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Review Article

Post-fire succession of black pine (*Pinus nigra*) forest vegetation under different fire regimes

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Abstract – The black pine is a characteristic Mediterranean pine species and extends from Spain eastward to Southern France, Italy, Austria, the Balkans and Türkiye. Black pine is a fire tolerator and has a distinctive natural fire regime differently from the serotinous red pine and Aleppo pine forests in Mediterranean. Black pine forests are one of the ecosystems that are most affected by changing fire regimes. Fires in these forests generally occur as low intensity surface fires. The black pine is a light-demanding species and in pure stands it forms single layer structure with self-pruning. It also has a thick bark. Therefore, heat during surface fires does not have a lethal effect on the trees and crown fires will not be generated due to self-pruning. However, with changing climatic conditions and forest structure based on human use and management, the fires in black pine forests have begun to become crown fires in large areas. Since the black pine does not have any adaptation to crown fires, the trees are killed and no regeneration occurs. This process results in the degradation of black pine forests into other vegetation types such as oak woodlands, rock rose (*Cistus* spp.) scrublands or bracken fern (*Pteridium aquilinum* L. (Kuhn)) herbaceous vegetation. This holds true for the whole of the distribution of the black pine in the Mediterranean. Therefore, a silvicultural approach ensuring fires occur as surface fires only should be employed in the existing black pine forests and the areas degraded after fires should be restored in an ecological way to re-establish the black pine.

Keywords: black pine, crown fire, degradation, fire regime, Mediterranean, succession, surface fire, vegetation

Introduction

The genus *Pinus* is represented by 122 species worldwide (POWO 2024). They are mainly distributed in the northern hemisphere and form forests in a wide geographical belt between the 2nd and 70th latitudes (Nobis et al. 2012). A widely distributed pine species is the black pine (*Pinus nigra* J.F.Arnold). It is a characteristic Mediterranean pine species with a natural geographical distribution extending from Spain eastward to Southern France, Italy, Austria, the Balkans and Türkiye (Christopoulou et al. 2014). It is also found in parts of north-west Africa, some Mediterranean islands (Corsica, Sicily, Cyprus and some Aegean islands) and the Crimean Peninsula in the Black Sea (Moreira et al. 2011). Within the Mediterranean basin, it has the widest distribution in Türkiye (Sevgi and Akkemik 2007).

The taxonomy of the species has a very complicated history (Akkemik 2020), but currently it includes five subspecies: *Pinus nigra* J.F. Arnold subsp. *nigra*, *P. nigra* subsp. *laricio* Palib. ex Maire, *P. nigra* subsp. *dalmatica* (Vis.) Franco, *P. nigra* subsp. *salzmannii* (Dunal) Franco and *P. nigra* subsp. *pallasiana* (Lamb.) Holmboe (Farjon 2010, POWO 2024). The distribution of these subspecies, which are scattered throughout the Mediterranean basin, varies geographically (Alptekin 1986, Enescu et al. 2016). *Pinus nigra* subsp. *nigra*, known as the Austrian black pine, extends from Austria to central Italy and has a natural distribution in Greece and the Balkans. The Corsican black pine (*P. nigra* subsp. *laricio*) is distributed in Southern Italy, Sicily and Corsica. The Dalmatian black pine (*P. nigra* subsp. *dalmatica*) is found in the north-east of the Adriatic coast and on the Croatian islands. The Pyrenean black pine (*P. nigra* subsp. *salzmannii*) occurs naturally in the Pyrenees Mountains, central and southern Spain and North Africa. The Anatolian black pine (*P. nigra* subsp. *pallasiana*) is distributed mainly in Anatolia, the Southern Carpathians, Crimea, Cyprus and Syria.

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The species is generally located in the supra-Mediterranean and sub-Mediterranean zones of the Mediterranean region and is a characteristic pine species of this region (Enescu et al. 2016). Forest fires have a decisive role in shaping the vegetation in the Mediterranean region (Pausas and Keeley 2009). Forests of the red pine (*P. brutia* Ten.), Aleppo pine (*P. halepensis* Mill.) and maritime pine (*P. pinaster* Aiton), which are widely distributed in the Mediterranean region (Bonari et al. 2021), are frequently exposed to fires and rapidly revegetate by means of their serotinous cones (Ne'eman and Arianoutsou 2021). Indeed, what is important here is not the ability of the species to adapt to fire, but their adaptation to the natural fire regime of the ecosystem (Sugihara et al. 2006, Keeley et al. 2011).

Fire regime is a concept that describes the mean and range of variation in characteristics like frequency, periodicity, intensity, severity and patchiness of fire (Krebs et al. 2010). There is a mutual interaction between the fire regime and vegetation; while the fire regime depends on the type of vegetation and its flammable load capacity, the vegetation can also tolerate the effects of fire with its adaptation capability (Sugihara et al. 2006). Therefore, if the fire regime experiences a major change, it may have a negative impact on the ecosystem's post-fire regeneration ability and changes in vegetation structure may occur (Keeley et al. 2011).

The majority of fires (more than 90%) in the Mediterranean basin are caused by human activities (San-Miguel-Ayanz et al. 2023). Ecosystems dominated by species that rejuvenate from seeds (obligate seeders) are particularly sensitive to changes in fire frequency (Pausas et al. 2008). The increased frequency of fire recurrence in red pine and Aleppo pine forests prevents these forests from reaching the maturity needed to create a sufficient crown seed bank. This causes species to fail to rejuvenate after fire, and forest ecosystems can be replaced by maquis or other vegetation types (Kavgacı et al. 2016).

Black pine forests too have a natural fire regime. However, this regime is characterized by a relatively high fire frequency and low intensity fires, unlike the thermo- and meso-Mediterranean pine ecosystems of red pine and Aleppo pine, which support highly flammable foliage and require fires with higher temperature to regenerate, but which cannot survive at high fire frequencies due to lack of sufficient time for canopy seed banking (Ne'eman and Arianoutsou 2021). As a result of the fire adaptation characteristics of black pine, it also differs notably from red pine and Aleppo pine. The triggering effects of both human activities and climate change on fires (Meehl and Tebaldi 2004, Dequé 2007, Beniston et al. 2007) are causing changes in the fire regime of black pine forests that affect vegetation recovery. This effect can be expected to be harsher than thermo- and meso-Mediterranean pine ecosystems, whose recovery after fire depends on a crown seed bank.

This study was prepared in this context and an assessment was done on the post-fire recovery of black pine forests in Mediterranean under the current fire regime and potential effects of a changing fire regime on post-fire vegetation dynamics. In order to accurately understand the interaction between the changing fire regime and black pine forests, it is important to know their biological, ecological and vegetative characteristics. Therefore, first the biology, ecology, general vegetation characteristics and structural features are explained. Subsequently, the interactions between black pine forests and fire are discussed, the changes that may occur in the vegetation structure under changing conditions are evaluated, and based on those, suggestions for post-fire restoration practices are submitted.

Biology and ecology of black pine forests

The black pine is a tree species that can reach 30-35 m height; mature stems have deep cracks and very thick bark (Yaltırık and Efe 1994, Fig. 1). Its resinous buds are cylindrical

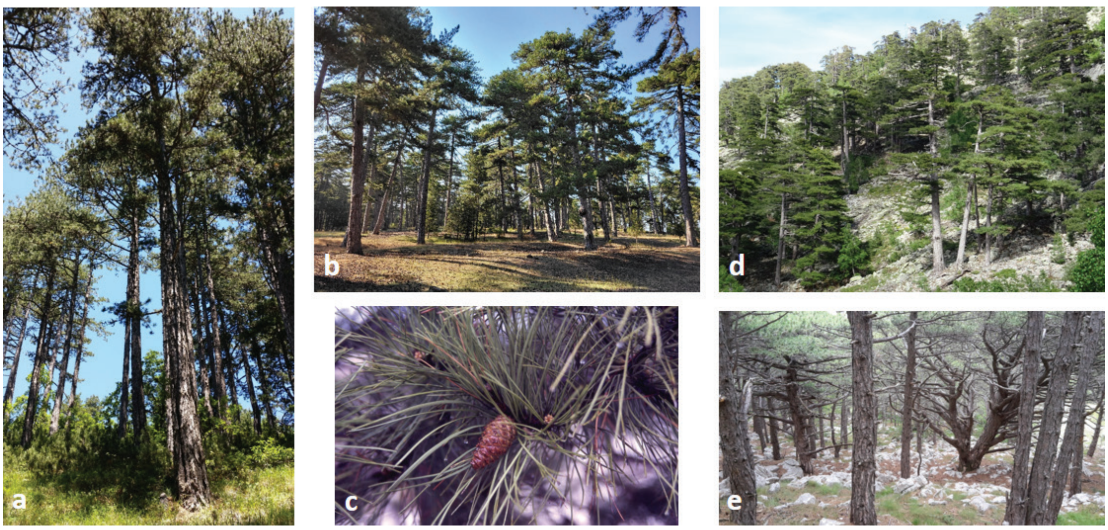

Fig. 1. Physiognomy of black pine forests in the Mediterranean: a – *Pinus nigra* subsp. *nigra* forests from Northern Macedonia, b – *P. nigra* subsp. *pallasiana* from Mugla in Türkiye, c – cone and shoot of *P. nigra* subsp. *salzmannii* from Spain, d – *P. nigra* subsp. *laricio* from Italy, e – *P. nigra* subsp. *dalmatica* from Croatia. Photo: D. Mandžukovski (a), E.S. Keleş (b), J. Loidi (c), G. Bonari (d), D. Krstonošić (e).

in shape and have a suddenly tapering structure at the ends. Leaves are 8-15 cm long, dark green and quite hard. The leaves at the ends of the shoots turn towards the bud, forming a bowl. Black pine is a monoecious species. The cones, 4-8 cm long and 2-4 cm wide, are stemless. Cones mature in two years and scatter their seeds from late autumn to early spring. When seeds are exposed to high temperatures for a long time, they lose their ability to germinate (Turna and Bilgili 2006). It is a relatively light-demanding tree, but it can tolerate shading to some extent at high productive sites.

Although the black pine is a species of the Mediterranean basin, it can appear under different ecological conditions within the basin. In addition to the Mediterranean distribution, it is also widely distributed in temperate-humid or cold-humid climates (Enescu et al. 2016). The coastal areas of the Black Sea, the mountainous regions of Northern Anatolia, the Balkans, central Europe and the Pyrenees are characterized by humid climate conditions, in which the black pine is abundant. The black pine also grows extensively in semi-humid and semi-arid climates such as the inner parts of the Black Sea and Sea of Marmara (Atalay and Efe 2012). The species is also distributed in the regions close to the steppe and has become evident as one of the pine species most frequently introduced into the steppe (Mayer and Aksoy 1986). Its optimum distribution appears to be between 700-1400 m above sea level (a.s.l.), but, it is also found in lower and higher elevation zones. It is resistant to both summer drought and heat and winter cold, grows on very different bedrocks such as limestone, ultramafic, dolomite and silicate. It is a moderate species in terms of soil requirements. The black pine is also widely planted outside of its natural distribution range (Mikulová et al. 2019, Čahojová et al. 2024).

Vegetation characteristics of black pine forests

As noted above the black pine has a broad geographic distribution and it is found in different climate zones, on different bedrocks and in an elevational gradient from meso- and supra-Mediterranean to sub-Mediterranean. These environmental differences cause a variation in species composition and thus the formation of different vegetation types. Since the post-fire regeneration capability of species differ, variation in species composition is important for post-fire vegetation dynamics.

According to Mucina et al. (2016), black pine dominated forests are classified in two classes. These are *Junipero-Pinetea sylvestris*, forming relict oro-Mediterranean and sub-Mediterranean orotemperate dry pine forest and *Erico-Pinetea* representing relict pine forests on calcareous and ultramafic substrates of the Balkans, the Alps, the Carpathians and Crimea.

Within *Junipero-Pinetea sylvestris*, the alliance *Berberido aetnensis-Pinion laricionis* represents the acidophilous dry pine forests in the supra-Mediterranean belt of Corsica, Sardinia, Sicily and Calabria. As an order the alliance is grouped under *Berberido creticae-Juniperetalia excelsae*.

Within *Erico-Pinetea*, there are six alliances, in which black pine dominated forests are classified. These are *Fraxino orni-Pinion nigrae* representing relic black pine forests on calcareous substrates of the South Adriatic, Central and Southern Balkans; *Junipero hemisphaericae-Pinion nigrae* for the natural black pine forests on calcareous substrates of the central-southern Apennines in the supratemperate thermotype; *Erico-Fraxinion orni*, which forms relict black pine forests on dolomite and ultramafic substrates of the Dinarides; *Chamaecytiso hirsuti-Pinion pallasianae* indicating relict black pine forests on calcareous, dolomitic and ophiolithic rocky slopes of the Southern Balkans and finally the Anatolian alliances *Cisto laurifolii-Pinion pallasianae* and *Adenocarpo complicati-Pinion pallasianae* distributed in temperate and Mediterranean Anatolia respectively (Kavgacı et al. 2021, 2023).

Apart from the Central and Southern Balkan and Apennine alliances, the others are classified under the order *Erico-Pinetalia*. *Fraxino orni-Pinion nigrae*, *Chamaecytiso hirsuti-Pinion pallasianae* and *Junipero hemisphaericae-Pinion nigrae* are classified under a newly defined order *Junipero communis-Pinetalia nigrae* (Biondi and Allegrezza 2019). Differently from all these vegetation units, the black pine forests in Spain were grouped within the *Querco-Fagatea* order (Regato-Pajeres and Elana-Rosselló 1995).

Effects of fire on black pine forest vegetation

Black pine forests are found in relatively fire-prone areas. With changing climatic conditions, these areas are likely to experience more frequent and potentially more intensive fires. And indeed, data show that in recent years, these forests have been exposed to fires more frequently and across larger areas than in the past (Christopoulou et al. 2013).

Pines are generally classified under two groups, as fire-avoiders and fire-adapted pines (Keeley 2012). Fire-adapted pines are also subdivided in accordance with their syndromes: fire-tolerator pine syndrome, fire-embracer pine syndrome

Tab. 1. Fire adaptation traits of pines (*Pinus*) frequently exposed to forest fires in the Mediterranean. + and – indicate whether the trait is present for the tree species or not. Based on Keeley (2012) and Ne'eman and Arianoutsou (2021).

Fire adaptation trait	*P. nigra*	*P. brutia*	*P. halepensis*	*P. pinaster*
Bark thickness	+	+/-	+/-	+
Self-pruning	+	–	–	+
Serotinous cones	–	+	+	–
Heat stimulated germination	–	+	+	–

and fire-refugia pine syndrome. Under these groups, the black pine is a fire tolerator species exposed to surface fires where trees survive following repeated fires by means of their height, self-pruning of lower branches, thick bark, and where their long, highly flammable needles foment frequent fire that kills competitors and reduces surface fuels (Tab. 1). Bark thickness in pines is a fire adaptation trait that originated during the Cretaceous Period at least 126 Ma ago in association with surface fires (He et al. 2012).

Within the natural fire regime, fires in black pine forests generally occur as surface fires. At this point a number of tree-ring based fire reconstructions have been carried out in black pine forests. All of these studies show active fire histories in black pine forests over many centuries, with fire return intervals linked to climate variation and human activities, and ranging from ca. 5-40 years (Touchan et al. 2012, Christopoulou et al. 2013, Şahan et al. 2021, 2022). Since the black pine is light-demanding and intolerant of shade, it generally forms a single-layer stand structure. However, it can also form layered stand structures depending on the site history, productivity, canopy and light conditions, and tree species mixture (Sevgi et al. 2022). Due to the presence of surface fuels, laddering from tall understory vegetation, and crown continuity, such sites are susceptible to crown fires, which are deleterious to black pines.

The black pine is an important tree species in Europe and the Mediterranean for commercial, restoration and conservation purposes (e.g. Isajev et al. 2004, Beltrán et al. 2018, Barčić et al. 2022, Vacek et al. 2023). Numerous studies have highlighted the threat that crown fires pose to black pine populations across its range (Christopoulou et al. 2013, Beltrán et al. 2018, Şahan et al. 2022). Suppression of low intensity fires, land abandonment, and inappropriate management practices have led to densification of black pine forests, invasion of fire intolerant species, and accumulation of live and dead fuels that in combination are changing the fire regime in these ecosystems (Moreira et al. 2020). In addition, the increasing risk of high severity fire in black pine forests is greatly exacerbated by current and projected climate trends (Moriondo et al. 2006). Below, we summarize the impacts of surface and crown fires on black pine forests and consider management implications of these important changes to black pine habitats. To conclude we suggest a set of management principles that will help ameliorate the threats posed to the black pine by the growing threat of catastrophic wildfire.

Surface fires in black pine forests

The main fire adaptation characteristics of black pine are thick stem bark, self-pruning and a dense shoot structure that protects the bud (Retana et al. 2002). The thick bark structure prevents the energy released in a surface fire from having a lethal effect on the cambium. Due to the self-pruning and the absence of an understory layer in a stand, surface fires cannot turn into crown fires. Additionally, owing to the dense shoot structure, fire intensity cannot have a negative effect on the buds. Thus, in a surface fire, the fire intensity remains low and the trees can continue their existence while preserving their vitality (Keleş and Kavgacı 2022, Tab. 2, Fig. 2a).

Tab. 2. Percentage and fidelity synoptic table of 2nd year vegetation sampling after the 2021 fire in Yılanlı, Muğla – Türkiye. First and second columns of each study area represent the percentage frequencies and fidelity measure of each species, respectively. Phi coefficient for fidelity is 0.30. Fidelity was calculated by using Juice program (Tichý 2002). Grey shaded species represent the diagnostic ones for each study area. The black pine either fails to rejuvenate in crown fire areas or shows very weak regeneration, insufficient to re-establish a forest. The nomenclature of species follows Euro+Med 2006+.

Study area number	1		2		3		4		5		6	
Fire severity	Surface		Surface		Crown		Crown		Unburned		Unburned	
Aspect	Northern		Southern		Northern		Southern		Northern		Southern	
Nr. of relevés	10		10		10		10		10		10	
Nr. of species	45		41		97		86		30		33	
Pinus nigra	100	25.8	100	25.8	40		10		100	25.8	100	25.8
Diagnostic species												
Pteridium aquilinum	90	61.2			10				50		20	
Crepis reuteriana	40	59.8										
Lathyrus cicera	30	41.8					10					
Securigera varia	30	41.8					10					
Digitalis cariensis	70	36.9			50		60	27.2	10			
Trifolium tomentosum			20	41.5								
Poaceae			20	41.5								
Acanthus spinosus	10		10		100	85	10					
Buglossoides arvensis			10		80	81.4						
Rubus canescens					90	78.3			30			
Trifolium tomentosum					60	74.5						

Tab. 2. Continued.

Hypericum perforatum			$60^{74.5}$			
Arabis verna	20		$90^{70.5}$		30	
Veronica cymbalaria			$60^{61.4}$	10	10	
Verbascum cheiranthifolium	40	40	$100^{60.9}$	30		
Trifolium arvense			$40^{59.8}$			
Senecio vulgaris		10	$50^{59.6}$			
Nepeta nuda	10		$70^{55.9}$	40		
Silene italica	30		60^{52}	10		
Galium setaceum			$30^{51.3}$			
Arrhenatherum palaestinum			$30^{51.3}$			
Cerastium brachypetalum	10		$60^{48.2}$	30		10
Bromus sterilis			$60^{44.7}$	40		20
Campanula lyrata	30		$70^{43.8}$		50	10
Allium scorodoprasum			$30^{41.8}$	10		
Filago arvensis		10	$30^{41.8}$			
Lactuca intricata			$30^{41.8}$	10		
Bromus tectorum			$30^{41.8}$	10		
Teucrium chamaedrys			$20^{41.5}$			
Cistus salviifolius			$20^{41.5}$			
Trifolium scabrum			$20^{41.5}$			
Centaurea virgata			$20^{41.5}$			
Vulpia myuros			$20^{41.5}$			
Asyneuma virgatum			$20^{41.5}$			
Bromus squarrosus			$20^{41.5}$			
Erysimum smyrnaeum			$20^{41.5}$			
Rhus coriaria		10	$40^{39.5}$	20		
Chondrilla juncea		10	$40^{35.1}$	30		
Briza humilis				$90^{93.9}$		
Valerianella species		10		$80^{81.4}$		
Alyssum simplex				$70^{81.3}$		
Trigonella spruneriana				$70^{81.3}$		
Velezia pseudorigida		10		$70^{74.5}$		
Ononis reclinata		20	40	$100^{74.2}$		
Astragalus oxytropifolius		10	10	$70^{68.9}$		
Glaucium corniculatum				$50^{67.4}$		
Linum corymbulosum		10	40	$80^{63.3}$		
Caryophyllaceae				$40^{59.8}$		
Alkanna tubulosa				$40^{59.8}$		
Origanum sipyleum	20	30	30	$80^{53.9}$		
Euphorbia falcata				$30^{51.3}$		
Polygonum species				$30^{51.3}$		
Clypeola jonthlaspi				$30^{51.3}$		
Echinops ritro		10		$40^{51.2}$		
Verbascum cariense			10	$40^{51.2}$		
Picnomon acarna	10	50	10	$70^{46.5}$	10	
Sanguisorba minor	40		30	$70^{46.5}$		10
Tragopogon porrifolius subsp. longirostris			10	$30^{41.8}$		
Centaurea urvillei			10	$30^{41.8}$		
Ziziphora tenuior			10	$30^{41.8}$		

Tab. 2. Continued.

Malva cretica				$20^{41.5}$		
Minuartia multinervis				$20^{41.5}$		
Astragalus condensatus				$20^{41.5}$		
Origanum minutiflorum				$20^{41.5}$		
Euphorbia rigida			10	$30^{35.1}$		10
Populus tremula					$60^{74.5}$	
Quercus cerris					$30^{51.3}$	
Turritis laxa	10				$30^{41.8}$	
Populus x canescens	50	30	60		$80^{40.2}$	
Cistus laurifolius	40	10	40	30	$70^{36.9}$	
Doronicum orientale	30	10	10		$40^{31.3}$	
Quercus coccifera						$80^{87.7}$
Genista anatolica						$70^{81.3}$
Dactylis glomerata			40			$80^{67.1}$
Trifolium grandiflorum						$40^{59.8}$
Trifolium lucanicum						$30^{51.3}$
Stipa bromoides						$20^{41.5}$
Pilosella hoppeana						$20^{41.5}$
Lolium rigidum						$20^{41.5}$
Rosa canina	20				20	$40^{35.1}$
Cephalanthera longifolia	$100^{54.8}$	$80^{36.5}$		20	30	10
Vicia cracca	$90^{51.6}$	10	$70^{32.8}$	30		10
Minuartia hybrida			$80^{59.9}$	$60^{38.8}$		
Trifolium campestre	10		$80^{53.9}$	$60^{33.7}$	10	
Sonchus asper	50	40	$100^{47.8}$	$90^{38.8}$		
Cichorium intybus			$50^{43.8}$	$40^{31.3}$		
Ajuga chamaepitys			$70^{43.8}$	90^{64}		
Lactuca serriola	60	70	$100^{41.8}$	$90^{32.9}$		
Verbascum glomeratum	10		$60^{38.8}$	$70^{49.3}$		
Anthyllis vulneraria		20	$60^{38.8}$	$60^{38.8}$		
Crepis foetida	20	40	$80^{38.3}$	$90^{47.5}$		
Capsella bursa-pastoris			$40^{35.1}$	$40^{35.1}$		
Conyza canadensis	10	60	$70^{32.8}$	$70^{32.8}$		
Other species appearing at more than 4 relevés						
Lens culinaris	30	50	50	40	10	
Poa bulbosa	10	10	30	50	10	50
Crataegus monogyna	30					30
Crepis sancta		20	30	10		
Polycarpon tetraphyllum			30	30		
Clinopodium vulgare	20		20		10	
Pilosella piloselloides			20	20		10

On the other hand, after surface fires, the floristic composition shows differences from unburned forests (Fig. 3).

However, cases where trees are damaged after a surface fire may occur. In this case, the reestablishment of the forest can be supplied by natural regeneration depending on the occurrence of the appropriate germination conditions in soil and the seed reserve in which seeds are still alive and germinate after dispersal (Fig. 2b). The important issue in this case is the amount of trees remaining alive and the size of the fire area. If there are not enough living trees in the burned area, the only seeding source are the trees at unburned areas. Since their seed dispersal distances would

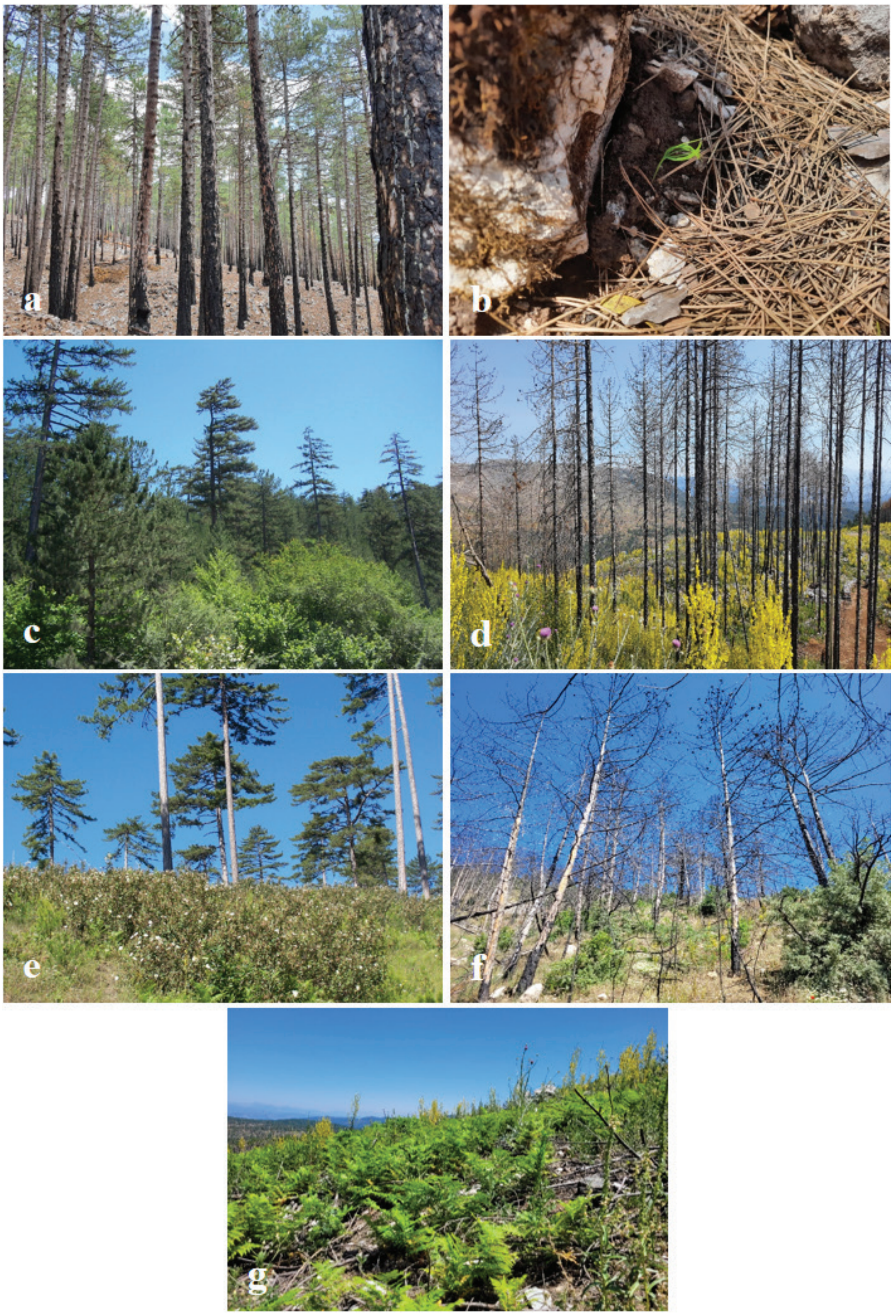

Fig. 2. Physiognomy of black pine forests before and after fire: a – surface fire, b – post-fire regeneration, c – black pine forest with dense underground layer, d – crown fire, e – black pine forest with *Cistus laurifolius*, f – crown fire with oak coppice after fire, g – *Pteridium aquilinum* vegetation after crown fire.

remain at a certain rate, there may be a possibility that the field will not be completely seeded. And this may cause a change in vegetation structure.

Stand age preventing tree bark from forming a sufficient thickness also has an effect on the lethality of fires on trees when the fire occurs as a surface fire. This reveals the importance of the age of a stand exposed to fire and indicates that mature black pine stands are more resistant to surface fires than young stands.

The lethal effect of surface fires may also closely be related to whether there is a dense shrub and herb layer in the forest. In relation to the increasing amount of fuel load, a dense shrub and herb layer may cause a higher intense surface fire resulting in a negative impact on trees. Although black pine forests generally do not include a dense scrub and herb layer, as is seen in the Tab. 2, it is possible to encounter such conditions especially at highly productive sites (Fig. 2c).

A sufficient post-fire regeneration of the black pine depends not only on the stand age but also the optimum number of trees and therefore crown coverage fostering the constitution of large amount of seed. The higher or lower number of trees necessary may have negative consequences in terms of post-fire regeneration. If the number is low, there may not be a sufficient cone reserve to seed the area, which

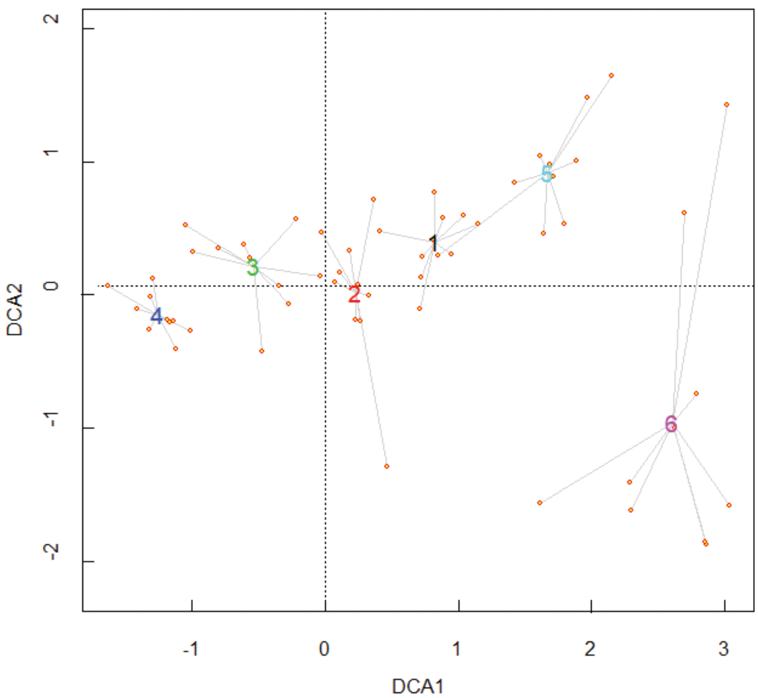

Fig. 3. Detrended correspondence analysis (DCA) ordination of 2nd year vegetation sampling after the 2021 fire in Yılanlı, Muğla - Türkiye. There is a clear floristic differentiation between crown fire (3, 4), surface fire (1, 2) and unburned areas (5, 6). The crown fire area is characterized by the low frequency of black pine juveniles which would not be sufficient to establish a forest canopy and a higher number of ruderal plants. DCA was done with R project (R Core Team 2021).

may lead to insufficient regeneration. On the other hand, in stands where the number of trees is higher, crown coverage may be weak due to competition among trees, and therefore inadequacies may occur in terms of cone and seed reserves (Christopoulou et al. 2014). This shows the importance of having an optimum number of trees with crowns that support high cone and seed production in stands. In a study by Arista and Talavera (1996), denser stands were found to have lower cone and seed production. This was associated with the reduced photosynthetic surface and increased competition between trees. Ordóñez et al. (2005) also reached similar results and detected a decrease in the amount of cones per tree and the amount of seeds per cone in too dense stands. This indicates the importance of silvicultural tending in stands to support the post-fire regeneration.

In terms of seed retention of black pine, there are differences between years (Odabaşı et al. 2004). Rich seed years of the species occur every 2-3 years. If the fire coincides with a seedless or poor seed year, it is not possible to re-establish a black pine forest in the area naturally, since there will be no seed reserve, even if there are viable trees in the burned area. In the case of natural regeneration after a fire, there may be variations in the amount of regeneration depending on site condition differences. In addition to the topographic conditions such as aspect, elevation and slope (Tavşanoğlu 2008), herbaceous plant competition, soil depth (Christopoulou et al. 2014), the presence of seed pests (Ordóñez and Retana 2004), branches, logs, burnt trees and other woody residues left on the field (Harmon et al. 1986, Harmon and Hua 1991) have an impact on these variations.

Briefly, if black pine forests are mature enough and the fire occurs as a surface fire, they can generally continue their existence. Natural regeneration mechanisms may also work in cases where the trees are even damaged. However, in addition to the changing climate conditions, forestry practices causing vertical and horizontal layered stand structures can cause the surface fires to turn into the crown fires covering large areas.

Crown fires in black pine forests

As a result of the heat generated by the fire, serotinous cones, which are a fire adaptation trait of coniferous species like red pine, Aleppo pine, maritime pine and cypress, open, and mass germination occurs after the fire (Thanos and Daskalakou 2000, Kavgacı et al. 2016). Unlike these species, the black pine, which is distributed in the supra- and sub-Mediterranean zones, does not have serotinous cones (Lanner 1998). Therefore, as a crown fire appears, the heat during the fire has a lethal effect on the seed reserves in the canopy and causes problems for the black pine to join and dominate the post-fire vegetation composition (Retana et al. 2002, Savage and Mast 2005, Pausas et al. 2008). An example of this kind of floristic change (Tab. 2, Fig. 3) and degradation (Fig. 2d) has been recently observed by Keleş and Kavgacı (2022) after forest fires occurred in black pine forests in Türkiye.

The opening of mature cones of black pine and seed dispersal occur from the late winter to early spring (Bolós and Vigo 1984, Laguna 1993, Skordilis and Thanos 1997). In the

Mediterranean region, fires occur frequently in the summer months. During this period, the seeds in cones are not mature enough or capable of germination (Peix 1999). Therefore, the only seed source that can contribute to regeneration after summer fire is the soil seed bank. Although black pine seeds are resistant to temperature shocks at certain levels (Ayan et al. 2020, Turna and Bilgili 2006), seeds in the soil cannot withstand the high temperatures reached during intense summer fires (Habrouk et al. 1999). Young black pine individuals in the understory layers (scrub and herb layers) are also burned during the fire. Therefore, after a crown fire, neither the crown seed bank, nor the soil seed bank, or young individuals can make a contribution to the survival of black pines after a fire, which prevents the natural regeneration of black pine.

In addition to the fact that, fires are beginning to occur as crown fires in mature black pine forests, the increase in fire frequency causes the stands to be exposed to fires during young stand ages and therefore in much drier site conditions (Gracia et al. 2002). Since sufficient stand height cannot be achieved in such forests, fires consume the entire fuel load including all the canopy and negatively affect seed stocks. The change of fire regime along with fire frequency, intensity and therefore severity causes the fire adaptation abilities of black pine to fail and different post-fire vegetation dynamics to emerge (Fyllas and Troumbis 2009, Keleş and Kavgacı 2022, Tab. 2, Fig. 3). Under these conditions, trees die completely and the seeds are damaged by fire due to the lack of the serotinous cone feature (Tapias et al. 2004). In such cases, the reemergence of a black pine forest depends only on the unburned stands at the edge of the burned area. This is also related to the size of the fire area, since most of the area would be not seeded in an optimum way after large fires.

The number of black pine seedlings decreases in the burnt area as the distance from the edge of unburned areas increases towards the core of the burnt area. Black pine seeds, like many other pine species, are dispersed by wind (Nathan et al. 2001). Seeds with wings can be dispersed over large area (Klaus 1989). Therefore, the seeds dispersed from unburned neighboring stands may seed the burned areas (Christopoulou et al. 2014). However, the optimal seed dispersal distance of trees is limited and for black pine, this is about 20-40 m (Odabaşı et al. 2004). In areas outside this distance, it does not seem possible for a forest structure to re-occur naturally. Therefore, if a crown fire area exceeds the optimum seed dispersal distance and there is not a sufficient amount of unburned patches (Christopoulou et al. 2014), the black pine may not realize a homogenous germination to survive in all the area of the fire and it will be replaced by a vegetation structure dominated by different species.

With the changes in the fire regime, especially with the increase in fire frequency, the obligate seeding tree species cannot naturally regenerate due to the damage in the crown seed bank and the vegetation is formed by other species (Pausas et al. 2003, Broncano and Retana 2004). One of the most important fire adaptation abilities of Mediterranean type ecosystems is obligate resprouting (Pausas and Keeley 2014). Many shrub and tree species dominating maquis and sclerophyllous forests are obligate resprouters. Since these species are also found in the underground layers of forests dominated by obligate seeding tree species, they can regenerate rapidly after fire and cause the formation of maquis and sclerophyllous forests instead of coniferous forests (Kavgacı et al. 2016). It is possible to accept that many maquis and sclerophyllous forests in the Mediterranean today, especially in high productive sites, were formed in this way.

A similar vegetation conversion is valid for black pine forests. In order to make an assessment of how this conversion happens or could happen, it is necessary to know the plants forming and dominating the underground layer of black pine forest and their fire adaptation characteristics. As the black pine vegetation composition in different geographical and environmental areas is examined, it is seen that there are other trees, shrubs and herbaceous plants that are obligate resprouterss, as well as obligate seeders based on a soil seed bank (Tavşanoğlu and Pausas 2018).

Post-fire survival through the soil seed bank is one of the most characteristic fire adaptations of plants in Mediterranean-type ecosystems. *Cistus laurifolius* L., which is a common element of black pine forest vegetation in the Eastern Mediterranean, is one of the species with this type of feature (Fig. 2e). It is known that *Cistus* species regenerate quickly after fire thanks to the soil seed bank (Tavşanoğlu 2011). If the black pine cannot regenerate due to fire frequency or crown fires, *C. laurifolius* germinates quickly and if there is no obligate resprouter tree or taller shrub species, it can dominate the vegetation (Ocak et al. 2007). As a matter of fact, currently, much of the *C. laurifolius* shrubland distributed in large areas in sub-Mediterranan and subeuxine regions are ecosystems that have replaced black pine forests that have suffered fires (Atalay and Efe 2010, Kavgacı et al. 2021).

Although black pine forest vegetation varies regionally, it can be seen that both deciduous and evergreen oak species are included in the floristic composition. Oak species are generally obligate resprouters and easily survive after fire (Pausas and Darwin 2001, Rodríguez-Trejo and Myers 2010, Kim et al. 2020). Deciduous oak species such as *Quercus cerris* L., *Q. pubescens* Willd. and *Q. infectoria* G. Olivier and evergreen ones like *Q. coccifera* L. often form mixed stands with black pine. In cases where black pine cannot regenerate after a fire, these species can resprout and dominate the vegetation (Keleş and Kavgacı 2012, Fig. 2f). Such a mixture of stands is not typical only for the natural distribution of black pine but also for plantations as, established in Croatia and Slovenia where deciduous were converted to black pine forests (Čahojová et al. 2024).

In the absence of woody species that accompany black pine or show vigorous renewal after fire, a herbaceous vegetation dominated by obligate resprouter grasses may occur. In fact, in humid environmental sites, *Pteridium aquilinum* L. (Kuhn) can be found densely in the herb layer of black pine forests (Kavgacı et al. 2013). The species regenerates quickly after a fire thanks to its underground rhizomes and covers the area (Keleş and Kavgacı, 2022, Fig. 2g). Vegetation conversion is managed not only by obligate seeders or resprouters but also colonizers like *Verbascum* ssp. as seen in Fig. 2d.

Conclusion

Studies indicate that there will be changes in fire regimes in the Mediterranean basin and fires will probably become more severe (Arca et al. 2010). Changing climatic conditions play a triggering role in fires occurring more frequently and at higher intensities. Under these conditions, it is expected that nonserotinous species will be more affected by the changes than serotinous ones. Therefore, it is predicted that black pine forests will be one of the most affected ecosystems due to the changing fire regime (Espelta et al. 2002).

Black pine forest ecosystems can continue to exist after low-intensity surface fires due to their adaptation. On the other hand, the decrease in fire frequency and the occurrence of high intensity crown fires create a problematic situation in terms of the continuity of black pine and cause the formation of different vegetation types because the fire adaptation capacity of the black pine is inadequate to overcome these changes.

In summary, changes in the fire regime have negative consequences for the continuity of black pine forests. Therefore, post-fire restoration of these forests becomes an important issue. It is crucial to adopt an ecologically based restoration approach after fire. A restoration plan that is appropriate to the ecology and biology of black pine, which prevents soil loss and erosion, promotes biodiversity and includes fire prevention measures, is necessary for the continuity of black pine forests. Since these forests are getting more prone to high-intensity fires, the black pine plantations, which are out of the species' natural distribution range and are exposed to crown fires should be converted to natural deciduous forests. This can easily be done by fostering the natural regeneration of post-fire resprouters, which are natural element of plantation flora and immediately emerge after fires, like oaks (Bergmeier et al. 2021, Čahojová et al. 2024).

Additionally, silvicultural treatments in the existing black pine forests should be carried out to promote a stand structure that is inclined to surface fires. Therefore, extending the harvesting period, fostering self-pruning, creating single layer stand structures but also a canopy supporting mass seed production should be the targets of silviculture. Additionally, to decrease the fuel load at ground layer, moderate grazing (Christopoulou et al. 2014) and prescribed burning (Ferrat et al. 2021) can be applied. This can reduce the fire intensity and ensure the black pine continuity not only by resistance but also by resilience.

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Author contribution statement

E.S.K. and A.K. jointly conceived and wrote this paper.

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Appendix: List of syntaxa mentioned in the text

Junipero-Pinetea sylvestris Rivas-Mart. 1965

- *Berberido creticae-Juniperetalia excelsae* Mucina 2016
  - *Berberido aetnensis-Pinion laricionis* (S. Brullo et al. 2001) Mucina et Theurillat 2016

Erico-Pinetea Horvat 1959

- *Erico-Pinetalia* Horvat 1959
  - *Erico-Fraxinion orni* Horvat 1959
  - *Cisto laurifolii-Pinion pallasianae*
  - *Adenocarpo complicati-Pinion pallasianae*
- *Junipero communis-Pinetalia nigrae* Biondi et Allegrezza 2020
  - *Fraxino orni-Pinion nigrae* Em 1978
  - *Chamaecytiso hirsuti-Pinion pallasianae* Barbero et Quezel 1976
  - *Junipero hemisphaericae-Pinion nigrae* Biondi et Allegrezza 2020