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ORIGINAL PAPER

Structure and dynamics of old-growth *Pinus nigra* stands in Southeast Europe

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Abstract

Pinus nigra has a scattered but widespread distribution across Mediterranean mountain regions, where it has often been planted to restore degraded sites, yet few studies have examined the dynamics of natural *P. nigra* stands. Old-growth *P. nigra* stands often occur on precipitous, rugged locations in the Southeastern Alps and Dinaric Mountain range, providing unique opportunities to study their natural dynamics and disturbance history. We quantified the structure and composition and used dendroecological methods to reconstruct disturbance history, including samples of fire-scarred trees, in two old-growth stands located in Slovenia and Bosnia-Herzegovina. The study stands were dominated by *P. nigra*, but also included a number of other thermophilic tree species, as well as shade-tolerant species common in the surrounding mountain forests. Both sites had an irregular uneven-age structure with several pulses of recruitment, perhaps indicating the influence of past fire events, and *P. nigra* regeneration was relatively abundant (> 3000 stems ha^{-1}). The most recent fires at each site burned in 1947 and 1969, and there was evidence of post-fire recruitment at the study sites. However, although tree cores sampled from fire-scarred trees suggest there were scattered, but infrequent fires over the past few centuries, we did not find evidence suggesting a regime of frequent recurring surface fires. The results suggest that rare surface fires may play a role in preventing successional replacement of *P. nigra* on productive sites, whereas steep, rocky sites likely support persistent populations in the absence of fire.

Keywords Age structure · Black pine · Dendroecology · Fire history · Fire regime · Stand dynamics

Introduction

Old-growth forests are an invaluable source of basic and applied information on ecosystem structure, composition, and natural processes (Foster et al. 1996; Nagel et al. 2013). Due to a long history of intensive land use, forests in an old-growth stage are rare across much of temperate Europe, particularly for common forest communities, such as oak, beech, or mixed mountain forests. However, small patches of old-growth may be widespread in areas with steep, inaccessible terrain in mountainous regions of Europe (Larson et al. 2000). A good example of this includes natural *Pinus nigra* Arn. Stands located across the Southeastern Alps and Dinaric Mountain range. Stands often occur on precipitous, rugged locations or inaccessible terrace positions in forests otherwise dominated by typical mixed mountain species, mainly including *Fagus sylvatica* and *Abies alba* (Poljansek et al. 2012; Nagel et al. 2017). Given their often inaccessible location, many of these stands have escaped historical logging and are in an old-growth stage.

Pinus nigra has a scattered but widespread distribution across mountain regions of the Mediterranean basin, ranging from Spain to Turkey (Enescu et al. 2016). Throughout much of the region, *P. nigra* is an important species for forestry, making a large contribution to timber production and the forest economy (Raptis et al. 2021; Seki and Sakici 2022). Moreover, it has often been planted on degraded sites throughout southern Europe to help restore soils and forest cover (Rey and Berger 2006; Zlatanov et al. 2010; Enescu et al. 2016). Finally, because *P. nigra* exhibits relatively good

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tolerance to a broad range of conditions, including cold-, heat-, and drought-stress, some studies have identified it as a potential candidate species to substitute native conifers (e.g., *Picea abies*) in Central Europe that are predicted to decline under future climate conditions (Huber 2011; Thiel et al. 2012). In the southern part of its range, however, a severe decline of *P. nigra* forests are predicted under future climate change projections (Navarro-Cerrillo et al. 2018; Fyllas et al. 2022).

Despite the importance of *P. nigra* both within and beyond its natural range, few studies have examined the dynamics of unmanaged old-growth stands. Understanding the dynamics of natural populations should provide important insight for future management and conservation of the species. Old-growth *P. nigra* stands are exceptionally rare in the Western part of the distribution range (e.g., Spain and France) (Fule et al. 2008; Tiscar and Lucas-Borja 2016), but more common toward the east (e.g., Bosnia-Herzegovina, Bulgaria, Turkey) (Poljansek et al. 2012; Shishkova and Panayotov 2013; Doğan and Köse 2015; Panayotov et al. 2017). Given the broad differences in bioclimate across this region, the structure, dynamics, and disturbance regimes in *P. nigra* forests are likely variable. The few studies that have been carried out on the dynamics of natural stands lend some support to this. For example, in mountains of Spain, Greece, and Turkey, regions influenced by a Mediterranean climate, studies in *P. nigra* forests show evidence of relatively frequent fire (with fire return intervals often less than 10 years) (Fule et al. 2008; Touchan et al. 2012; Christopoulou et al. 2013; Sahan et al. 2021; Sahan et al. 2022), suggesting that surface fires play a key role in stand dynamics.

In the Southeastern Alps and Dinaric Mountains, where the climate is more continental and annual precipitation is quite high (> 1500 mm) (Poljansek et al. 2012; Nagel et al. 2017), fire may not play as prominent a role as in other parts of the range of *P. nigra*. If fire is absent or infrequent, then dynamics may be regulated by competition for light with other more shade-tolerant species on sites with sufficient soil depth, perhaps allowing for long-term successional replacement of *P. nigra* following past disturbance. On sites where growing conditions are too harsh for most tree species, such as on steep, rocky slopes with shallow and erodible soils, populations may be relatively stable, with periodic recruitment replacing old individuals resulting in all-aged population structure (Abrams and Orwig 1995; Williams 1998).

We examine stand age structure and dynamics based on dendroecological data collected from two old-growth *P. nigra* stands located in Slovenia and Bosnia and Herzegovina. This work contributes to a small number of studies on the dynamics of natural *P. nigra* forests, which have mainly been carried out in more fire prone regions of the species range. We ask the following questions: 1) Does the age structure indicate an all-aged population with continuous recruitment and replacement of the overstory, or is the age structure irregular, indicating pulsed recruitment? 2) Is there evidence of past fire or post-fire recruitment in the studied stands? 3) Is there evidence of successional replacement by other more shade-tolerant species?

Materials and methods

Study areas

This study was conducted in the Hude Stene (HS) (46°31' N, 14°49' E) forest reserve in the Kamniška Alps of Slovenia and the Perućica (PE) (43°32' N, 18°71' E) forest reserve in Sutjeska National Park located in the central Dinaric Mountains of Bosnia-Herzegovina (Table 1, see Figure S1 for a map of the study sites). The HS forest reserve covers 43 ha and is located on a steep, rocky NE slope above the Kokra river valley. The HS site was chosen because it contains one of the most well preserved old-growth *P. nigra* stands in Slovenia (Dakskobler et al. 2015). The site is located at about 700–1100 m a.s.l. on dolomite bedrock with shallow rendzina soil, with a mean annual temperature range of 6–8 °C and a mean annual precipitation range of 1600–1800 mm (based on the Slovenian climate atlas, period 1981–2010, Ministry of the Environment and Spatial Planning). The PE forest reserve is located in Sutjeska National Park, where old-growth *P. nigra* stands frequently occur on steep, rocky slope positions (Fig. 1a and b). We chose a stand that was accessible from the main road near Dragos sedlo. The site is characterized by limestone rock outcrops and cliffs, with *P. nigra* growing on moderate to steep SW slopes at approximately 1300–1600 m a.s.l. The mean annual temperature is 6 °C and mean annual precipitation is

Table 1 Site characteristics of the two old-growth *Pinus nigra* stands

	Huda stena (HS)	Perućica (PE)
Coordinates	46°31' N, 14°49' E	43°32' N, 18°71' E
Mean annual temperature (°C)	6–8*	6**
Mean annual precipitation (mm)	1600–1800*	1800**
Bedrock type	Dolomite	Limestone
Elevation range (m a.s.l.)	700—1100	1300—1600
Predominant aspect	NE	SW
Slope (°) range (mean)	30–50 (39)	8–45 (25)
Rock cover (%) range (mean)	5–65 (26)	0–10 (6)
Herb cover (%) range (mean)	35–95 (74)	40–90 (79)

*Range 1981–2010, based on the Slovenian climate atlas, Ministry of the Environment and Spatial Planning; **Bajić and Trbić 2016

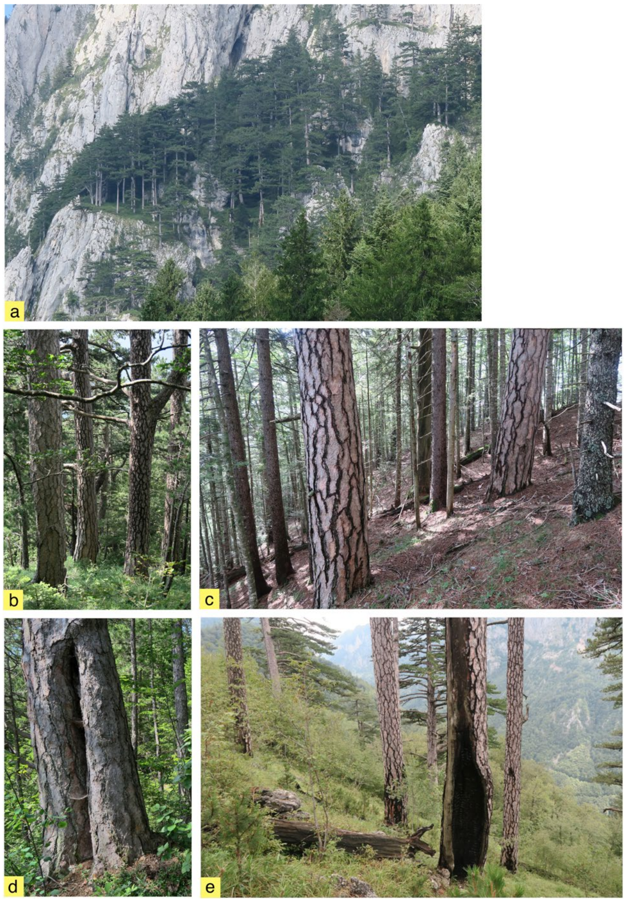

Fig. 1 Structural patterns of old-growth *Pinus nigra* stands: (**a**) *P. nigra* dominated stand growing on a steep rocky slope at the Perućica site; (**b**) part of the PE site with a high density of large *P. nigra* trees; (**c**) old *P. nigra* growing on a more productive, moderately sloped site undergoing successional replacement by shade-tolerant conifers; (**d**) old fire-scarred tree used for fire history reconstruction; (**e**) open stand structure with evidence of recent fire

1800 mm (Bajić and Trbić 2016). Herbaceous plants were abundant in the understories of both sites, with mean percent cover of 74% and 79% at HS and PE, respectively. Rocky outcrops were more common across plots at HS (26% cover) compared to PE (6%).

Field sampling

Field sampling was carried out in the summers of 2016 and 2017. Eight circular plots were established in each of the two study areas using a roughly systematic sampling design: transects running parallel to the slope contour were placed at low, mid, and upper portions of each stand, with 2–3 plots per transect. However, due to the rugged nature of the terrain (e.g., rock outcrops and cliffs), plots could not always be systematically spaced along transects; in such cases, plot centers were shifted along the transect until sampling could be safely done. Plot size (horizontal projection) was 200 m^2 at the PE site and ranged from 200 to 400 m^2 at the HS site; the larger size was used when tree density was very low and the terrain safely allowed placement of a larger plot.

Within each plot, we recorded the species and diameter at breast height (dbh) for all live trees > 5 cm dbh (total sample sizes were 295 trees at HS and 192 at PE). We tallied regeneration of each tree species present in the plot within three height classes (10–50 cm; 51–150 cm; > 150 cm-5 cm dbh). Site characteristics of the plots, such as geographical coordinates, elevation, aspect, slope, and ground cover (% cover of rocks and herbs) were recorded. Increment cores were sampled from all trees ≥ 10 cm dbh within each plot. One core was extracted from each tree at approximately 1 m in height and parallel to the slope contour. Cores were also extracted from trees between 5 and 9.9 cm dbh in circular sub-plots of 150 m^2 at the HS site, but not at PE in order to reduce sampling effort due to time constraints. We also searched entire stands, including areas outside plots, for fire-scarred trees. Because we did not have permission to sample partial cross sections from live trees, we extracted several tree cores crossing the callus wood formed at scar junctions on fire-scarred trees (Vasileva and Panayotov 2016). In a few cases at the HS site, we sampled cross sections from downed and dead logs with fire scars.

Dendroecological analysis

All cores samples were air-dried, glued to wooden holders, and sanded with progressively finer sandpaper (Stokes and Smiley 1996). The wood samples were then visually cross-dated using pointer years based on consistently narrow rings (Yamaguchi 1991). Cores were scanned using the software ATRICS 1.2 (Levanic 2009), and ring width was measured to the nearest 0.01 mm using WinDENDRO software (Regent Instruments Inc.). For cores samples that did not contain the pith, the number of missing rings was estimated based on the arching pattern of tree rings and growth rate of the last five visible rings. At HS, we estimated the ages of the non-cored black pines belonging to the 5—9.9 cm dbh class based on the age distribution of trees cored in sub-plots.

Tree-ring cores were used for dating past fire events, both directly by inspecting cores for fire scar wounds (e.g., cambial injury with discolored wood and callus tissue), and indirectly by identifying abrupt growth releases and suppressions of radial growth. Previous work indicates that both growth release and more commonly, growth suppressions, occur following known fire events (Vasileva and Panayotov 2016). Each sampled fire scar was dated to the exact year or to a range of years, which was commonly the case for tree cores that intersected fire scars. Such samples were difficult to cross-date due to missing rings near the fire scar zone.

Growth releases and suppressions were identified by first calculating percent growth change values in yearly increments for each tree-ring series using the running mean technique of Nowacki and Abrams (1997). Percent growth change (% GC) for a given year is equal to [(M2—M1)/M1] * 100, where M1 is equal to average radial growth over the preceding ten-year period (inclusive of the year for which %GC is being calculated), and M2 equals the average radial growth over the subsequent ten-year period. The maximum % GC value for each growth pulse exceeding 50% (absolute value) associated with each release or suppression was selected as the disturbance year (Nowacki and Abrams 1997). However, release and suppression events were only included in the disturbance history chronologies if they lasted a minimum of 10 years based on a visual inspection of the cores. Releases were further categorized as minor (50–100%) and major releases (> 100%). Disturbance chronologies were constructed based on the number of cores showing a release or suppression each decade. The chronologies were truncated when the sample depth dropped below 15 trees. Finally, we searched archival literature (e.g., newspaper records, local forest management records, etc.) for any documented evidence of wildfires in the two study areas.

Results

Stand structure and composition

Tree density (dbh ≥ 5 cm) was high at both sites, with an average of 1049 trees ha^{-1} at HS and 1313 trees ha^{-1} at PE. The mean basal area at HS and PE was 34.7 and 103.0 m^{2}ha^{-1}, respectively. Note that per hectare values of both tree density and basal area are likely biased toward higher values given our sampling design, whereby we avoided rugged areas with low tree density on sample transects. *Pinus nigra* was dominant at both sites, representing 92 and 82% of the total basal area at PE and HS, respectively. In terms of tree density, *P. nigra* made up 50 and 70% of the stand at PE and HS, respectively. A number of other tree species comprised the remainder of the stands at both sites in terms of density. At HS, *Ostrya carpinifolia* (10%), *Larix decidua* (7%), *Fagus sylvatica* (5%), and *Picea abies* (5%) were present, as well as a minor component of thermophilic species (< 2%), including *Sorbus aria*, *Fraxinus ornus*, and *Sorbus aucuparia*. At PE, *Abies alba* (24%), *P. abies* (15%), and *O. carpinifolia* (8%) were relatively abundant, followed by *F. sylvatica* (3%) and *S. aucuparia* (1%).

The diameter structure at both sites was uneven (Fig. 2), with *P. nigra* occurring in all size classes, reaching a maximum dbh of 62 cm at HS and 87.3 cm at PE. Unlike HS, the PE site was notable for having a high density of large trees > 50 cm dbh. At both sites, all of the other tree species were mainly present in smaller dbh classes below 35 cm.

A total of 160 and 129 cores were sampled at HS and PE, respectively. However, due to incomplete cores with rotten centers or difficulties distinguishing annual growth rings, particularly for *O. carpinifolia*, age structures were reconstructed from a sample of 128 cores at HS and 124 cores at PE. HS includes dated stems from 5 to 10 cm dbh sampled in subplots ($N = 18$), as well as estimated ages for trees in this size class sampled in the full plot size ($N = 28$). Note that PE does not include stems below 10 cm dbh. Both sites show irregular, multi-aged structures (Fig. 2). HS shows two age class peaks, one from 20 to 30 years and another from 70 to 130 years; most of the other tree species recruited during the latter peak. A low density of *P. nigra* is present in scattered age classes > 200 years up to a maximum age of 461 years at HS. At PE, *P. nigra* is present in nearly all age classes from 90 years to a maximum age of 434 years, with a relatively high abundance of stems > 200 years old. The age structure at PE exhibits a broad peak from around 1820–1920, during which time most of the other tree species recruited. Compared to HS, there is a notable lack of stems < 50 years old at PE, but this is likely a sampling artifact.

The density of tree regeneration (all species and height classes combined) was 5686 stems ha^{-1} at HS and 3256 stems ha^{-1} at PE, with most stems occurring in height classes below 150 cm (Table 2). *Pinus nigra* regeneration was abundant at HS, making up 64% of the total density, followed by *P. abies* (20%) and *L. decidua* (13%). At PE, the dominant species in the regeneration layer included *P. nigra* (25.9%), *A. alba* (25.5%), *S. aria* (24.4%), and *P. abies* (12.3%).

Disturbance history

For the HS site, we identified a total of 77 release and 68 suppression events in the disturbance chronology beginning in 1860 (the sample depth was below 15 trees prior to 1860) (Fig. 3). Five fire-scarred cross sections collected at HS all show a fire event in 1969. This event was also published in the archives of the local fire department, which describe a wildfire burning the slope of the forest reserve in 1969. The disturbance chronology also shows a large number of suppression events in the 1970s and 1980s. The 2000 decade shows a peak of release events, but it is not clear if this is a delayed reaction to the 1969 fire event. The 1930s show a small peak in suppressions, perhaps indicating a past fire event, but no other fires were recorded in the sampled cross sections. At PE, we identified a total of 172 release and 131 suppression events in the chronology beginning in 1700. Our archival search revealed a wildfire that burned the slope in the vicinity of our study site in 1947 (Fukarek 1970). Given

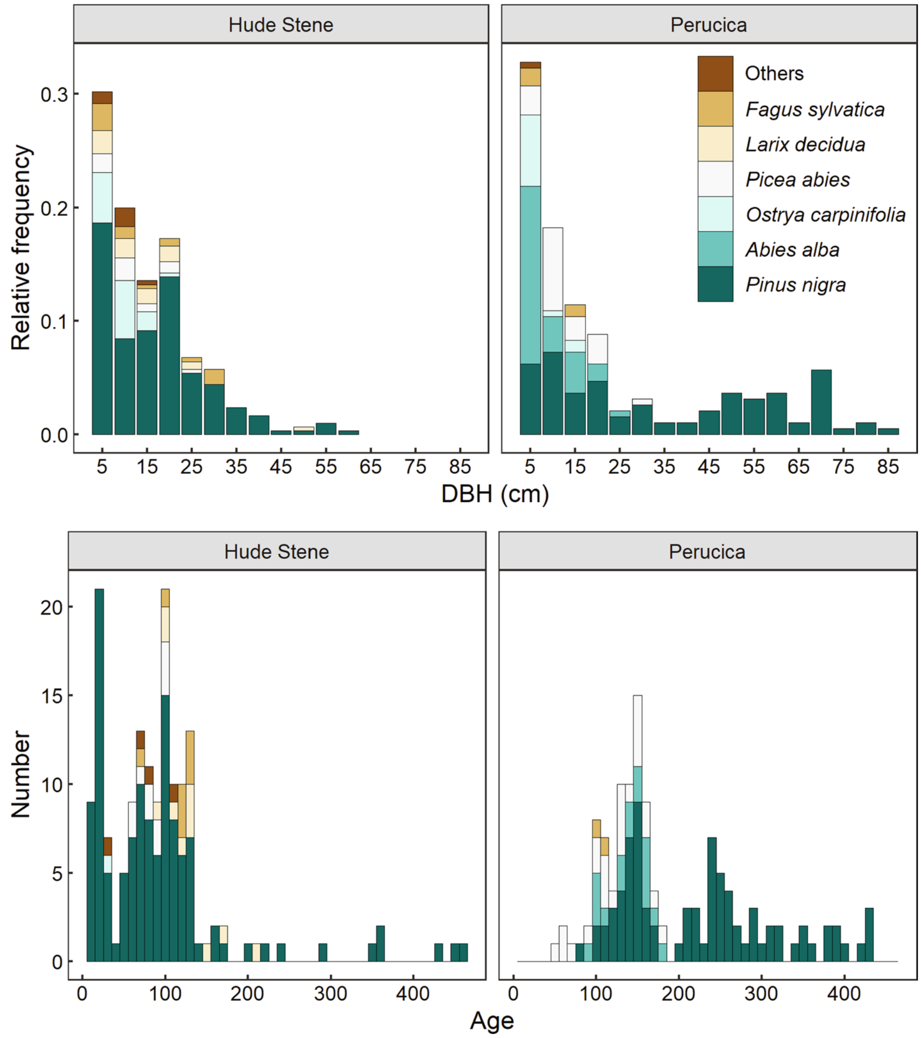

Fig. 2 Diameter (dbh) and age distributions by species for the two study sites. Trees were cored at a height of approximately one meter, such that ages represent recruitment into the population at this height. Note that Hude stene includes core samples from trees 5–10 cm dbh, while Perućica only includes trees > 10 cm dbh

Table 2 Regeneration density (N-ha^{-1}) by tree species and height class at the two study sites

	Huda Stena			Perućica		
Height (cm)	10–50	51–150	> 150	10–50	51–150	> 150
Pinus nigra	1391	1422	836	588	213	44
Picea abies	486	571	65	113	219	69
Larix decidua	283	306	150	0	0	0
Ostrya carpinifolia	163	13	0	0	44	44
Sorbus aria	0	0	0	31	688	75
Abies alba	0	0	0	13	644	175
Others*	0	0	0	44	156	100

**Acer pseudoplatanus, Fagus sylvatica, Fraxinus ornus, Juniperus communis, Sorbus aucuparia*

the large peak in suppression events in the 1950s, followed by several decades with high numbers of minor and major release events, it seems likely that this fire burned the study site. We extracted cores from 10 trees with old scars that may have been created by past fires at PE. Five trees had scars dated to the 1820s (1821, 1822, 1823, 1823, 1826), which was likely a single event that could not be precisely dated due to missing rings near the scar juncture. However, the disturbance chronology does not show a clear peak of either suppression or release during this time period. Other scarred trees had single scars present in cores that dated to 1664, 1772, 1810, 1842, and 1874, but none of these approximate scar dates were recorded on more than one tree, making it difficult to conclude if these were related to fire events

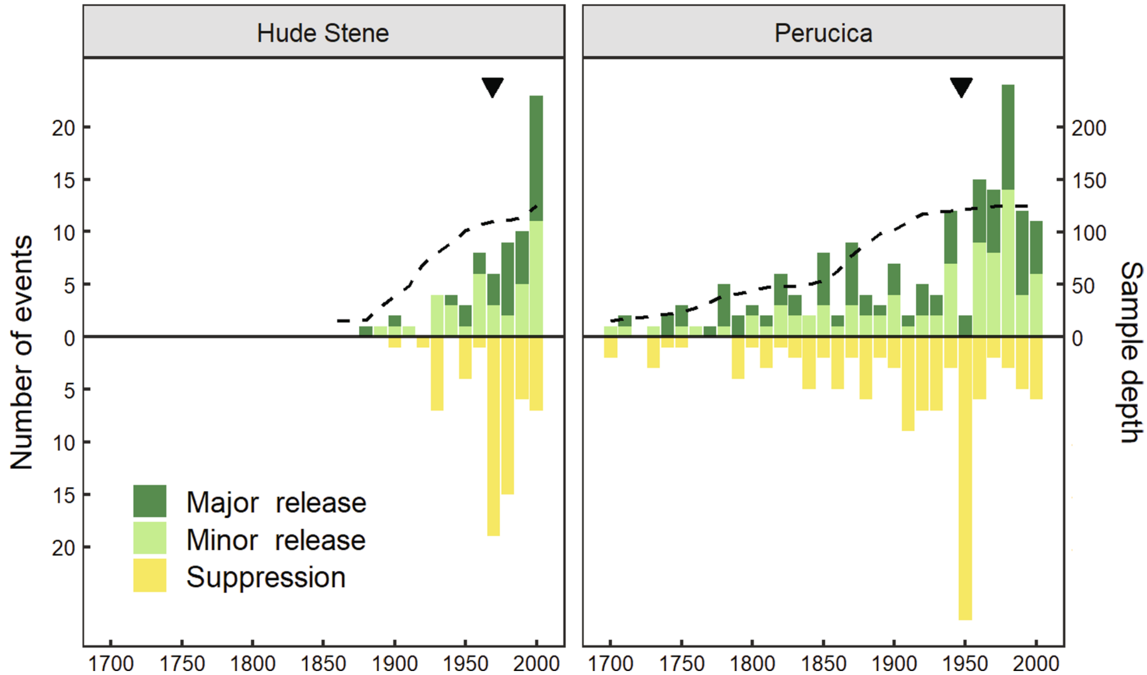

Fig. 3 Disturbance chronologies for both study sites. Upward facing bars show the number of major releases and minor releases each decade, while downward facing bars show suppression events. Chronologies are truncated when the sample depth dropped below 15 trees. The black arrows indicate known fire events from historical archives

that burned the surrounding stand, lightning strikes, or other types of injuries.

Discussion

Taken together, the results suggest that both environmental conditions and disturbance history influence forest dynamics at the study sites. *Pinus nigra* populations at both sites have an uneven-age structure, with canopy individuals reaching ages well over 300 years. However, the age structures do not resemble a typical negative exponential distribution that would indicate continuous recruitment and replacement of the overstory. Rather, the age structure is irregular with several pulses of recruitment, perhaps indicating the influence of past fire events or favorable environmental windows for seedling establishment and growth.

There was evidence of wildfire at both sites, including written documentation of the most recent fire at each site. Both the 1947 fire at PE and 1969 fire at HS were recorded in tree growth patterns via a large number of suppression events. However, there is no strong evidence suggesting that these sites burn relatively frequently. We did not encounter fire scarred trees with typical "cat faces" showing multiple scars that recorded a history of recurring fire, or open forest structures dominated by large widely spaced trees, both of which are consistent with *Pinus* forests that experience frequent surface fires (Keeley and Zedler 1998; Fule et al. 2008). The scarred trees that we found at the PE site had single old scars that were nearly healed over (Fig. 1d). Scars in five of these trees at PE dated to around 1820, which we suspect was a fire event, but we cannot rule out anthropogenic causes, such as resin collection. Although our evidence is limited, the data suggest that low intensity fires burn episodically on these sites. One potential explanation for a low fire frequency is that while thunderstorms and lightning are frequent in the region, they are often accompanied by heavy precipitation, which likely limits the ignition and spread of fire (Nagel et al. 2017).

Even if fires are relatively infrequent, recruitment patterns indicate they may play an important role in forest dynamics. For example, there was a protracted pulse of tree recruitment starting after the 1820s event at PE, when all the species other than *P. nigra* recruited (Fig. 2). Likewise, there was a recruitment pulse of *P. nigra* after the 1969 fire at HS. Low intensity surface fire may remove competition from understory shrubs and thermophilic tree species, and provide recruitment opportunities for *P. nigra* and other shade-tolerant late successional species, such as *A. alba* and *P. abies* observed at PE. Occasional fire may also be important for reducing competition with thin-barked late successional species, which have lower resistance to fire compared to thick-barked *P. nigra* (Fernandes et al. 2008), especially on sites with more productive edaphic conditions that support these species. The age structure and composition patterns at PE lend partial support to successional replacement of *P. nigra* in the long-term absence of fire on more moderately sloped plots. For example, on the two steepest plots (39 and 45°), *P. nigra* made up 80% of the stems, while the remaining stems were mainly understory *O. carpinifolia*, another species able to tolerate steep, rocky sites. On the more moderately sloped plots (cca 10–20°), *A. alba* and *P. abies* made up 50% of the stems (Fig. 1c). At HS, where nearly all plots were located on steep, rocky site conditions, very slow growing *P. nigra* and *O. carpinifolia* were the dominant species, and there was no evidence of successional replacement by shade tolerant, late successional species.

There are few studies in the region to compare with our results. The only other study on the dynamics of old-growth *P. nigra* was carried out in the central Dinaric Mountains of Bosnia-Herzegovina by Accetto (1979). He examined the age structure and fire history of a stands growing on steep, rocky slopes, similar to the stands in our study. His study also documented irregular multi-aged stands with pulses of past recruitment over four centuries. Based on 57 cross sections of mature trees, he identified six trees with individual fire scars between 1667 and 1882, and only two trees recorded the same fire date. He suggested that these scars were caused by low intensity surface fires that played little role in forest dynamics, although a fire date in 1744 is synchronized with a large recruitment pulse in his published age structure. Other studies have documented the occurrence of wildfires in *P. nigra* stands in the Southeastern Alps and Dinaric regions (Urbancic and Dakskobler 2001; Poljansek et al. 2012; Nagel et al. 2017), and field reconnaissance of other old-growth stands in Sutjeska National Park had evidence of fire (scorched trees) (Fig. 1e), indicating that these stands occasionally burn.

Our results suggest that the structure and dynamics of old-growth *P. nigra* stands in the study region differ from those in other Mediterranean mountain regions that are regulated by more frequent fire (Fule et al. 2008; Touchan et al. 2012; Christopoulou et al. 2013; Sahan et al. 2022). Fule et al. (2008), for example, working in old-growth relict stands in eastern Spain, found multi-aged stands with open structure dominated by large *P. nigra* trees (i.e., 99% of tree species composition) that had survived many surface fires. They also reported patchy and low overall densities of *P. nigra* regeneration (196 stems ha^{-1}), along with higher densities of *Quercus* and *Juniperus* regeneration, suggesting the recurring surface fires are important for maintaining forest structure and composition at these sites. In another old-growth stand in southern Spain, again dominated by *P. nigra* (representing 98% of basal area in the study), Tiscar and Lucas-Borja (2016) also reported multi-aged structure dominated by large trees, and a low density of *P. nigra* regeneration; they suggest that *P. nigra* recruits episodically during a favorable combination of environmental factors (Tiscar 2007). By comparison, the mean density of regeneration at our sites was > 3000 ha^{-1} and was often dominated by *P. nigra* in many plots, suggesting that *P. nigra* is able to maintain a bank of advance regeneration in areas with sufficient understory light.

Conclusions and management implications

This study contributes to a small body of literature on the dynamics of old-growth *P. nigra* stands in Europe, where few natural old-growth forests remain across much of the range of this species. Unlike other stands in the Mediterranean region that support frequent surface fire and open structures dominated by *P. nigra*, our study stands were comprised of mixed tree species and higher tree densities. Within stands, *P. nigra* was dominant on steep, rocky slope positions, while late successional shade-tolerant tree species were developing in the understory of *P. nigra* on more productive, moderate slope positions. Both sites have burned over the past century, but we did not find evidence of frequent recurring fire. We suggest that rare surface fires may play a role in preventing successional replacement of *P. nigra* on productive sites, whereas steep, rocky sites likely support persistent populations in the absence of fire. Further fire history studies and post-fire recovery studies in recently burned stands across a range of edaphic conditions would be important to further generalize these results.

There are several important implications of this study for the conservation of natural *P. nigra* forests. Because *P. nigra* often occurs on rugged inaccessible locations that have escaped past logging activities, many stands in the Southeastern Alps and Dinaric Mountains are in an old-growth stage of development, yet many of these areas are not formally protected in forest reserves. Other forest communities that mix with *P. nigra*, such as low statured thermophilic forests dominated by *O. carpinifolia* and other broadleaf species that grow on steep, south facing slopes, may also occur in an old-growth stage throughout this region, yet have received very little attention compared to old-growth forests on productive sites. *Pinus nigra* stands support a high diversity of understory herbs and shrubs (Accetto 1979; Dakskobler et al. 2015), and perhaps other taxa that have not been adequately studied. Given their importance for natural heritage and biodiversity, coupled with the vulnerability of *P. nigra* to climate change (Fyllas et al. 2022), formal protection of larger landscapes containing old-growth *P. nigra* may be prudent. If possible, managers should avoid suppressing low intensity surface fires caused by lightning in protected areas with natural *P. nigra* forests, where fires may play an important role in removing competing species.

The results may also help to guide management of production forests, particularly with regard to aging *P. nigra* plantations that are common across Southern Europe. One potential management option that may restore the long-term functionality of these plantations is to convert them to uneven-aged stands that can be maintained with natural regeneration, which would emulate the age structure of natural stands. This could be done using variable retention harvests with canopy openings sufficiently large for *P. nigra* recruitment (Palik and D'Amato 2019). One challenge is that plantations often have an understory component dominated by herbaceous plants and shrub-like broadleaf species, such as *Fraxinus ornus*. This understory layer both competes with *P. nigra* regeneration, and also contributes to a thick layer of organic matter, which inhibits seedling establishment of *P. nigra*. A potential solution to both of these obstacles is to use prescribed fire, which should emulate the low intensity surface fires that occur in natural *P. nigra* stands. In *P. nigra* forests managed for multiple functions in Spain, for example, prescribed burning has been successfully used to reduce fuel levels and vulnerability to crown fire, facilitate natural regeneration by burning competitive understory shrubs, and maintain open canopy stands with old-mature trees (Domènech et al. 2018). We therefore suggest that future research should explore a combination of uneven-aged silviculture and prescribed fire treatments to restore and enhance forest functions in aging *P. nigra* plantations.

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Authors' contributions TAN and MC carried out the field measurements. MC and TAN carried out the laboratory work and analyzed the data. TAN conceived the study and wrote the manuscript, with help from MC.

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Data availability The data are available from the corresponding author upon request.

Declarations

Conflicts of interest The authors declare no competing interests.

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