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Short-term drivers of post-fire forest regeneration in the Western Alps

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Abstract

Background The Mediterranean basin is currently facing major changes in fire regimes as a result of climate and land-use changes. These alterations could affect the ability of forests to recover after a fire, hence triggering degradation processes and modifying the provision of fundamental ecosystem services. Examining patterns and drivers of post-fire forest recovery, particularly for obligate seeders without specific fire-adaptive traits, thus becomes a priority for researchers and land managers. We studied the post-fire dynamics of Scots pine (*Pinus sylvestris* L.) stands affected by a mixed-severity fire in North-Western Italy, aiming to understand the impact of fire on soil properties and assess drivers, spatial distribution, and characteristics of short-term post-fire recovery.

Results We observed that fire did not significantly affect soil organic carbon (OC) content, while we detected significantly lower nitrogen (N) content in severely burnt sites. Regeneration density was particularly abundant in medium-severity areas, while it drastically decreased in high-severity patches. The most abundant tree species in the regeneration layer was Scots pine, followed by goat willow (*Salix caprea* L.), European aspen (*Populus tremula* L.), and, to a lesser extent, European larch (*Larix decidua* Mill.). Slope, fire severity, and distance from seed trees emerged as the most important drivers of post-fire forest regeneration patterns.

Conclusions Our results highlight the importance of preserving seed trees from salvage logging, even if they are damaged and have a low survival probability. Active post-fire management, such as tree planting, should be limited to large and severely burnt patches, where natural forest regeneration struggles to settle, increasing the risk of ecosystem degradation. These findings could be useful for informing land managers, helping them to enhance potential mitigation strategies in similar ecosystems and plan appropriate restoration approaches.

Keywords Biological legacies, Fire regime, Global change, *Pinus sylvestris*, Post-fire regeneration, Scots pine stands, Seed trees, Western Alps

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Resumen

Antecedentes La cuenca del Mediterráneo está actualmente enfrentando grandes cambios en los regímenes de fuego, como resultado de cambios en el clima y usos de la tierra. Estas alteraciones pueden afectar la habilidad de los bosques para recuperarse luego de incendios, y por lo tanto disparar procesos de degradación y modificar la provisión de servicios ecosistémicos fundamentales. El examen de los patrones y conductores de la recuperación post-fuego, particularmente para especies que regeneran exclusivamente de semillas sin características adaptativas al fuego, se transforma entonces en una prioridad para los investigadores y gestores de recursos. Estudiamos la dinámica post-fuego de rodales de pino silvestre (*Pinus sylvestris* L.) afectados por incendios de severidad mixta en el noroeste de Italia, con el objetivo de entender el impacto del fuego en las propiedades del suelo y determinar la dinámica, distribución espacial y características de la recuperación post-fuego en el corto plazo.

Resultados Observamos que el fuego no afectó significativamente el contenido de carbono orgánico del suelo (CO), mientras que detectamos una menor cantidad de contenido de nitrógeno (N) en lugares severamente quemados. La densidad de la regeneración fue particularmente abundante en áreas quemadas a severidad media, mientras que decreció drásticamente en parches de alta severidad. La especie arbórea con mayor abundancia en el estrado regenerativo fue el pino silvestre, seguido del sauce de montaña o sauce cabruno (*Salix caprea* L.), luego el álamo temblón (*Populus tremula* L.), y en menor medida el alerce europeo (*Larix decidua* Mill.). La pendiente, la severidad del fuego, y la distancia a los árboles semilleros emergieron como los conductores más importantes de los patrones de la regeneración post-fuego de estos bosques.

Conclusiones Nuestros resultados resaltan la importancia de preservar árboles semilleros en una eventual tala rasa post-fuego aún si estos resultan dañados o con pocas probabilidades de sobrevivir. El manejo activo post-fuego como la replantación, debe ser limitado a parches grandes y severamente quemados, donde la regeneración natural lucha para establecerse, incrementando el riesgo de degradación del ecosistema. Estos resultados pueden ser útiles para ilustrar a gestores de tierras, ayudándolos a incrementar las estrategias potenciales de mitigación en ecosistemas similares y planificar combinaciones de restauración apropiadas.

Background

Climate and land-use changes are currently modifying the disturbance regimes under which forest landscapes have been shaped for millennia (Pausas et al. 2008; Turner 2010; Leverkus et al. 2019; Mantero et al. 2020; Pausas and Keeley 2021). These alterations could affect the ability of forests to recover after a disturbance, which could in turn trigger degradation processes (Dury et al. 2011; Johnstone et al. 2016; Fernandez-Vega et al. 2017), thus modifying the provision of fundamental ecosystem services (Turner et al. 2013; Seidl et al. 2016; Thom and Seidl 2016; Kulakowski et al. 2017).

The potential ecosystem transformations resulting from global change and altered disturbance regimes are becoming a pressing issue (Littlefield et al. 2020). The increasing number of large stand-replacing fires, the shortening of the return intervals, as well as the post-fire climatic conditions, often characterized by severe droughts, all raise concerns about regeneration recruitment, particularly for obligate seeders (Enright et al. 2015; Turner et al. 2019). Examining patterns and drivers of post-fire forest recovery thus becomes a priority for researchers and land managers.

Mediterranean mountain forests are particularly sensitive to global change due to the historical anthropogenic pressure and their low resilience (San Roman Sanz et al. 2013; Doblas-Miranda et al. 2017). In these areas, the widespread land abandonment acts synergistically with climate change (Bebi et al. 2017; Kulakowski et al. 2017), and with harsher environmental characteristics, possibly hindering regeneration dynamics (Castro et al. 2004a, b; Marzano et al. 2013). Under these new conditions, large and severe wildfires often occur in stands characterized by species lacking specific fire-related traits (e.g., Scots pine, *Pinus sylvestris* L.). After these events, a deficiency or a delay in the establishment of natural regeneration has been observed, often due to the cascading effects of post-fire management interventions, most likely resulting in degradation processes (Beghin et al. 2010; Marzano et al. 2013).

Salvage logging is still one of the most common post-disturbance practices. It consists of the harvesting of dead or damaged trees from sites after disturbance events, sometimes followed by plantation (Lindenmayer and Noss 2006; Lindenmayer et al. 2008). However, several negative consequences on natural regeneration processes and on the provision of ecosystem services have been demonstrated to occur after this practice (Donato et al. 2006; Leverkus et al. 2018a,b), acting as a second disturbance with combined effects that could be more than simply additive (Leverkus et al. 2018b). Consequently, lower-impact post-fire management activities are increasingly considered (Moreira et al. 2012; Vallejo et al. 2012; Marques et al. 2016; Wohlgemuth et al. 2017; Leverkus et al. 2021). Passive restoration is often the most ecologically appropriate solution (Beghin et al. 2010; Moreira et al. 2012; Honey-Rosés et al. 2018; Chazdon et al. 2021), but active intervention is required whenever degradation processes may affect natural dynamics (Stewart et al. 2003).

Whatever the chosen post-disturbance management strategy, taking advantage of natural regeneration can reduce costs and be more effective. Natural regeneration indeed ensures the presence of a plant community adapted to site conditions, enhances species diversity, limits soil erosion, and increases soil fertility (FAO 2019; Shono et al. 2020). Natural regeneration can be passive, or it may be assisted or managed (Di Sacco et al. 2021), with an approach to forest restoration spanning a gradient of active anthropic interventions, from assisted natural regeneration (ANR) to applied nucleation (Zahawi et al. 2013; FAO 2019; Shono et al. 2020; Di Sacco et al. 2021). These practices could facilitate post-disturbance ecosystem recovery, avoiding degradation processes, but this requires accurate planning and an in-depth understanding of all the factors affecting regeneration dynamics, including the characteristics of the fire event, the environmental conditions of the affected area, and the pre-fire forest attributes (Martín-Alcón and Coll 2016). Among them, disturbance severity has been shown to strongly influence seedling recruitment (Turner et al. 1999, 2003; Jayen et al. 2006; Maia et al. 2012; Hollingsworth et al. 2013). In particular, fire can produce different impacts on the below- and above-ground components of forest ecosystems. Depending on the magnitude of the event, soil organic matter, and mineral phases can be heavily affected (Knicker 2011; Jordanova et al. 2019), even if a fire-induced increase in temperatures is generally limited to the top five cm (Neary et al. 1999) due to low soil thermal conductivity (DeBano et al. 1998). Also, fire severity affects the type, amount, and quality of biological legacies like soil and crown seed banks or deadwood. Biological legacies can have positive effects on ecosystem recovery, promoting regeneration settlement and establishment (Franklin 1990; Peterson and Leach 2008; Castro et al. 2012). Deadwood, for instance, provides safe microsites for recruitment, particularly in harsh environmental conditions (Coop and Schoettle 2009; Grenfell et al. 2011; Marzano et al. 2013; Marcolin et al. 2019; Marangon et al. 2022). Another key aspect affecting post-fire regeneration, especially for obligate seeders, is the distance from seed sources, including both forest edges and isolated seed trees or green islands inside burnt areas. The survival of a crown seed bank, together with seed dispersal ability, has been recognized as the most important factor in propagule provisioning for conifers, as the soil seed bank is often destroyed by fire (Krüssmann 1983; Zasada et al. 1992; Greene et al. 2005; Donato et al. 2009).

Short-term (< 5 years) post-fire recovery shapes future stand trajectories, directing forest dynamics in the long-term (van Mantgem et al. 2006; Swanson et al. 2011; Meng et al. 2015). The increase in the size and frequency of high-severity fires (Seidl et al. 2017; Mantero et al. 2020) and the trends of increasing temperature and water deficit are threatening tree seedling establishment and survival potentially leading to shifts from forest types to shrublands or grasslands (Stevens-Rumann et al. 2017; Haffey et al. 2018). The uncertainty about post-fire recovery of conifer-dominated stands (Harvey et al. 2016; Stevens-Rumann et al. 2017; Serra-Diaz et al. 2018), especially in sensitive forests characterized by species lacking direct post-fire regeneration mechanisms, is mounting concern about ecosystem resilience (Harvey et al. 2016; Stevens-Rumann et al. 2017).

The unprecedented wildfires that struck North-Western Italy in early fall 2017 offered an opportunity to study post-fire forest regeneration patterns, focusing specifically on tree regeneration from seeds, under the new environment generated by global change. The present study aimed to investigate short-term forest recovery after the largest of these fires, characterized by a high spatial heterogeneity resulting from varying levels of fire severity on the predominantly forested landscape. We thus assessed the post-fire regeneration dynamics in Scots pine stands affected by a mixed-severity fire in the Western Alps (Italy) to answer the following research questions: (i) What is the impact of fire on soil properties across a fire severity gradient? (ii) What are the short-term regeneration patterns? (iii) What are the most important drivers influencing post-fire regeneration by seeds?

Methods

Study area

The study area was located in the municipalities of Bussoleno and Mompantero (45.15°, 7.067°) (Susa Valley, Piedmont, North-Western Italy). The altitude of the study area ranged between 500 and 2500 m a.s.l. and the soils are Cambisols according to the Working Group World Reference Base for Soil Resources (WRB) (IUSS Working Group WRB 2014). The mean annual precipitation was approximately 800 mm and the mean annual temperature was 12 °C. Vegetation was dominated by downy oak (*Quercus pubescens* Willd.) and shrubs at lower elevations and Scots pine, European beech (*Fagus sylvatica* L.), and

European larch (*Larix decidua* Mill.) at higher elevations. Silver fir (*Abies alba* Mill.) stands, sweet chestnut (*Castanea sativa* Mill.) stands, and mixed broadleaves (*Acer pseudoplatanus* L., *Tilia platyphyllos* Scop. and *Fraxinus excelsior* L.) stands were sporadically present.

Autumn 2017 was characterized by an uncommon fire season in Piedmont (North-Western Italy) that was triggered by exceptional weather conditions, which were dominated by high temperatures and scarce rainfall (Bo et al. 2020; Rita et al. 2020). The average temperature of October 2017 was 2.9 °C higher than the 1970–2000 period and the average precipitation was 98% lower (Arpa 2017). The extreme climatic conditions were further exacerbated by the intense local phenomena of foehn, a dry and warm down-slope wind. As a result of these extraordinary meteorological conditions, between late October and early November 2017, 10 large fires struck the Region, burning about 9700 ha (7200 ha covered by forests), a much larger area than the annual average (2800 ha) of the previous 20 years (Arpa 2017). The Susa fire was the largest event, with an extent of around 4000 ha (2500 ha of forests). The fire resulted in a complex mosaic of high-severity patches (13%) within a matrix of low and medium-severity patches (44% and 43%, respectively) (Morresi et al. 2022).

Sampling design and data collection

We adopted a stratified random sampling design based on the fire severity map produced in a previous study (Morresi et al. 2022), obtained by integrating both field and satellite (Sentinel-2) data, with fire severity expressed as Relative differenced Normalized Burn Ratio (RdNBR) (Miller and Thode 2007) and classified in three categories: unburnt to low, medium, and high. The adopted fire severity map did not discriminate between unburnt and low-severity classes due to uncertainties related to the remote sensing approach. We conducted field surveys only in pure Scots pine stands. We organized the data collection according to the study aims, using three sets of data, with sampling plots partially overlapping.

Fire severity and soil properties

In July 2020, we randomly selected soil sampling points (defined as “soil plots,” $n=48$) among the plots also used for analyzing short-term seedling regeneration patterns (see the following paragraph for details). Soil plots were distributed as follows: 26 in high-severity patches, 13 in medium-severity patches, and 9 in unburnt to low-severity patches. After litter removal, visual inspection revealed the presence of a superficial blackish horizon (at most sites), a typical feature that can be found in fire-affected soils (Certini et al. 2011). We collected the superficial (blackish) and underlying sub-superficial organo-mineral A horizons to a depth <5 cm, so as to sample the portion of the pedon most heavily affected by the fire. We air-dried, sieved (2 mm mesh), ground (0.5 mm mesh), and stored soil samples at room temperature until laboratory analysis.

We measured soil pH in a 1:2.5 soil:deionized water suspension after 2 h shaking (van Reeuwijk 2002). We determined total carbon (C) and nitrogen (N) by dry combustion with a Unicube CHNS Analyzer (Elementar, Langenselbold, Hesse, Germany). We evaluated carbonate content volumetrically after soil treatment with HCl (Nelson 1982) and we subtracted inorganic C content from total C to obtain organic carbon (OC) content.

Short-term seedling regeneration patterns

We measured a total of 100 plots (defined as “time series plots”) at the end of the first post-fire growing season (autumn 2018) and we remeasured them in the two following years (autumn 2019 and 2020). We spatially distributed the time series plots as follows: 66 plots in high-severity patches, 15 in medium-severity patches, 19 in unburnt to low-severity patches. Each plot consisted of two concentric subplots of 2 and 5 m radius. We assessed pre- and post-fire tree structure and composition in the 5 m plot, by collecting species and status (dead or alive) of each tree individual (DBH >7.5 cm). We recorded abundance and species of all tree seedlings and ground cover in the 2 m plot. We attributed ground cover classes on the field by visually estimating the percent cover of Gramineae, forbs, bare soil, shrubs, coarse woody debris (CWD), and rocks.

Drivers of forest recovery

We collected environmental drivers, obtained from both field surveys and GIS-derived data (Table 1), in 213 circular plots sampled in autumn 2020 (defined as “drivers plots”, including the 100 “time series plots”). Plots were distributed as follows: 156 plots in high-severity areas, 37 in medium-severity areas, and 20 in unburnt to low-severity areas. We applied the same sampling design adopted for the time series dataset.

We derived topographic variables from a 5 m resolution digital terrain model (DTM; Regione Piemonte 2011) obtaining raster datasets of slope, elevation, Heat Load Index (HLI) (McCune and Keon 2002), and roughness. We obtained the HLI through the R package spatialEco (Evans 2021). We calculated roughness using the R package terra (Hijmans 2022). The roughness value for each pixel is calculated as the difference between the maximum and the minimum elevation value among a 3×3 moving window around the pixel (Wilson et al. 2007).

Table 1 Variables used to assess the main drivers of forest seedling regeneration in the Susa fire (Susa Valley, Italy). Dash (-) indicates the absence of the spatial resolution (*i.e.*, field measurement) or unit (i.e., dimensionless indices)

Variable code	Description	Spatial resolution	Unit	Data source
Elevation	Elevation	20 m	m a.s.l	DTM
HLI	Heat Load Index (McCune and Keon 2002)	20 m	-	DTM
Slope	Slope	20 m	°	DTM
Roughness	Degree of irregularity of the surface	20 m	m	DTM
Fire severity (RdNBR)	Fire severity based on Morresi et al. (2022)	20 m	-	Morresi et al. 2022
Gramineae	Gramineae cover	-	%	Field
Forbs	Forbs cover	-	%	Field
Bare soil	Bare soil cover	-	%	Field
Shrubs	Shrubs cover	-	%	Field
CWD	Coarse woody debris cover	-	%	Field
Rock	Rock Cover	-	%	Field
Distance to seed trees	Distance from the nearest seed tree	20 m	m	RapidEye
Seedlings density	Density of seed-origin individuals	-	Seedlings number ha^{-1}	Field

To map seed trees, i.e., those individuals with some green foliage during the first growing season after the fire, surrounding each plot, we established a relation between the percentage of seed trees in the plots surveyed in 2018 and a vegetation index derived from satellite imagery. Specifically, we computed the Normalized Difference Red-Edge (NDRE) index using a RapidEye multispectral image (5 m spatial resolution), acquired on 30 June 2018. This image was obtained from the ESA RapidEye Full archive (https://earth.esa.int/eogateway/catalog/rapideye-full-archive-and-tasking) processed according to Level 3A (radiometric, sensor, and geometric corrections). NDRE is similar to the Normalized Difference Vegetation Index (NDVI) but it uses the red-edge wavelength instead of the red wavelength. NDRE is well suited for fire severity mapping as it is particularly sensitive to variations in chlorophyll content (Chuvieco et al. 2006; Korets et al. 2010; Fernández-Manso et al. 2016).

To map living trees, we classified NDRE values using a threshold discriminating between RapidEye pixels containing only dead trees and those with some survived individuals. We first selected plots with no survived trees, as assessed during field surveys, and computed the average NDRE value at the plot level, using pixels whose centroid fell within that plot. We then computed the 95th percentile of their NDRE values, equal to 0.25, and considered pixels with values higher than this threshold as likely containing living trees. Afterwards, we calculated the Euclidean distance from each plot to the nearest pixel containing seed trees in a GIS environment. We aggregated the cells of all the variables in raster format to 20 m to match the resolution of the fire severity map.

Data analysis

We performed all the statistical analyses using the R language (R Core Team 2022). We assessed differences in soil characteristics according to fire severity classes by analyzing the following parameters: organic carbon content (OC), nitrogen content (N), carbon-to-nitrogen ratio (C/N), and pH. We employed the Kruskal–Wallis test (Kruskal and Wallis 1952). to detect significant differences in soil parameters according to the fire severity classes since normality assumptions were not satisfied (Shapiro–Wilk test; Shapiro and Wilk 1965). In case of a significant difference among groups, we used Dunn's test to perform pairwise comparisons (Dunn 1964).

We assessed short-term seedling regeneration dynamics using the time series dataset (2018–2020 period). We assessed patterns in ground cover, seedling density, and species composition throughout the study period. We calculated the Brillouin index as a measure of species diversity (Brillouin 1956) with the R package vegan (Oksanen et al. 2020). Since the assumptions of normality were not satisfied, we used PERMANOVA (Anderson 2017) to assess the differences in ground cover among the three fire severity classes, while we used the Kruskal–Wallis test by rank to test for significant differences in seedling density and species diversity among the different fire severity classes. We performed pairwise comparison by using Dunn's test.

We predicted the total seedling regeneration density based on several environmental drivers (Table 1) through a Random Forest (RF) regressive model (Table 1). We employed the randomForestSRC R package to build the RF model (Ishwaran and Kogalur 2022). We calculated variable importance (vimp) through the Breiman-Cutler permutation (Breiman 2001), and we obtained partial dependence plots through the ggRandomForests R package (Ehrlinger 2016). We created partial dependence plots for the three most important variables by integrating the effects of variables according to the covariate of interest, and we constructed graphs by selecting evenly-spaced points alongside the distribution of the covariate. We evaluated the model performance by using the out-of-bag (OOB) R^2. We performed the same model to assess Scots pine and broadleaf seedling density based on the environmental drivers in Table 1, evaluating differences in species dispersal capacity and colonization ability (See Supplementary Material, Figs. S2, S3, S4, and S5).

Results

Fire severity and soil properties

Topsoils in unburnt to low-severity plots were characterized by an average OC content of 42.47 g kg^{-1} (± 21.02 g kg^{-1}) (Fig. 1a) and an average N content of 3.17 g kg^{-1} (± 1.28 g kg^{-1}) (Fig. 1b). High-severity plots showed lower N contents ($P = 0.046$; Fig. 1b) compared to unburnt to low-severity plots. C/N values (Fig. 1c), in the range of 8.60 to 17.40 (± 2.01), did not vary significantly along the fire severity gradient ($P > 0.1$), as well as soil pH ($P > 0.1$) (Fig. 1d; mean value 5.63 ± 0.78), and OC content ($P > 0.1$; Fig. 1a).

Short-term seedling regeneration patterns

Bare soil was the dominant ground cover class in the entire study area, but fire severity classes showed different responses (Fig. 2). Bare soil, from the first to the third year since the fire, decreased from 81 to 64% in medium-severity areas and from 78 to 48% in high-severity areas. We observed a gradual increase of shrubs, Gramineae, and forbs throughout the years, mainly in high-severity areas (Fig. 2). We found differences in ground cover (between medium and high-severity in 2019 ($P = 0.054$*)* and between unburnt to low and high-severity in 2020 ($P = 0.09$).

We found the highest values of seedling regeneration density in the medium-severity areas for all 3 years of observation (mean = 42,138 seedlings number

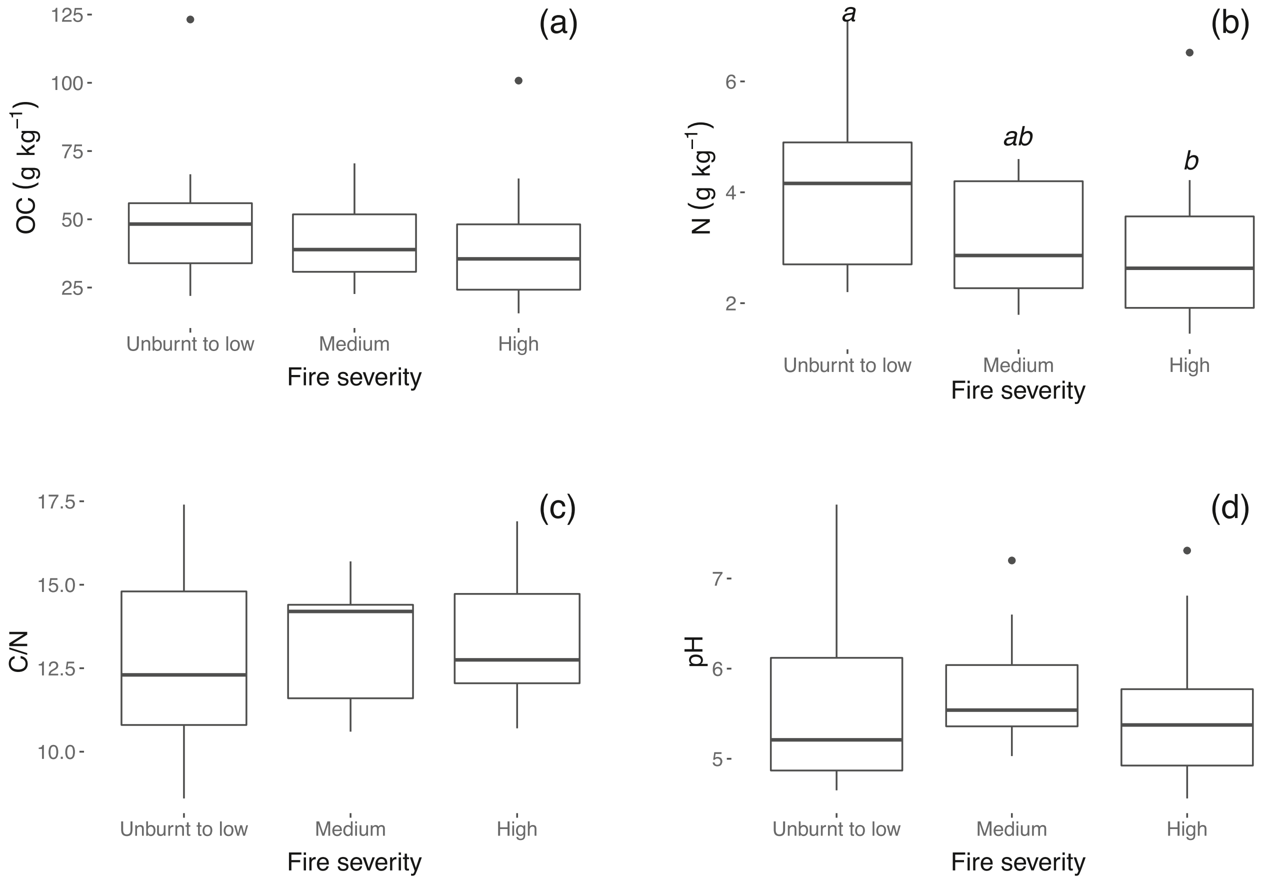

Fig. 1 **a** Soil organic carbon content (OC) (g kg^{-1}), **b** nitrogen content (N) (g kg^{-1}), **c** carbon-to-nitrogen ratio (C/N) and **d** pH in the four fire severity classes in 2020 in the Susa fire (Susa Valley, Italy). Different letters indicate significant differences among fire severity classes according to Dunn's post hoc tests for pairwise comparisons

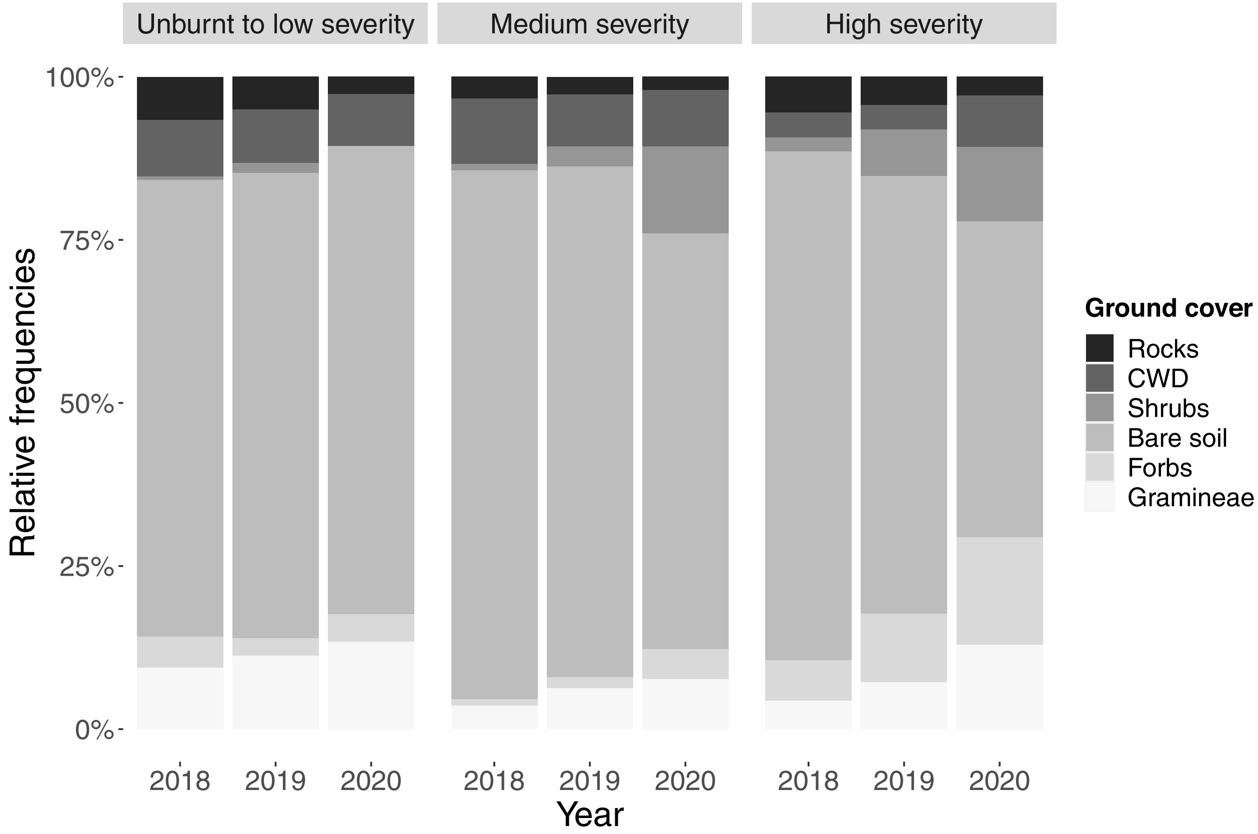

Fig. 2 Ground cover percentage according to fire severity classes in 2018, 2019, and 2020 in the Susa fire (Susa Valley, Italy)

ha^{-1}), while high-severity areas had the lowest density (mean = 6509 seedlings number ha^{-1}; Fig. 3). There were differences in terms of density among all fire severity classes ($P < 0.05$). The pairwise comparisons among group levels showed that seedling regeneration density in medium-severity areas was higher than in the other fire severity classes for all the years of observation ($P < 0.05$) (Fig. 3). We observed an increase in Scots pine density between 2018 and 2019, followed by a sharp decrease in 2020. This trend was common among all fire severity classes, but the only slightly significant difference was found in unburnt to low-severity between 2018 and 2019 density ($P = 0.059$) (Table 2).

In terms of species composition, Scots pine was the most abundant species in the fire severity classes and post-fire years, with the only exception of goat willow (*Salix caprea* L.) in high-severity areas in 2020 (Table 2; See Supplementary Material, Fig. S1). The presence of other tree species was rather sporadic, apart from goat willow and European larch. In medium-severity areas, Scots pine was by far the most widespread species, with seedling density after the first post-fire growing season being more than 10 times higher than in unburnt to low plots ($P = 0.0003$), almost 3 times in the second year post-fire ($P = 0.008$), and more than 5 times in the third year post-fire ($P = 0.016$). Goat willow and European larch were respectively the second and third most abundant species in the medium-severity class. High-severity areas were also dominated by Scots pine, but with much lower density compared to medium-severity. Other relevant species, in the case of high-severity, were goat willow and European aspen (*Populus tremula* L.) (Table 2).

The Brillouin diversity index showed the highest values in medium-severity areas, with an increasing trend from 2018 (0.62) to 2020 (0.90) (See Supplementary Material, Table S1). The only significant difference was between unburnt to low and medium-severities in 2018, immediately after the fire ($P = 0.024$), and between unburnt to low and high-severity in 2019 ($P = 0.062$).

Drivers of forest recovery

The variable importance from the RF model identified slope as the most important factor influencing seedling density, followed by fire severity and distance from seed trees (Fig. 4). The out-of-bag (OOB) R^2 obtained from the RF was 0.42.

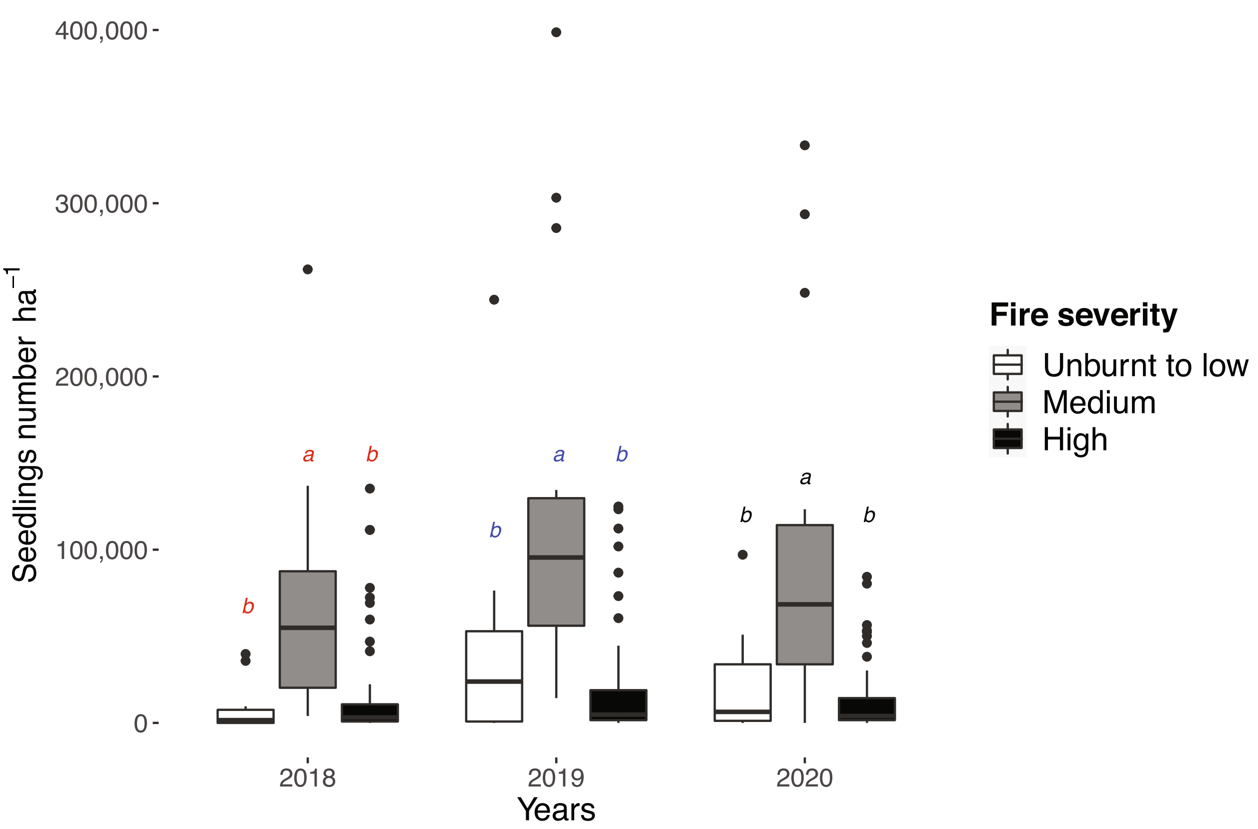

Fig. 3 Box plots of seedling regeneration density in unburnt to low, medium, and high-severity areas for 2018, 2019, and 2020 in the Susa fire (Susa Valley, Italy). Different letters indicate significant differences among fire severity classes according to Dunn's post hoc tests for all pairwise comparisons

Table 2 Annual mean seedling density (seedlings number ha^{-1}) and standard deviation (SD) for the main tree species in the different fire severity classes in 2018, 2019, and 2020 in the Susa fire (Susa Valley, Italy)

Seedling density															
Year	**Fire severity**	***Pinus sylvestris***		***Populus tremula***		***Salix caprea***		***Populus alba***		***Larix decidua***		***Abies alba***		***Other broadleaves***	
		Mean	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
2018	Unburnt to low	4398	7523	0	0	1508	4707	0	0	0	0	42	183	335	765
	Medium	45,784	47,582	424	1079	17,613	21,458	1538	4536	1220	2914	159	616	0	0
	High	9127	21,770	1784	2981	3629	9526	277	647	157	508	48	275	60	212
2019	Unburnt to low	28,983	43,625	209	447	4272	9008	0	0	1927	7634	586	641	209	584
	Medium	81,859	62,975	1910	2653	22,706	25,157	690	1851	17,454	36,601	690	788	106	411
	High	7729	18,476	2833	3735	6101	11,186	494	891	301	749	277	783	48	191
2020	Unburnt to low	10,596	13,260	335	667	3937	8763	0	0	4063	10,429	544	653	209	520
	Medium	51,778	50,702	3395	4826	26,526	28,398	902	1616	19,788	36,783	424	591	0	0
	High	4063	9707	1833	2489	5474	8815	555	1108	434	840	229	736	109	520

According to the partial dependence plot, seedling regeneration density was scarce in steep slopes, showing an exponentially decreasing trend with increasing slope (Fig. 5a). The model predicted the maximum of seedling density in medium-severity areas, while high-severity areas were associated with lower forest seedling

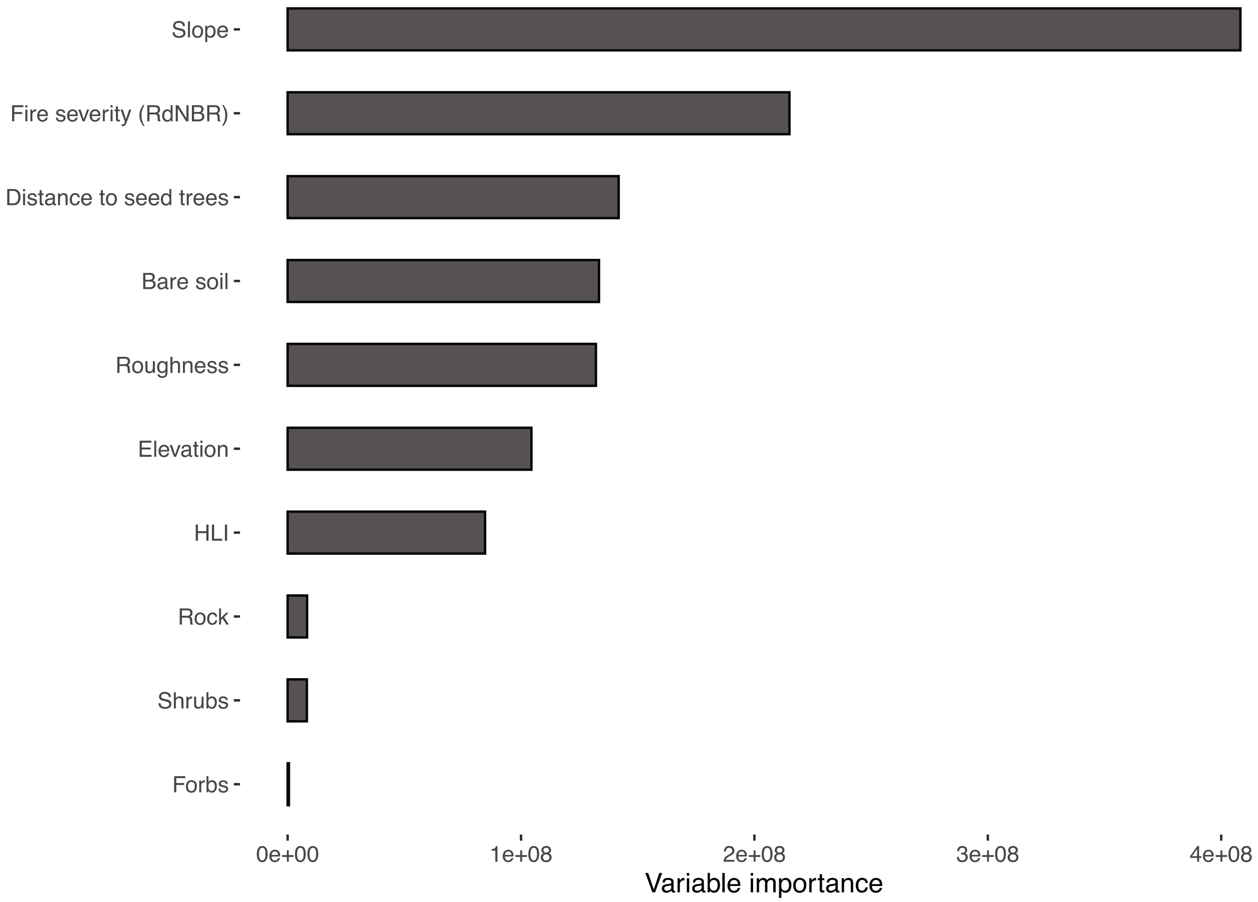

Fig. 4 Variable importance (vimp) for seedling regeneration density (seedlings number ha^{-1}). The plot details vimp ranking for the regeneration density baseline variables, from the largest (slope) at the top, to the smallest (forbs) at the bottom. Vimp measures are shown using bars to compare the scale of the error increase under permutation. Only the first 10 variables are shown

regeneration abundance (Fig. 5b). We found maximum seedling regeneration density close to seed trees, showing again an exponentially decreasing trend that reached a plateau around 50 m from the seed trees, where seedlings were very few (Fig. 5c).

Scots pine and broadleaf RF models showed similar results to those obtained for the total seedling regeneration density (See Supplementary Material, Figs. S2, S3, S4, and S5). Scots pine seedling density was mainly influenced by bare soil, fire severity, and distance to seed trees (See Supplementary Material, Fig. S2). Predicted seedling density was positively correlated to bare soil, with an abrupt increase for percentage cover values higher than 70% (See Supplementary Material, Fig. S3a). Fire severity and distance to seed trees showed a trend similar to the one of total seedling regeneration density (See Supplementary Material, Figs. S3b and S3c). The main drivers of broadleaf seedling regeneration density were fire severity, elevation, and slope (See Supplementary Material, Fig. S4).

Discussion

Shedding light on short-term seedling regeneration patterns following a wildfire and their key drivers is essential to develop appropriate management strategies in the current context of global change. Early post-fire recovery and regeneration dynamics in Scots pine stands of the Alpine Region is a poorly explored issue that needs to be monitored. This species lacks a resilience strategy (e.g., serotiny) to promptly recover after a fire (Tapias et al. 2004), and is particularly sensitive to crown fires with no direct post-fire regeneration mechanisms (Pausas et al. 2008; Vilà-Cabrera et al. 2011; Martín-Alcón and Coll 2016). Nevertheless, the fire regime in the Alpine Region will likely be altered because of global change, and the limited post-fire regeneration capacity of Scots pine could lead to a transition in species composition (Rodrigo et al. 2004; Vilà-Cabrera et al. 2011). In addition to fire regime alteration, the increase in drought periods and temperature due to climate change is already causing a decline in Scots pine stands, especially at the

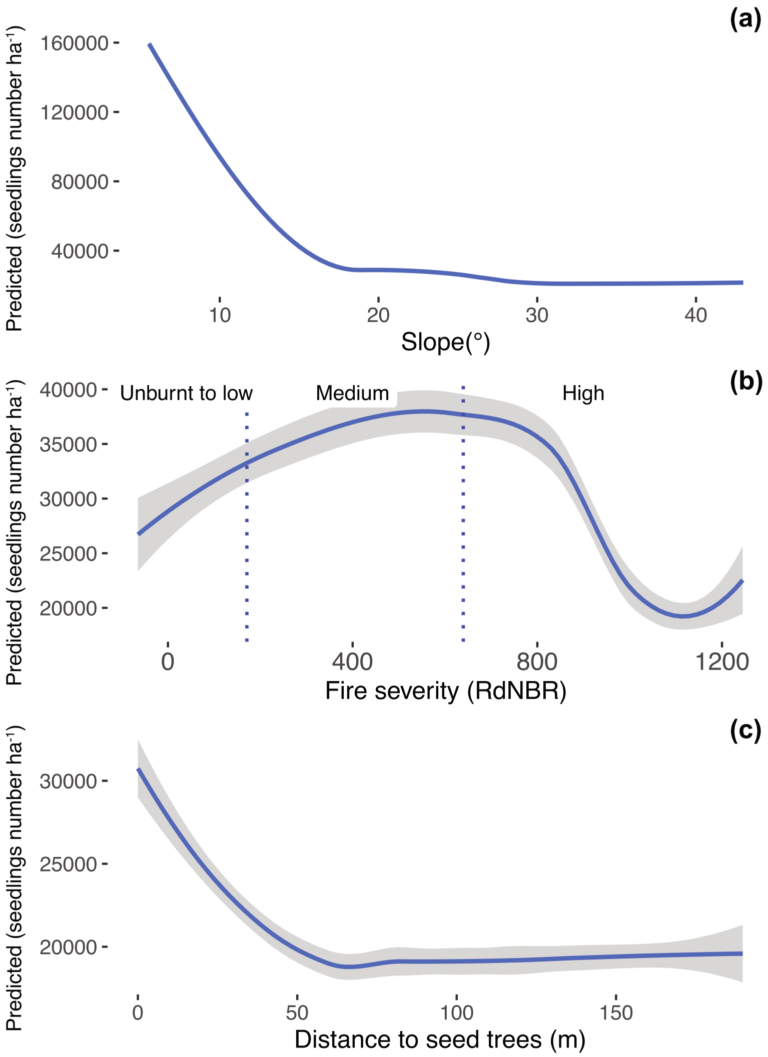

Fig. 5 Partial dependence plots from RF of post-fire seedling regeneration density for the three main driver variables: **a** slope, **b** fire severity, **c** distance to seed trees. A partial dependence plot shows the effect of a particular predictor on the response variable after integrating the effect of the rest of the predictors. The blue line indicates the average value over individual marginal effects of the variables, while the gray ribbon indicates the standard deviation of individual marginal effects. **b** Dotted vertical lines indicate thresholds for fire severity classes (Morresi et al. 2022)

southern fringes of its distributional range, as in the Alpine Region (Mátyás et al. 2004; Rebetez and Dobbertin 2004; Hanewinkel et al. 2013; Dyderski et al. 2018; Sáenz-Romero et al. 2019).

Fire severity and soil properties

Fire severity did not significantly affect the monitored soil chemical parameters. We did not find any significant effect of fire severity on soil OC content, while existing studies reported a decrease in soil OC content in severely burnt areas (Certini 2005), contrasting (Neary et al. 2005) or mostly unchanged values (Fernández-García et al. 2019). We found instead a decreasing pattern in total N content from unburnt to low to high-severity, as expected due to its volatilization caused by the fire (Raison 1979; Grogan et al. 2000; Smithwick et al. 2005). We found C/N values that are in line with existing data of fire-affected forest soils (Knicker et al. 2006) and, as in our case, increasing fire severities do not always affect this parameter (Certini et al. 2011). An increase in soil pH frequently occurs after the passage of a wildfire (Badía and Martí 2003; Pereira et al. 2017). Yet, the alkalizing effect induced by ash incorporation within the soil matrix (Certini et al. 2011) was not always found to persist over long time periods (Zavala et al. 2014). However, we did not find any statistically significant effect of fire severity on soil pH.

In other forest environments, changes in soil OC and N were documented to be fundamental in ruling post-fire vegetation recovery (Caon et al. 2014). It is possible that other soil characteristics or nutrient availability would be more fitting to explain the effects of fire severity on soil and the potential implication for vegetation recovery, rather than OC content, N content, and pH alone. However, the objective of this work was to evaluate the role of typical chemical indicators on post-fire regeneration dynamics according to different levels of fire severity.

Short-term regeneration patterns

Since the first 3 years post-fire, seedling regeneration showed the highest density as well as the greatest diversity in species composition in medium fire severity areas. The most abundant regenerating species was Scots pine, probably due to the almost pure species composition of the previous stand. Nevertheless, 3 years after the fire (2020), goat willow showed a greater density than Scots pine in high-severity areas, suggesting a potential shift from conifer to broadleaf species in stand replacing patches. Medium-severity areas presented a significant regeneration density of larch as well, probably due to the seed dispersal ability of this species. Larch was mostly located on the upper slopes of the study area, where fire severity was lower (personal observation). The most common broadleaves in the seedling layer were goat willow and European aspen, mainly in medium and high-severity area. The density of these pioneer broadleaf species is mainly due to their strong seed dispersal ability through anemochory (Myking et al. 2011; Tiebel et al. 2019). All the observed regenerating species were early successional and were therefore able to establish and grow under the favorable conditions (i.e., increased availability of light, exposed mineral soil, and favorable seed beds) created post-fire (Reinhardt et al. 2001; Nuñez et al. 2003; Úbeda et al. 2006).

Drivers of forest recovery

The importance of fire severity in determining seedling density also emerged from the RF model, confirming that medium-severity conditions maximize the probability of having high seedling densities for the species under investigation. In these areas, the wider presence of Scots pine seedlings, compared to the one observed in both unburnt to low and high-severity areas, was probably related to more favorable conditions required for seedling recruitments.

Nevertheless, the most important parameter in influencing seedling abundance was slope, with a higher density in flat areas and almost no seedlings on slopes greater than 30°. This is confirmed in several studies analyzing post-fire regeneration recovery (e.g., Tsitsoni 1997, Han et al. 2015; Sass and S, Sarcletti. 2017). Steeper slopes are more prone to soil surface erosion phenomena and, consequently, to seed run-off, while in flatter areas seeds tend to accumulate and there are more favorable moisture conditions (Tsitsoni 1997; Pausas et al. 2004; García-Jiménez et al. 2017; Ziegler et al. 2017).

We observed an exponential decrease in the abundance of seedlings at increasing distances from seed trees, reaching a plateau at a value of 50 m (< 5000 seedlings ha^{-1}). Similarly, Vilà-Cabrera et al. (2011) found that 90% of Scots pine seedlings were in the first 25 m from the seed source (50% within the first 10 m). Debain et al. (2007) also observed that Scots pine regeneration density decreased 50 m away from seed trees. In comparison with other pine species (*Pinus heldreichii* Christ*, P. peuce* Griseb., *P. uncinata* Mill.), Scots pine resulted as the one with the lowest dispersal distance, comparable only to *P. uncinata* (4.2 and 3.7 m, respectively; Vitali et al. 2019). Thus, seed trees need to be preserved, even in the case of damaged individuals with a low probability of survival.

Alteration in fire regimes will likely cause an increase in the extent of high-severity patches (Miller et al. 2012), making recovery harder because of the greater distance from seed sources (Harvey et al. 2016). A proper management of seed trees inside high-severity patches will become increasingly important. The key role of seed sources in this study is likely linked to fire severity and to the loss of the soil seed bank in medium and high-severity areas, due to the high soil temperature reached during the fire. In several studies (e.g., Escudero et al. 1997, Reyes and Casal 1995, Nuñez and Calvo 2000), a decrease in germination was observed for temperatures higher than 90° C and an exposure time greater than 5 min.

According to the RF model, ground cover classes did not show a great influence on total seedling density, while bare soil emerged as the most important factor positively affecting Scots pine abundance (See Supplementary Material, Figs. S2 and S3). This finding aligned with the ecological needs of this species (Castro et al. 2005). We found coarse woody debris to be unrelated to seedling abundance, which is in contrast to what has been observed in other studies in the North-Western Italian Alps (Beghin et al. 2010; Marzano et al. 2013). This might be due to the overall sufficient presence of seed trees, even inside high-severity patches, with the distance from seed sources seldom being a limiting factor in the Susa fire. Widespread seed availability likely reduced the importance of facilitation mechanisms on regeneration, such as those provided by shield objects like deadwood. However, where large stand-replacing fire patches are present, "safe-sites", those with favorable microclimatic conditions created by deadwood, are fundamental for seedlings establishment and survival (Marzano et al. 2013). Unlike other studies, the presence of shrubs and herbaceous species after the Susa fire did not seem to strongly affect regeneration density yet, as assessed in the RF model. This indicates that competition had minimal importance during the first years after fire, even if interspecific competition is usually considered a key factor in the regeneration process (Nuñez et al. 2003). However, it is likely that the spreading of dense and continuous shrub or herbaceous layers in the area observed throughout the study period will lead in the near future to an increase in competition for light and nutrients and to the death of those seedlings that are still growing under these layers.

Management implications

Our results provide implications for the management of mountain conifer forests affected by shifts in their fire regime and without specific fire-adaptive traits. Given the abundance of seedling regeneration in medium-severity patches close to seed trees, we recommend leaving any potential seed source, including damaged individuals, to promote postfire forest recovery. The removal of damaged trees should be restricted to sensitive areas, where the fall of these individuals could pose a risk for humans or their assets. Salvage logging practices should be therefore limited, since they can slow down or inhibit natural recovery processes, reducing regeneration density and influencing the specific composition and structure of future stands (Leverkus et al. 2018a,b).

Proper planning and management of areas affected by a wildfire are often necessary, especially to define the actual need for intervention and organize appropriate and targeted measures. Active intervention should be devoted to those situations in which natural regeneration is unable to establish, for example in large high-severity patches, or likely to be affected by degradation phenomena, such as soil erosion, or where a decrease in the provision of ecosystem services and potential cascading disturbance effects are foreseen. In those contexts, where natural successional dynamics are delayed, it could be useful to adopt ANR approaches, like for instance removing competitive, non-woody species and grasses (Zahawi et al. 2013) or taking advantage of facilitation mechanisms. Methods like applied nucleation can be also implemented to accelerate natural dynamics. Applied nucleation, enhancing seed dispersal and improving establishment conditions, can be particularly useful in wide high-severity patches where the seed rain from forest edges and green islands is insufficient. Spatial prioritization of nuclei location combined with ANR allows active restoration efforts to be implemented only in areas where natural regeneration is lacking or more prone to post-disturbance degradation phenomena, also resulting in lower costs compared to a traditional regular plantation. This follows within the framework of precise forest restoration (PFR) (Castro et al. 2021), aiming to improve planting (or seeding) efficiency, by focusing on site selection and preparation, postplanting care, and monitoring.

Conclusions

Our investigation of the Susa fire provided information on the spatial distribution and characteristics of short-term post-fire recovery after a large mixed-severity event in Scots pine stands. These findings could be useful for informing land managers, helping them to enhance potential mitigation strategies in similar ecosystems. The most frequently applied restoration techniques applied after large fire events are often not up-to-date and suited to the ecological context and to the consequences of global change. More ecologically appropriate restoration approaches are needed as land managers increasingly request for restoration strategies and guidelines. The necessity of appropriate strategies is even more pressing in the case of sensitive ecosystems, where natural balances could be altered by changes in disturbance regimes, and human intervention can either facilitate ecosystem recovery or trigger further degradation phenomena. In this perspective, it is crucial to reconsider current post-disturbance policies to identify strategies that promote and maintain ecosystem functions of severely affected forests, whether through active or passive management.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s42408-023-00182-7.

Additional file 1: Table S1. Brillouin index values (0 to 1) according to fire severity classes in Susa fire (Susa Valley, Italy) in 2018, 2019, and 2020. **Figure S1.** Proportion of seedlings of each tree species according to fire severity classes in 2018, 2019, and 2020 in the Susa fire (Susa Valley, Italy). **Figure S2.** Variable importance (vimp) for Scots pine density (seedlings number ha^{-1}). The plot details vimp ranking for the regeneration density baseline variables, from the largest (bare soil) at the top, to the smallest (shrubs) at the bottom. Vimp measures are shown using bars to compare the scale of the error increase under permutation. Only the first 10 variables are shown. **Figure S3.** Partial dependence plots from RF of Scots pine density for the three main driver variables: (a) bare soil, (b) fire severity, (c) distance to seed trees. A partial dependence plot shows the effect of a particular predictor on the response variable after integrating the effect of the rest of predictors. The blue line indicates the average value over individual marginal effects of the variables, while the grey ribbon indicates the standard deviation of individual marginal effects. (b) Dotted vertical lines indicate thresholds for severity classes (Morresi et al., 2022). **Figure S4.** Variable importance (vimp) for broadleaf density (seedlings number ha^{-1}). The plot details vimp ranking for the regeneration density baseline variables, from the largest (fire severity) at the top, to the smallest (bare soil) at the bottom. Vimp measures are shown using bars to compare the scale of the error increase under permutation. Only the first 8 variables are shown. **Figure S5.** Partial dependence plots from RF of broadleaf regeneration density for the three main driver variables: (a) fire severity, (b) elevation, (c) slope. A partial dependence plot shows the effect of a particular predictor on the response variable after integrating the effect of the rest of predictors. The blue line indicates the average value over individual marginal effects of the variables, while the grey ribbon indicates the standard deviation of individual marginal effects. (b) Dotted vertical lines indicate thresholds for severity classes (Morresi et al., 2022).

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Authors' contributions

GM, EL, EB, MG, and RM contributed to the conception and design of the study. MG and RM obtained funding. GM and SN collected the data. GM, DM, SN, and NA analyzed and interpreted the data. GM and SN drafted the manuscript. All authors contributed editorial input during manuscript preparation. All authors have read and approved the submitted version. All authors have agreed both to be personally accountable for the author's own contributions and to ensure that questions related to the accuracy or integrity of any part of the work, even ones in which the author was not personally involved, are appropriately investigated, resolved, and the resolution documented in the literature.

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Availability of data and materials

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

Declarations

Ethics approval and consent participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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