e Resilienza (PNRR) – MISSIONE 4 COMPONENTE 2, INVESTIMENTO 1.4 – D.D. 1032 17/06/2022, CN00000022).

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/ffgc.2023.1177551/full#supplementary-material>

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