



ORIGINAL RESEARCH

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Topographic conditions dominate tree species recovery over 15 years post-fire in a temperate *Pinus sylvestris* forest

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Abstract

Background Intensifying fire regimes and changing climatic conditions raise concerns about the capacity of forests to naturally recover after fire. Linking long-term observations of post-fire natural tree regeneration with the environmental and spatiotemporal context is thus becoming increasingly important to guide restoration efforts worldwide. Especially where fires have been rare, snapshot and short-term monitoring efforts prevail, thereby failing to recognize the post-fire species dynamics and wider community trends. Using multivariate Bayesian and spatial point process modeling, we evaluated the main environmental drivers of post-fire tree species recovery, its compositional and structural components, and species' spatiotemporal co-occurrence patterns over 15 years post-fire in a Central European *Pinus sylvestris* forest.

Results Topography-related conditions and ground cover were the prevalent drivers of tree species responses. In addition to diverse species-specific and size-dependent responses, higher site moisture and moss cover were beneficial for most species, while steep and warm habitats with exposed mineral soil and lack of litter mostly represented harsh conditions. We demonstrate the transition of the *Pinus sylvestris* forest to early successional broadleaves. *Betula pendula* seedlings and saplings began to dominate 10 and 5 years after the fire, respectively. *Pinus sylvestris* seedlings showed a similar abundance to *Betula pendula* and *Populus tremula* 5 years after the fire but declined sharply thereafter. We identified synchronized but species-specific patterns of seedling decline and sapling basal area build-up in early successional broadleaves. *Fagus sylvatica*, *Picea abies*, and *Pinus sylvestris* saplings showed synchronized recovery 15 years post-fire.

Conclusions We highlight the need for a detailed recognition of species-environment relationships, particularly where species with diverse levels of natural recovery are challenged along wide topographic gradients. Our findings also demonstrate that the compositional and structural components of post-fire recovery were shaped by species and wider community dynamics depending on time since fire. Exploring these species' unique and synchronized trajectories through spatiotemporal co-occurrence patterns is essential for setting realistic expectations of future forest recovery and can also help guide active restoration efforts in various post-disturbance contexts.

Keywords Natural regeneration, Forest recovery, Fire disturbance, Species co-occurrence patterns, Species-environment relationships, Sandstone landscapes, *Pinus sylvestris*

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Resumen

Antecedentes La intensificación en los regímenes de fuego y los cambios en las condiciones climáticas, incrementan la preocupación sobre la capacidad de los bosques de recuperarse naturalmente luego de incendios. El relacionamiento entre las observaciones de largo plazo sobre la regeneración natural de árboles y el contexto ambiental y espaciotemporal, está siendo incrementalmente importante para guiar los esfuerzos de restauración en todo el mundo. Especialmente donde los incendios han sido particularmente raros, prevalecen las observaciones instantáneas y los esfuerzos de monitoreo a corto plazo, lo que impide reconocer la dinámica de las especies y su tendencia en el desarrollo de la comunidad en el post fuego. Usando modelos multivariados bayesianos y de puntos espaciales, evaluamos los principales conductores ambientales en la recuperación post fuego de especies de árboles, sus componentes composicionales y estructurales, y los patrones de co-ocurrencia espacio temporal por 15 años después de un incendio en un bosque de pino silvestre en Europa Central.

Resultados Las condiciones relacionadas con la topografía y la cobertura del suelo fueron los conductores prevalentes en las respuestas de las especies de árboles. Adicionalmente a las respuestas de diversas especie-específicas y de tamaño- dependientes, la humedad más alta de algunos sitios y con cobertura de musgos, fueron beneficiosos para la mayoría de las especies, mientras que sitios con pendiente y hábitats cálidos con suelo mineral expuesto y sin mantillo, presentaron condiciones más severas. Demostramos la transición entre de bosques de pino silvestre a una etapa sucesional temprana de latifoliadas. Las plántulas y brinzales de *Betula pendula* comenzaron a dominar entre cinco y diez años luego del fuego, respectivamente. Las plántulas de pino silvestre mostraron una abundancia similar a *Betula pendula* y *Populus tremula* cinco años luego del incendio, pero declinaron rápidamente de ahí en más. Identificamos patrones sincrónicos especie-específicos de declinación de plántulas y el crecimiento del área basal de brinzales de latifoliadas en estadios tempranos de la sucesión. Las plántulas de *Fagus sylvatica*, *Picea abies*, y pino silvestre mostraron una recuperación sincronizada 15 años luego del incendio.

Conclusiones Subrayamos la necesidad de un detallado reconocimiento de las relaciones entre las especies y su ambiente, particularmente donde las especies con diversos niveles de recuperación natural se enfrentan con amplios gradientes topográficos. Nuestros resultados también demuestran que los componentes composicionales y estructurales de la recuperación estuvieron modelados por las especies y la amplia dinámica de la comunidad, dependiendo del tiempo desde el incendio. El explorar las trayectorias únicas y sincronizadas de estas especies a través de los patrones de co-ocurrencia espacio-temporales, se torna esencial para determinar expectativas realistas de la recuperación futura del bosque, y puede también ayudar a guiar en los esfuerzos de restauración activa en varios contextos del post-disturbio.

Background

Understanding the compositional and structural components of post-fire forest recovery over space and time is critical to guide restoration efforts worldwide (Baltzer et al. 2021; Cerioni et al. 2024; Harvey et al. 2016). The need has become more pressing due to increases in the frequency of extreme fire weather (Jain et al. 2022), forest biomass burned (Patacca et al. 2023), and the strength of fire impacts on ecosystem services (Thom and Seidl 2016) over recent decades. The primary concern centers on whether the process of natural tree regeneration can facilitate post-fire recovery or if active restorative interventions are needed (Crouzeilles et al. 2017; Mantero et al. 2024; Souza-Alonso et al. 2022). Natural tree regeneration often represents the most ecological and cost-effective strategy to restore locally adapted tree communities with native species diversity and structural complexity (Beghin et al. 2010; Cerioni et al. 2024; Crouzeilles et al. 2017; Di Sacco et al. 2021) and to prevent ecosystem degradative processes such as soil erosion

(Shakesby 2011). Specific species regenerative strategies, such as long-distance seed dispersal and vegetative regrowth, can particularly facilitate rapid post-fire recovery (Donato et al. 2009; Nolan et al. 2021). On the other hand, the ecosystem's capacity to naturally recover can be exhausted under certain conditions, in which case alternative restoration strategies may be necessary (Larson et al. 2022; Souza-Alonso et al. 2022). For instance, large high severity fires and short-interval reburns can substantially inhibit natural recovery, especially when seed trees are depleted (Coop et al. 2020; Stevens-Rumann and Morgan 2019). Natural recovery can also be challenging on fire-degraded soils (Souza-Alonso et al. 2022) and during periods of severe post-fire drought (Moser et al. 2010).

Forecasting future forest composition relies on the assumption that the composition of tree regeneration early after fire is closely linked to that of a mature forest (Baltzer et al. 2021; Johnstone et al. 2020). However, the temporal context of post-fire forest recovery needs to

be comprehensively recognized to validate this assumption (Stevens-Rumann and Morgan 2019). The longest post-fire observations of tree regeneration in temperate and boreal forests span up to several decades (Baltzer et al. 2021; Donato et al. 2016; Johnstone et al. 2004). Yet, the majority of observational studies only document a few years or a handful of time points after fire. Snapshot and short-term observations may thus fail to document changes in vegetation trajectory at longer time scales due to biotic processes such as competition and tree interactions with pathogens and herbivores (Boulanger et al. 2018; Walter et al. 2023).

Predicting forest recovery is further complicated by site differences in pre- and post-fire biophysical conditions (Baltzer et al. 2021; Harvey et al. 2016). Especially in topographically rugged regions, tree regeneration patterns can arise from a broad array of environmental conditions (Adámek et al. 2016; Larson et al. 2022). Steep habitats with southern exposures and shallow soils can represent harsh conditions for many tree species (Mantero et al. 2023; Petrie et al. 2023). Another source of uncertainty arises from how fire impacts the forest stand (Becker and Lutz 2023b; Churchill et al. 2022), influencing factors such as the survival of pre-fire trees (Fernandes et al. 2008), forest floor conditions (Dzwonko et al. 2015; Mantero et al. 2023), and seed banks (Reid et al. 2023; Shi et al. 2022).

The post-fire trajectories of individual tree species and their position along environmental gradients can vary widely (Harvey et al. 2016). Surprisingly, there is little information about the long-term establishment success of individual tree species in the post-fire context, making predictions about their roles within the broader forest community unreliable (but see Andrus et al. 2022; Becker and Lutz 2023a; Harvey et al. 2016; Jorgensen et al. 2023). However, understanding both species and wider tree community dynamics through observations of natural regeneration patterns and their distribution over space and time is vital for predicting post-fire recovery and guiding active restoration efforts (Di Sacco et al. 2021; North et al. 2019). For instance, identifying habitats where certain species show greater establishment success can be used to determine habitat suitability for planting and ensure alignment with an appropriate species composition (North et al. 2019).

High fire activity was an integral part of forest dynamics in the coniferous forests of Central Europe at least until the Mid-Holocene, but it declined later due the expansion of *Fagus sylvatica* (Bobek et al. 2019, 2018; Feurdean et al. 2020). However, fires have a well-documented, continuous history in the topographically complex *Pinus sylvestris* forests of central European sandstone landscapes throughout the Holocene to the present days (Adámek

et al. 2015, 2018; Bobek et al. 2019). Periodic fires, occurring at least once in 200 years, have been hypothesized to maintain *P. sylvestris*-dominated forests by stimulating its regeneration and impeding late-successional tree species that are more sensitive to fire than *P. sylvestris* (Adámek et al. 2016). Evidence on historical fire frequency suggests that it may have fluctuated substantially, with fire return intervals ranging from a few years to over a hundred years (Seiler et al. 2013; Šamonil et al. 2018). Moreover, some *P. sylvestris* forests in the sandstone landscape are situated within larger protected areas where nature conservation regulations mostly preclude conventional forest management, including the use of fire treatment. Relatively extensive recent fires in these areas have raised questions about the appropriate post-disturbance approach in forests that are expected to remain free from any large-scale interventions due to conservation objectives (Kudláčková et al. 2024; Trochta et al. 2012).

To set realistic expectations of future forest recovery through ecological processes, linking long-term observations after fire with the environmental and spatiotemporal context is becoming increasingly important (Adámek et al. 2016; Lindenmayer et al. 2019; Stevens-Rumann and Morgan 2019). The overarching goal of this study was to evaluate the main environmental drivers and spatiotemporal aspects of tree species recovery over 15 years after a fire in a central European temperate forest dominated by *P. sylvestris*. We specifically detailed post-fire: (1) shifts in tree species composition, structure and diversity, (2) spatial and temporal species co-occurrence patterns and (3) seedling and sapling species' responses to environmental conditions.

Methods

Study site

The study was carried out at the Havraní skála site in the Bohemian Switzerland National Park, which is characterized by heterogeneous landscape of dry rock outcrops, narrow humid valleys and gorges, and mesic plateaus lined with steep rock walls (Adámek et al. 2016; Novák et al. 2019). The bedrock is formed by quartzose sandstone rocks and occasional outcrops of tertiary volcanic rocks (Adámek et al. 2016). The rugged relief of Havraní skála is characterized by a sandstone ridge with central sandstone rock formations flanked by deep valleys. The sandstone ridge lies in NE-SW direction and is ca 350 m long. The elevation ranges from 245 to 393 m. The slope ranges from 0 to 90° (Trochta et al. 2012). The interannual mean $\pm$ standard deviation for the period of 1991–2023 was 8.58 ± 0.72 °C for temperature and 827 ± 137 mm for precipitation. Most precipitation falls evenly throughout the year (Czech Hydrometeorological Institute, <https://chmi.cz/>). Based on the forest management records, the

pre-fire forest stand was approximately up to 130 years old and was dominated by *P. sylvestris*. Other species present in the pre-fire forest stand were *Betula pendula*, *Fagus sylvatica*, *Picea abies*, *Quercus petraea*, and *Pinus strobus*. In July 2006, one of the largest wildfires in the contemporary history of the Czech Republic burned 17.9 ha of forests at the Havraní skála site. Historical fires in this region over the past 200 years were rare and typically smaller than the 2006 fire event (Adámek et al. 2016; Tinner et al. 2005), with the exception of the 1842 fire, which burned about 180 ha (Seiler et al. 2013).

A smaller part of the burned area, 13.6 ha large, was selected as a study site to avoid the impact of tourists entering the burned site from a nearby hiking trail. The event was a stand-replacing fire, characterized by a combination of canopy and ground fire that eventually killed most canopy trees (Trochta et al. 2012). It was presumably much more severe than historical fires over the past two centuries which, while substantially reducing tree survival, did not remove the tree canopy completely (Adámek et al. 2016). Because *P. strobus* is considered an alien species in this region and throughout Europe (Puchałka et al. 2023), its saplings were partly cut out in 2016. However, forest management is typically prohibited under national park regulations.

Study design

One year after the fire, we established a regular network of 135 sampling points, spaced 30 m apart. Each point was permanently marked with one wooden and one iron stake. We set up one square and one circular sampling plot at each point to record all tree seedlings and saplings, defined as < 130 cm and ≥ 130 cm tall, respectively. The iron stake marked the lower-left corner of the square plot and the center of the circular plot. Post-fire tree resprouting was not observed, likely because tree regeneration was poor prior to the fire.

On square plots (2.25 m²), seedlings were counted, identified to species and sorted into the following four height classes: < 30 cm, 30–59 cm, and 60–130 cm. On circular plots (28.3 m²), saplings were counted, identified to species and sorted into several classes based on their diameter at breast height (DBH). Although the definition of DBH classes varied between survey years (Appendix A Table S1), we were able to group saplings into the following three DBH classes: < 3 cm, 3–6.9 cm and > 7 cm. We also calculated the sum of basal area of each sapling species. Due to discrete DBH classes, we used a central value of each DBH class to calculate sapling basal area. We sampled seedlings and saplings over a 15-year period following the fire. Seedlings were sampled yearly from 2007 to 2011, and then again in 2016 and 2021. The same

applied to saplings, except that we were unable to collect the data in 2016.

In the central part of the study site, a large-scale census plot (100 m × 100 m) was established 15 years after the fire (2021) to serve as a permanent research infrastructure for detailed spatiotemporal evaluation of post-fire forest dynamics. This plot overlapped with some of the square and circular sampling plots. The most extreme topographical conditions of the study area represented by rock outcrops were avoided on the census plot. All tree individuals ≥ 1 cm DBH that regenerated after the fire were mapped, identified to species and measured for DBH on the census plot in 2021. Although this size definition targeted larger tree individuals than those sampled on circular plots, we classify them as saplings due to a significant overlap in size structure. Pre-fire trees were dead and therefore not mapped.

Fire characteristics and environmental conditions

We gathered diverse biophysical characteristics that have previously been shown to be the key drivers of post-fire tree regeneration (Mantero et al. 2023; Povak et al. 2020). To characterize canopy and ground fire severity, we used remote sensing data on post-fire tree crown defoliation and field observations of flame height, as detailed in our previous study (Trochta et al. 2012). Tree crown defoliation was based on a supervised classification of green tree canopy cover using orthophoto maps from the pre-fire year 2005, and two post-fire years 2006 and 2007. Crown defoliation in 2006 was calculated as a difference in the average percentage of green crowns in a circle with 7.5 m radius between 2006 and 2005. Crown defoliation in 2007 was calculated as a difference between 2005 and 2007. In 2007, we measured a maximum flame height on all pre-fire trees within a 7-m radius of each sampling point and calculated the mean of these measurements (Trochta et al. 2012). We characterized ground cover in the first post-fire year for each square and circular plot by visually estimating the percent cover of deadwood, graminoids, forest floor litter, mineral soil (uppermost mineral A horizon), mosses, and rock (Table 1).

Topographic variables for each sampling plot were obtained from a 1-m resolution digital terrain model. It included elevation and slope as direct measures of topography, and topographic proxies for site climate (Table 1), such as potential heat load (heat load index; McCune 2007) and moisture availability (topographic wetness index; Beven and Kirkby 1979; wind effect; Gerlitz et al. 2015). Heat load index uses slope, aspect and latitude to estimate the intensity of solar heating, with lower values indicating cooler sites (McCune 2007). Topographic wetness index is estimated as a ratio of upstream catchment area and slope, with lower values indicating drier

Table 1 A summary of predictor variables used in the JSDMs. Dash indicates dimensionless indices. DTM stands for Digital Terrain Model. The scores of the first two principal components (Ground 1, Ground 2) were used as predictors instead of the original ground cover variables. Highly correlated variables, which were excluded prior to analyses, are not shown

Group	Variable	Unit	Range	Mean	Median	Data source
Ground cover	Deadwood	%	0–100	4.19	0	Field
	Graminoid	%	0–5	0.16	0	Field
	Litter	%	0–100	49.11	50	Field
	Mineral soil	%	0–100	16.71	0	Field
	Moss	%	0–95	17.65	5	Field
	Rock	%	0–100	12.41	0	Field
Topography	Elevation	m a.s.l	248.87–390.54	317.75	320.22	DTM
	Slope	°	6.09–65.58	33.66	34.10	DTM
Proxies for site climate	Heat load index (HLI)	-	0.15–0.99	0.65	0.63	DTM
	Topographic wetness index (TWI)	-	0.38–7.52	3.69	3.66	DTM
	Wind effect (WE)	-	0.76–1.31	0.96	0.90	DTM
Fire severity	Crown defoliation	%	0–100	97.81	100	Orthophoto
	Flame height (FlameH)	m	0–0.90	0.28	0.2	Field

sites (Beven and Kirkby 1979). Wind effect uses wind direction to calculate the potential exposure to wind and precipitation, with high values indicating wind exposed sites (Böhner and AntoniĆ 2009). To calculate wind effect for our study site, we derived mean interannual wind direction data at 10 m height for the longest available period (2006–2018) from the New European Wind Atlas (<https://map.neweuropeanwindatlas.eu/>). Other potentially relevant variables were excluded from our study due to high correlations (> 0.8) with either slope or elevation (Appendix A Fig. S1). The plot-level values of topographic variables were computed using bilinear interpolation.

Data analyses

We used several techniques to address our objectives. To summarize shifts in tree seedling and sapling composition and structure over 15 years after the fire, we adopted an approach of confidence interval inference (Di Stefano 2004; Donato et al. 2016). We used this approach to be versatile and informative enough to describe the abundances of a relatively few species that varied widely within and between years, thereby often resulting in data distributions with excessive number of zeros. As a method robust to abundant zeros, we constructed non-parametric bias-corrected and accelerated 95% confidence intervals based on 10,000 bootstrap resamples for the mean abundance of seedling and sapling species with at least five occurrences on sampling plots (square or circular) in each year (Efron and Tibshirani 1993). Such estimates of mean abundance were similarly calculated for each seedling species $\times$ height class $\times$ year and each sapling species $\times$ DBH class $\times$ year combinations. We also

calculated these 95% confidence intervals for the sum of basal area of each sapling species. As a measure of species relative abundance, we calculated the seedling and sapling proportion of the plot-level total abundance for each species and also for each species $\times$ size class combination. We report the abundances of tree seedling and sapling species at roughly regular time steps of 1, 5, 10, and 15 years after the fire.

Moreover, we evaluated the diversity of seedling and sapling species as species richness (the actual number of species), the effective number of species (ENS) and the Gini-Simpson index (GS index; Tuomisto 2010). Compared to species richness, ENS and GS index consider relative abundances, making them more suitable for assessing tree species diversity, particularly when species abundances substantially vary. If species are equally abundant, ENS corresponds to species richness, in other cases, it is lower than species richness. GS index represents the probability that two randomly selected individuals are heterospecific and increases with species richness (Tuomisto 2010). We used nonparametric Kruskal–Wallis and Dunn tests with Bonferroni-corrected p -values to compare species richness, ENS and GS index between years. The species diversity of seedlings was compared across 1, 5, 10, and 15 years after the fire. Due to unavailable data, the species diversity of saplings was only compared across 1, 5, and 15 years after the fire. Because ENS and GS index based on the number of stems and basal area were comparable, we report the results based on stem abundances.

We fitted joint species distribution models (JSDMs) within a multivariate Bayesian generalized linear mixed modeling framework (Tikhonov et al. 2020) to evaluate

seedling and sapling species responses on square and circular sampling plots to environmental conditions while accounting for the post-fire spatiotemporal context of the study site. This modeling framework explicitly assumes that multiple species respond jointly to the environment and to each other, thereby providing more complete picture on species-environment relationships than single-species models (Warton et al. 2015). It can also be used when many species are rare in the community because information is borrowed across species (Ovaskainen et al. 2016). This is a typical situation of post-fire forest recovery when, for instance, late-successional species remain rare for decades after fire but are important for post-fire vegetation trajectories in the long-term (Adámek et al. 2016).

For seedlings and saplings separately, we fitted probit models based on presence-absence and log-normal Poisson models based on abundance conditional on species presence (Ovaskainen and Abrego 2020). We also fitted a linear model for saplings based on basal area conditional on species presence. Due to high variation in species basal area, we transformed these data with the binary logarithm. In each model, we included nine environmental characteristics as fixed effects. To avoid overly complex models and multicollinearity, we reduced the number of ground cover variables by performing a principal component analysis (Appendix A Fig. S2). The scores of the first two principal components were used as fixed effects instead of the original six ground cover variables. The first principal component was associated with higher cover of mineral soil and rock, and lower cover of litter (Ground 1). The second principal component was associated with higher cover of moss (Ground 2). Another seven fixed effects represented topography (elevation, slope), topographic proxies for site climate (HLI, TWI, WE) and fire severity characteristics (tree crown defoliation, flame height). We used two types of seedling responses (presence-absence and abundance) and three types of sapling responses (presence-absence, abundance and basal area) per each species to calculate the proportion of seedling and sapling species showing positive and negative responses to each environmental predictor with at least 95% posterior probability.

To account for the spatial and temporal structure of the study design and variation unexplained by the nine environmental predictors, we included sampling plot and survey year as community-level random effects. Using these random effects, we separately estimated spatial and temporal species co-occurrence patterns based on the residual species-to-species variance-covariance matrices that accounts for environmental predictors. They can be interpreted as data-derived approximations of species interactions. Using these

matrices, we evaluated for each species pair if species are spatially and temporally associated more or less often than expected by chance (Ovaskainen et al. 2016). However, we were unable to examine species co-occurrence both over space and time, because models with a random effect at the sampling unit level (sampling plot $\times$ survey year) showed poor convergence.

For each of the five models, we applied an MCMC posterior sampling procedure and evaluated their convergence and performance (see Appendix B for details). For each species, we performed variance partitioning to evaluate the contribution of individual fixed and random effects to the explained variance (Tikhonov et al. 2020).

For sufficient statistical power and reliable estimates of species co-occurrence patterns, we included in the analyses only those seedling and sapling species that occurred at least on 10 sampling plots (Ovaskainen and Abrego 2020). We included 11 species, *Betula pendula*, *Carpinus betulus*, *Fagus sylvatica*, *Larix decidua*, *Picea abies*, *Pinus strobus*, *Pinus sylvestris*, *Populus tremula*, *Quercus petraea*, *Salix caprea*, and *Sorbus aucuparia*, to quantify seedling responses, and eight species, *Betula pendula*, *Fagus sylvatica*, *Picea abies*, *Pinus strobus*, *Pinus sylvestris*, *Populus tremula*, and *Salix caprea*, to quantify sapling responses. We report the results of *P. strobus* regeneration with caution, due to an attempt to remove the species from the burned site in 2016.

To evaluate the effect of environmental conditions on the spatial distribution of trees, we fitted log-Gaussian Cox process (LGCP) models to presence-only data of trees mapped within the census plot (Renner et al. 2015). These spatial point process models are extensions of inhomogeneous Poisson process models, which assume that tree locations are independent of each other and that the expected number of trees per unit area (intensity) varies spatially (see Appendix B for details; Baddeley et al. 2015; Renner et al. 2015). Five topographic variables based on the 1 m resolution digital terrain model, elevation, slope, HLI, WE, and TWI, were included in the model as spatial environmental predictors. Some other variables were excluded due to high correlations (> 0.8) with either slope or elevation (Appendix A Fig. S3).

The goodness-of-fit of LGCP models was evaluated by Monte Carlo simulations. To assess if the choice of the LGCP models was appropriate for our presence-only data, we evaluated the goodness-of-fit of structurally less complex models (see Appendix B for details; Baddeley et al. 2015; Bagchi and Illian 2015). We used data on the locations of *B. pendula* (4235 stems) and *P. tremula* saplings (364 stems) to fit single-species models. Other species were represented by less than 40 individuals, which was insufficient to fit individual models.

Data wrangling and analyses were carried out in R 4.2.1. (R Core Team 2023) and QGIS (version 3.28; QGIS.org 2022). Topographic variables were calculated using the R packages *RSAGA* (Brenning et al. 2022), *spatialEco* (Evans and Ram 2023) and *terra* (Hijmans et al. 2024). JSDMs were performed with the package *hmsc* (Tikhonov et al. 2020) and spatial point process models with the package *spatstat* (Baddeley et al. 2015).

Results

Species diversity, composition and structure over time

Seedling species richness, the GS index and ENS peaked 5 years post-fire and then gradually decreased over the following 10 years (Fig. 1). These seedling diversity indices were comparable between 1 and 15 years post-fire. Sapling species richness increased over the whole period, while the GS index and ENS remained similar between 5 and 15 years post-fire (Fig. 1).

One year after the fire *P. tremula* seedlings were the most abundant (34%), followed by *B. pendula* (23%) and *S. caprea* seedlings (16%). Other seedling species were rare (< 3%; Fig. 2). Five years post-fire, *P. tremula* and *B. pendula* seedlings were equally abundant and dominated in the community (22% and 23%, respectively; Fig. 2). The abundance of *P. sylvestris* and *P. strobus* seedlings peaked 5 years post-fire (18% and 8%, respectively; Fig. 2). *B. pendula* seedlings were the most dominant 10 and 15 years

after the fire (Fig. 2). All seedling species except *P. abies* exhibited a decrease in abundances 10 and 15 years post-fire (Fig. 2).

The abundance and basal area of *P. sylvestris* and *P. abies* saplings were low but dominated 1 year post-fire (Fig. 3). From 5 to 15 years post-fire, *B. pendula* was the most abundant sapling species (Fig. 3). The abundance of *P. abies*, *P. sylvestris* and *F. sylvatica* saplings slightly increased 15 years post-fire, each showing a similar abundance as *P. tremula* (Fig. 3a). Except for *B. pendula*, the basal area (but not abundance) of *P. abies* saplings (8%) exceeded that of all other sapling species 15 years post-fire (Fig. S4). Other seedling and sapling species were rare throughout the entire period (< 2%; Figs. 2 and 3). Temporal shifts in the height, diameter, and basal area structure of tree regeneration were more nuanced but aligned with the patterns described above (Appendix A Figs. S4–S8).

Species co-occurrence patterns

The MCMC convergence diagnostics showed good convergence in all JSDMs (Appendix A Table S2). All JSDMs had high explanatory power on average ($R^2 = 0.33$ – 0.54) and expectedly lower predictive power ($R^2 = 0.18$ – 0.35). Based on the random effects of JSDMs, the prevalence of positive seedling species associations was detected at the plot level (Appendix A Fig. S9a, b). The occurrence

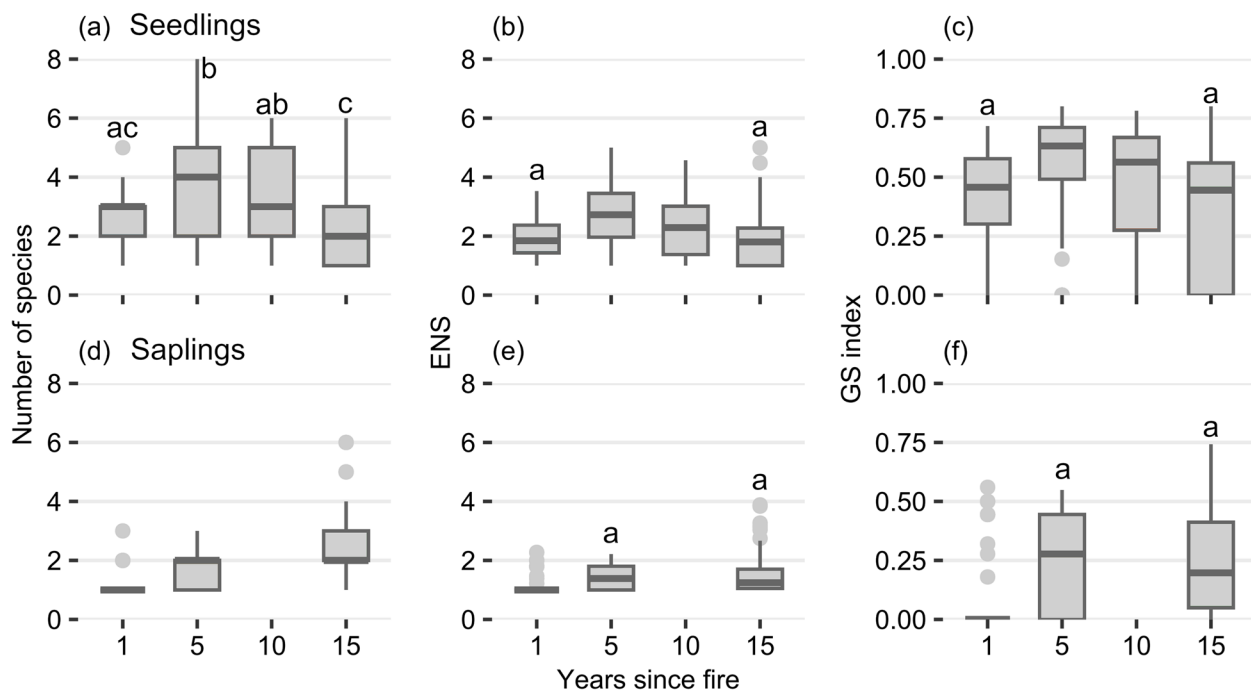


Fig. 1 Seedling (a–c) and sapling diversity (d–f) evaluated as the number of species, effective number of species (ENS) and Gini-Simpson (GS) index. Boxplots with the same letters indicate that diversity indices did not vary significantly between years since fire. All other comparisons were significant, with p -values < 0.05

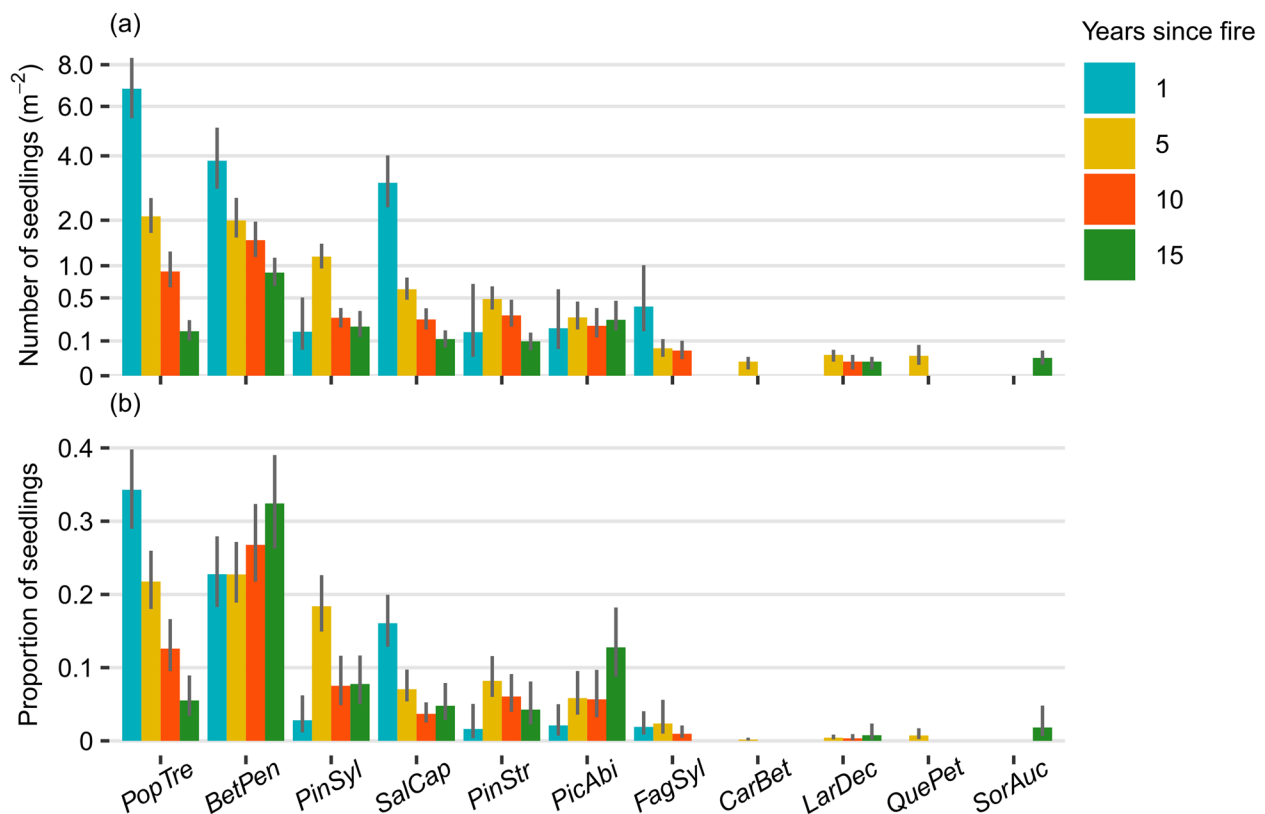


Fig. 2 Observed number of seedlings (a) and their proportion of the plot-level total (b) depending on the number of years since fire. Error bars indicate 95% confidence intervals based on 10,000 bootstrap resamples. Seedling species are ordered on the x-axis from the most to the least abundant based on their proportion of the total seedling sample size during the whole 15-year period after the fire. The y-axis in a was transformed with a square root function to effectively display species with widely varying abundances. The full species names are: *Populus tremula* (PopTre), *Betula pendula* (BetPen), *Pinus sylvestris* (PinSyl), *Salix caprea* (SalCap), *Pinus strobus* (PinStr), *Picea abies* (PicAbi), *Fagus sylvatica* (FagSyl), *Carpinus betulus* (CarBet), *Larix decidua* (LarDec), *Quercus petraea* (QuePet), and *Sorbus aucuparia* (SorAuc)

or abundance of some seedling species were positively associated at the survey year level, e.g., the association between *P. sylvestris* and *P. strobus*, or among *B. pendula*, *S. caprea*, and *P. tremula* (Appendix A Fig. S9c, d). Sapling species associations were less common (Appendix A Fig. S10). *B. pendula*, *P. tremula*, *S. Caprea*, and *F. sylvatica* sapling occurrence showed positive associations at the plot level (Appendix A Fig. S10a), while *P. abies*, *F. sylvatica*, and *P. strobus* sapling occurrence exhibited positive associations at the survey year level (Appendix A Fig. S10d). The basal area of *B. pendula*, *P. tremula*, and *S. caprea* saplings was positively associated at the survey year level (Appendix A Fig. S10f). The occurrence of *P. sylvestris* and *S. caprea* was negatively associated at the survey year level (Appendix A Fig. S10d).

Environmental and spatiotemporal context of tree regeneration

Variance partitioning based on JSDMs indicated that among the fixed effects, topography and topographic

proxies for site climate had the strongest effect on seedling and sapling responses (Figs. 4, 5, Appendix A Fig. S11). Ground cover was nearly twice as important for seedlings than fire severity (Fig. 4), yet they influenced sapling responses to a similar degree (Fig. 5, Appendix A Fig. S11). Most seedling and sapling responses, primarily of *B. pendula*, *P. tremula*, *S. caprea*, *P. Sylvestris*, and *P. strobus*, were explained by temporal variation (the random effect for variation between the survey years) much more than spatial variation (the random effect for variation among plots; Figs. 4b, 5, Appendix A Fig. S11).

Seedling and sapling responses were most often positively associated with TWI, WE and moss cover (Ground 2; Fig. 6, Appendix A Table S3). Seedlings and saplings of several species, such as *B. pendula*, *P. tremula*, and *P. sylvestris*, responded positively to either tree crown defoliation or flame height (Fig. 6). Seedlings were most often negatively associated with slope, HLI, high rock cover and low litter cover (Ground 1; Fig. 6, Appendix A Table S3). Moreover, seedlings of mainly *B. pendula*, *P. tremula*,

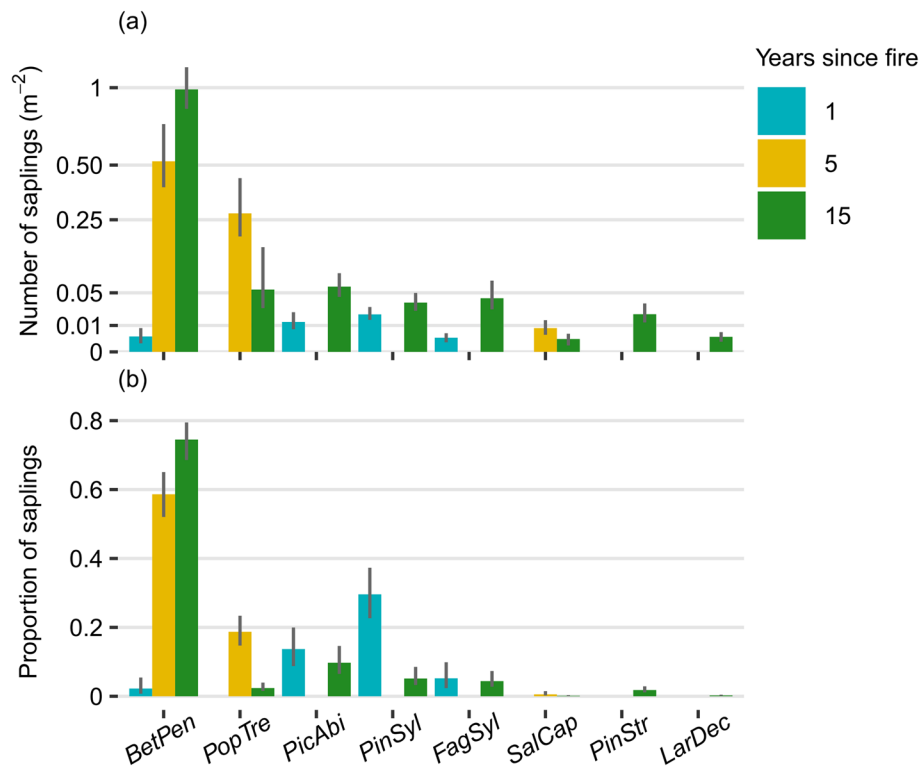


Fig. 3 Observed number of saplings (a) and their proportion of the plot-level total (b) depending on the number of years since fire. Sapling species are ordered on the x-axis from the most to the least abundant based on their proportion of the total sapling sample size during the whole 15-year period after the fire. Sapling data are not available 10 years after the fire. See Fig. 2 for other conventions

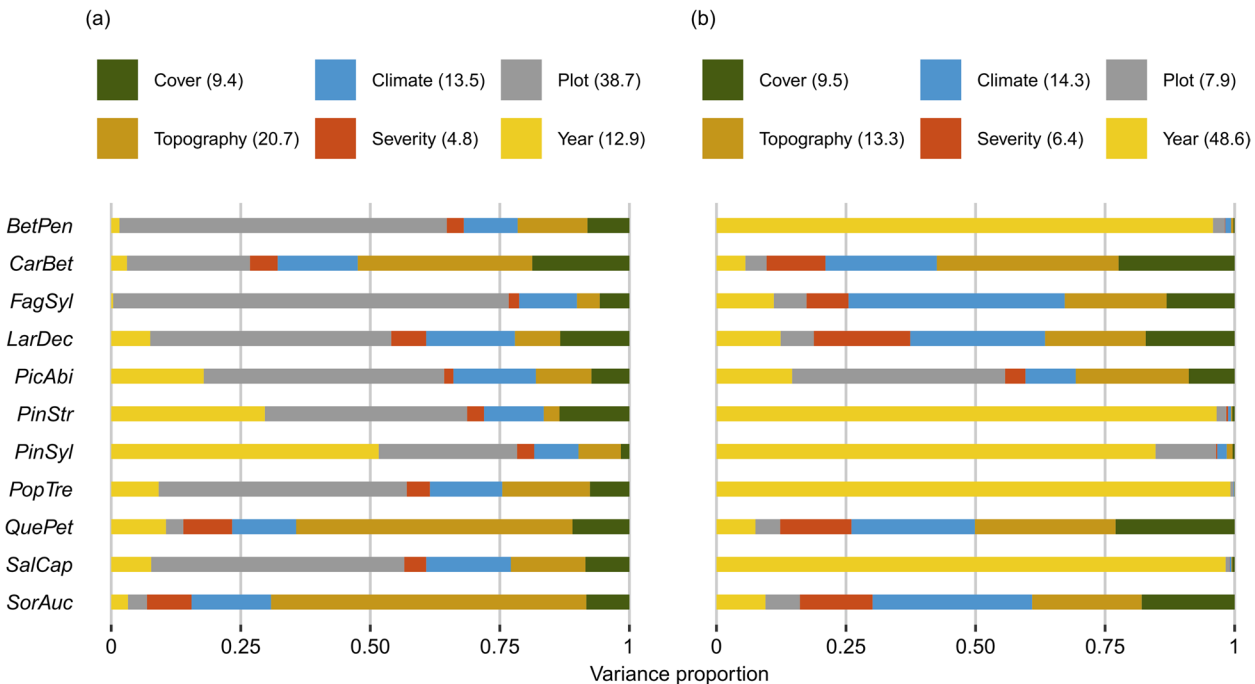


Fig. 4 Variance partitioning into the random effects (plot, year) and different groups of fixed effects for seedling species based on posterior parameter estimates from the JSDMs of presence-absence (a) and abundance (b). Groups of fixed effects follow Table 1. The mean proportion of variance explained by each model component is shown in brackets

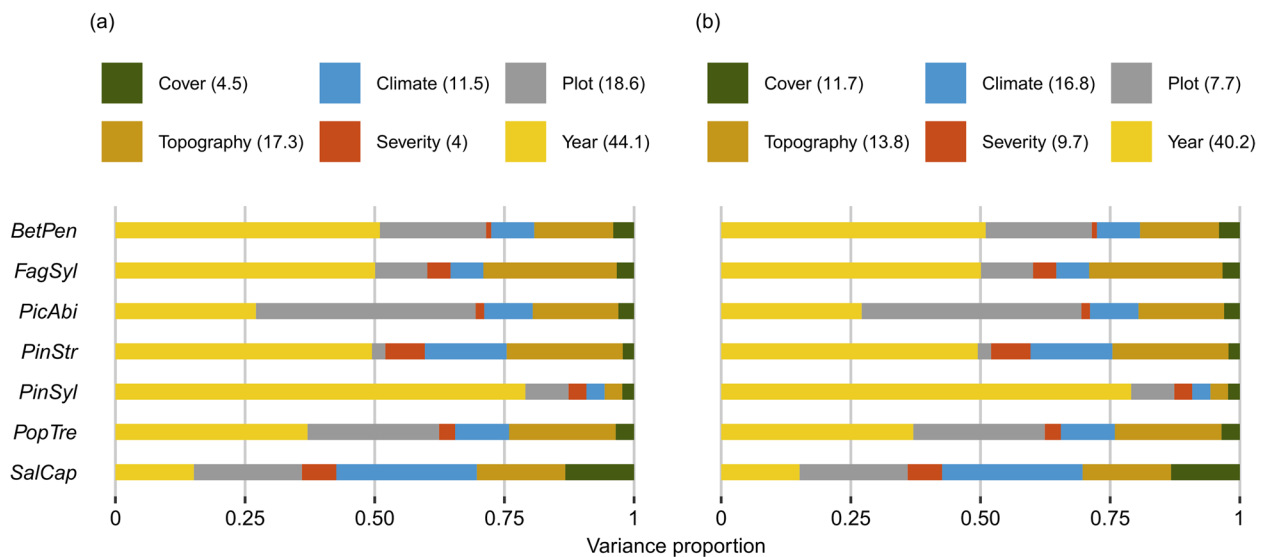


Fig. 5 Variance partitioning into the random effects (plot, year) and different groups of fixed effects for sapling species based on posterior parameter estimates from the JSDMs of presence-absence (a) and abundance (b). Groups of fixed effects follow Table 1. The mean proportion of variance explained by each model component is shown in brackets

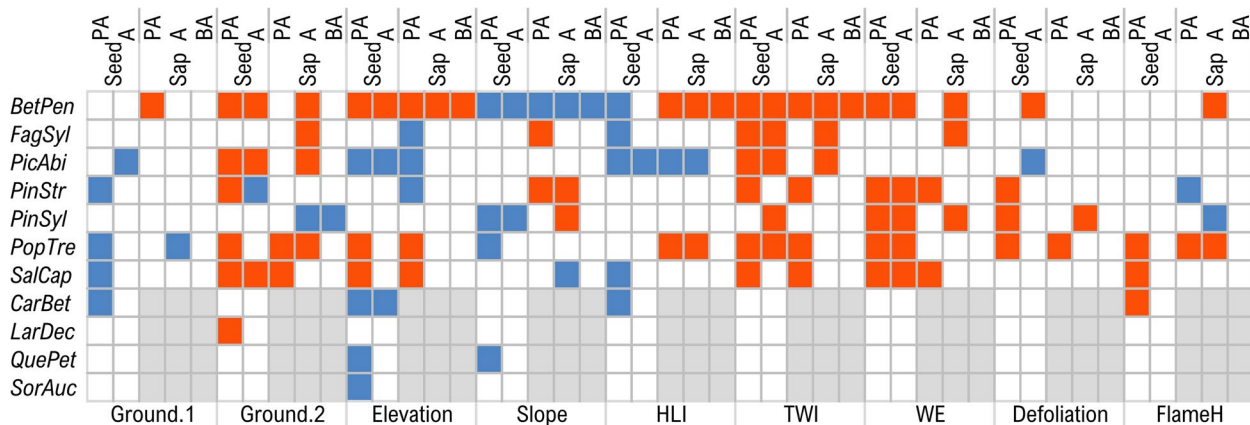


Fig. 6 Seedling (seed) and sapling (sap) responses to environmental conditions for the JSDMs of presence-absence (PA), abundance (A) and basal area (BA). Responses (β parameters) with at least 95% posterior probability of being positive (red) and negative (blue) are shown. Some sapling species responses were not estimated for the lack of data (grey). The full species names are shown in Fig. 2

and *S. caprea* were positively associated with elevation, while those of *C. betulus*, *P. abies*, *Q. petraea*, and *S. aucuparia* responded negatively to elevation (Fig. 6). Depending on tree species, saplings demonstrated both positive and negative responses to elevation, slope, HLI and flame height (Fig. 6, Appendix A Table S3). The basal area of sapling species rarely showed significant response to environmental conditions (Fig. 6).

LGCP models that estimated both environmental conditions and additional sources of tree clustering demonstrated an adequate fit (Appendix A Figs. S12c, f, S13c, f; Table S4), while those models that did not completely

account for these factors showed a lack of fit (Appendix A Figs. S12, S13). The spatial distribution of *B. pendula* saplings was negatively associated with slope based on LGCP models (Fig. 7a), while that of *P. tremula* saplings was positively associated with TWI and elevation (Fig. 7b).

Discussion

Post-fire tree regeneration patterns

Our findings demonstrate the transition of the pre-fire *P. sylvestris*-dominated forest to early successional broad-leaf species, mainly to the post-fire dominant *B. pendula*.

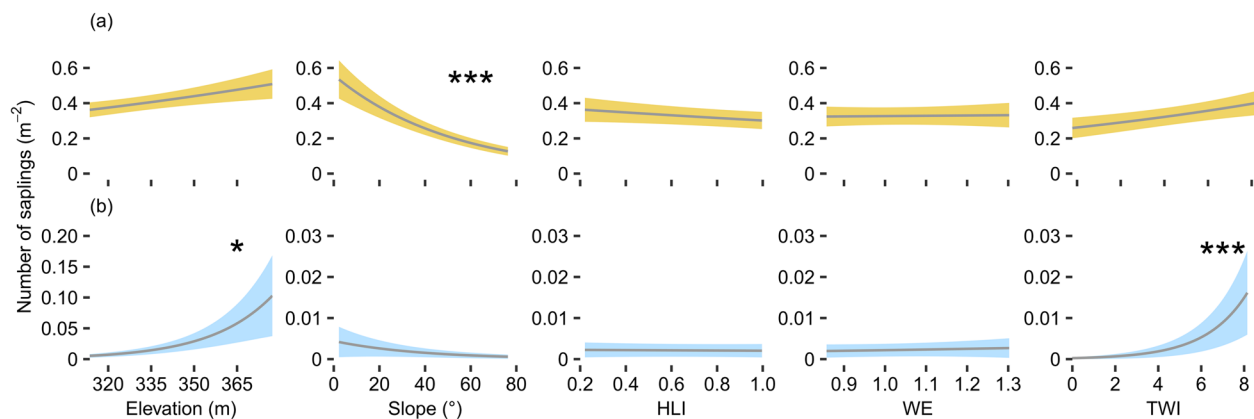


Fig. 7 The effect of environmental conditions on the spatial distributions of *B. pendula* (a) and *P. tremula* (b) represented by the predicted number of saplings per m². The 95% confidence intervals around the estimate (solid line) are shown as outputs of the LGCP models. Significant environmental effects are shown by * and *** for p -values < 0.05 and < 0.001, respectively. Model parameters are shown in Table S3

With almost 10,000 saplings per hectare, it overwhelmingly outnumbered all other species 15 years after the fire. We show that the transition likely did not result from low seed availability or low seedling establishment success of *P. sylvestris* as reported in some Mediterranean regions (Rodrigo et al. 2004; Vilà-Cabrera et al. 2012), because *P. sylvestris*, *B. pendula*, and *P. tremula* seedlings were the most abundant seedling species 5 years after the fire. With approximately 11,000 seedlings per hectare, *P. sylvestris* abundance was comparable (Mantero et al. 2023; Marozas et al. 2007) or even higher than that reported for *P. sylvestris* at different post-fire sites in Europe (Dzwonko et al. 2015; Retana et al. 2002; Schüle et al. 2023; Vilà-Cabrera et al. 2012). *P. sylvestris* began to decline between 10 and 15 years along with most other species at our site, likely due to extensive density-dependent seedling mortality under increasingly shaded canopy conditions (Holík et al. 2021). The early post-fire mortality of *P. sylvestris* trees at our site (Trochta et al. 2012) also rendered *P. sylvestris* establishment in the following post-fire years, which might compensate for abundance losses, rather unlikely. With around 350 saplings per hectare, *P. sylvestris* began to recover 15 years after the fire, following a medium-term recovery trend similar to that of *F. sylvatica* and *P. abies* saplings. Surprisingly, the alien *P. strobus*, a species known to recover well after various types of disturbances (Weyenberg et al. 2004), showed a post-fire trajectory similar to that of *P. sylvestris*. An attempt to remove it from the burned site 10 years post-fire was likely unsuccessful, suggesting it could contribute to future community composition if not effectively eliminated.

In forests where *P. sylvestris* was the pre-fire dominant, several explanations have been proposed for the lack of its post-fire self-replacement. At severely burned sites,

fire can substantially increase the mortality of *P. sylvestris* trees in the first years (Adámek et al. 2016; Trochta et al. 2012) through crown and cambium damage (Fernandes et al. 2008). Moreover, with most *P. sylvestris* seeds falling up to 50 m from seed trees (Mantero et al. 2023; Schüle et al. 2023), seed dispersal from outside the severely burned area can mainly contribute to the establishment of this species at the site's edges (Retana et al. 2002; Vilà-Cabrera et al. 2012). Large burned areas may then be much less colonized by *P. sylvestris*, while early successional broadleaf species usually take over due to their high capacity for yearly seed production, long-distance seed dispersal and resprouting (Schüle et al. 2023; Tiebel et al. 2020, 2019), none of which is typical for *P. sylvestris* (Mantero et al. 2023; Schüle et al. 2023; Vander Wall 2023). The resilience of *P. sylvestris*, as well as many other species, to fire is further limited at dry sites (Donato et al. 2016; Vilà-Cabrera et al. 2012) and by post-fire drought periods (Harvey et al. 2016; Moser et al. 2010).

In addition to the dynamic changes in *P. sylvestris* abundance and size structure, we observed a synchronous decline in the seedling abundance of early successional broadleaves, *B. pendula*, *P. tremula* and *S. caprea*, followed by species-specific levels of sapling abundance build-up during the post-fire period. Indeed, temporal variability (variation between the inventory years) was especially important for seedlings of early successional species, perhaps because these fast-growing species usually experience strong density-dependent thinning in early life stages (Zhu et al. 2018). An increase in *P. tremula* sapling basal area 15 years after the fire suggests that some proportion of *P. tremula* seedlings eventually recruited. On the other hand, a modest increase in *S. caprea* sapling basal area with a recent decline in sapling abundance points to the uncertain role of this species in

the post-fire community and likely reflects the medium-term decline in shade-intolerant tree species after fire (Adámek et al. 2016; Johnstone et al. 2004). Conversely, *B. pendula* seedlings and saplings dominated 10 and 5 years after the fire, respectively, despite its seedlings being less abundant in the first years than those of *P. tremula*. It can be speculated that the decline of *P. tremula* and *S. caprea* could be attributed to a higher deer preference for these species than for *B. pendula* (Bergman et al. 2005; Didion et al. 2009) or perhaps to the higher competitive ability of *B. pendula* (Dehlin et al. 2004). However, our findings do not indicate any negative associations between early successional broadleaves.

Findings from European forests about temporal shifts in post-fire tree regeneration patterns are rather fragmented, with most studies documenting snapshot or short-term forest recovery. However, this is a widespread limitation even in regions where fire is thought to be one of the main drivers of community assembly (Stevens-Rumann and Morgan 2019). Post-fire transitions to broadleaved forests have been documented throughout Europe for different number of years since fire. In line with our findings, *P. tremula* and *Betula* spp. dominated tree regeneration 5 years after fire in hemiboreal forests in south-central Sweden (Gustafsson et al. 2021). However, *P. tremula* seedlings were the most abundant up to 3 years after the fire in a lowland forest in north-eastern Germany (Schüle et al. 2023) and 16 years after the fire in mountainous forests in north-western Italy (Mantero et al. 2024). *B. pendula* was the most abundant species throughout the whole 14-year period following the fire in a lowland forest in southern Poland (Dzwonko et al. 2015). *S. caprea* seedlings dominated 1 year after the fire in boreal forests in central Sweden (de Chantal and Granström 2007). Transitions to broadleaved *Quercus* forests have also been documented 3 years after fire in the Mediterranean (Retana et al. 2002) and are also predicted to replace *P. sylvestris* forests at its southern distribution in the future (Vilà-Cabrera et al. 2012). On the other hand, some studies reported high resilience of *P. sylvestris* to stand-replacing fires in some temperate and boreal forests, showing its seedling dominance in low- and medium-severity patches up to 3 years (Mantero et al. 2023) and 12 years after fires in mountainous forests in north-western Italy (Beghin et al. 2010), up to 4 years after fires in southern Lithuania (Marozas et al. 2007), and 31 years after fire in north-western Russia (Lampainen et al. 2004).

Shifts in seedling and sapling diversity largely reflected compositional and structural patterns in post-fire community throughout the 15-year period after the fire. Seedling species richness and evenness initially increased 5 years after the fire, which can be explained by the

contribution of both surviving pre-fire species and new post-fire colonizing species to community composition (Abella and Fornwalt 2015). The abundance of several species (*P. abies*, *P. sylvestris*, *P. strobus*) increased in these first 5 years and some others appeared for the first time in the seedling assembly (*C. betulus*, *L. decidua*, *Q. petraea*), all contributing to higher seedling diversity. Sapling diversity similarly increased 5 years following the fire. While sapling diversity leveled off between 5 and 15 years post-fire, seedling diversity decreased due to the combination of species' decline and loss. The highest plant species richness has similarly been documented in our study region during the first 6 years after fire (Adámek et al. 2016). Short-term increase in tree seedling diversity was reported at sites with medium-severity fires in mountainous forests in north-western Italy (Mantero et al. 2023). The diversity of different plant groups also increased in the medium-term with time since fire in the western USA (Abella and Fornwalt 2015; Odland et al. 2021).

Environmental context of post-fire tree regeneration

Efforts to identify the range of favorable and harsh habitats for post-fire tree recovery have been central to many studies due to the diversity of implications they can have for post-fire forest management. Using multivariate and spatially explicit modeling approaches, our findings demonstrate that topography-related conditions (elevation, slope, TWI, WE) and moss cover were the most prevalent drivers of tree species responses. Favorable habitats for tree regeneration were indicated by higher site moisture availability (TWI, WE). This effect was broadly pervasive for *P. tremula*, influencing its seedling and sapling responses, and spatial distribution. Soil moisture availability is considered to improve seedling establishment (Petrie et al. 2023). It was an important driver of post-fire vegetation recovery in boreal forests (Jorgensen et al. 2023) and in subalpine forests in North America (Harvey et al. 2016), but conversely played a minor role in tree recovery after bark beetle outbreaks in the US Rocky Mountains (Rodman et al. 2022) and after various types of disturbances in European temperate forests (Cerioni et al. 2024). Higher moisture availability can further be expected in wind-exposed sites due to higher probability of precipitation on windward slopes (Böhner and AntoniĆ 2009). In addition, the positive effects of windward slopes could translate into higher seedling establishment due to the increased input of wind-dispersed seeds. Indeed, prevailing wind direction drives seed dispersal of these species (Wagner et al. 2004), which could elucidate why mainly the seedlings of wind-dispersed species (e.g., *B. pendula*, *P. tremula*, *S. caprea*, *P. sylvestris*) were favored at higher levels of wind exposure. Seedlings and saplings

also benefited from higher moss cover at our site, yet its effect on tree regeneration is generally less consistent, with studies showing no (Moser et al. 2010), positive (Hanssen 2003) and negative effects (Valkonen and Maguire 2005). Some mosses could represent a favorable seedbed for some tree species by indirectly enhancing seedling establishment through moist conditions or the potential effects of preserved mutualistic soil biota (Ibáñez et al. 2022).

Steep slope represented harsh conditions for tree regeneration in our study, perhaps due to the broad array of processes such as soil erosion and runoff (Shakesby 2011). Slope extensively regulated the population of the post-fire dominant *B. pendula*, exhibiting fewer seedlings and saplings, and also less clustered spatial pattern on steeper slopes. This aligns with findings on lower seedling establishment success on steeper slopes after fire (Mantero et al. 2023) and on topographic heterogeneity as a driver of tree species distributions (Shen et al. 2013; Wang et al. 2024). Although species' responses to slope were mostly consistent, it is interesting that steep slope was a limiting factor for *P. sylvestris* seedlings, while it was beneficial for its saplings. This observation largely corresponds with the historical perspective on the *P. sylvestris* position along the environmental gradients of sandstone regions. It suggests that *P. sylvestris* could maintain its dominance at exposed rocky sites throughout the Holocene but became outcompeted in other habitats due to the expansion of several late-successional tree species (Novák et al. 2019). Similarly to our observations, warmer sites (high HLI) negatively affected tree recovery at post-windthrow sites in Europe, suggesting that cooler sites recovered better (Cerioni et al. 2024).

We found the effect of elevation to vary between species. Because lower elevations were also closer to the fire perimeter at our site, we assume that species with larger seeds could spread primarily from outside the burned area (e.g., *C. betulus*, *F. sylvatica*), as indicated by their positive association with these places. The establishment success of early successional broadleaves was conversely greater at higher elevations, i.e. more central parts of the site. These parts initially exhibited the greatest crown defoliation (Trochta et al. 2012). Indeed, we demonstrate that early successional broadleaves were associated with high canopy and ground fire severity, perhaps due to the enormous capacity for seed production, dispersal and more effective soil nutrient exploitation compared to other species (Dehlin et al. 2004; Schüle et al. 2023; Tiebel et al. 2020). Higher establishment of early successional broadleaves at high fire severity sites has been reported throughout temperate and boreal forests (Harvey et al. 2016; Johnstone et al. 2010; Mantero et al. 2023). Higher canopy fire severity (crown defoliation)

was also beneficial for *P. sylvestris* and *P. strobus* in our study, while higher ground fire severity (flame height) was impeding for their saplings. Canopy and ground fire severity might perhaps act independently (Johnstone et al. 2020) and influence tree regeneration of some species through varying biotic and abiotic pathways (Kardol et al. 2023). It is possible that higher ground severity was adverse for *Pinus* regeneration due to impacts on ectomycorrhizal fungi in the soil (Pressler et al. 2019; Su et al. 2022). Mycorrhizal symbionts could be essential for *Pinus* recruitment, but perhaps less important for some early successional broadleaf species (Ibáñez et al. 2022). Their post-fire recovery can conversely be more dependent on the short-term release of soil nutrients from the combustion of organic material (Dzwonko et al. 2015). Previous observations from our and other nearby sites also suggest that the unburned organic soil layers were depleted at higher levels of flame height (Adámek et al. 2016; Trochta et al. 2012), a frequent indication of fire impacts on biotic (Su et al. 2022) and abiotic soil components (Li et al. 2021). It is unclear if a high exposure of mineral soil and low litter cover observed in our study directly indicated high ground fire severity, yet those conditions were adverse for the seedlings of many species at our site. The contrary has often been found in other post-fire contexts, with less litter and more mineral soil being beneficial for tree regeneration (Mallik et al. 2010; Mantero et al. 2023). We assume that litter could be a favorable seedbed for most species by maintaining higher soil moisture (Zhang et al. 2022), because the exposed mineral layers of sandy soils at our site are more prone to drying out and erosion, or may indicate a post-fire lack of soil mutualists (Su et al. 2022), thereby inhibiting tree regeneration.

Conclusions

Our findings from a burned unmanaged temperate *P. sylvestris* forest provide a detailed picture of natural tree species and wider community dynamics over the 15 years following the fire. Due to their enormous capacity to colonize the burned site, *P. sylvestris* and the early successional broadleaf species *B. pendula*, *P. tremula*, and *S. caprea* established to a similar extent during the first 5 years. However, *B. pendula* seedlings and saplings began to dominate 10 and 5 years after the fire, respectively, contributing to the growing evidence on the medium-term post-fire transition of Central European *P. sylvestris* forests to early successional broadleaves (Dzwonko et al. 2015; Moser et al. 2010; Schüle et al. 2023). *P. tremula* and *S. caprea* gradually declined with time since fire, which aligns with the broader medium-term trend of shade-intolerant species decline after fire (Adámek et al. 2016; Johnstone et al. 2004). On the other hand, the synchronized

recovery of *F. sylvatica*, *P. abies*, and *P. sylvestris* saplings 15 years post-fire indicates an initial shift in community structure towards shade-tolerant species (Donato et al. 2016), and partly towards the pre-fire dominant *P. sylvestris*. Future community pathways depend on how these species vary in their contributions to a forest structure currently dominated by *B. pendula*, which is eventually expected to recede in the long term due to its high susceptibility to snow and ice damage in unmanaged stands (Hynynen et al. 2009) or as it reaches senescence (Adámek et al. 2016).

We suggest that exploring these species' unique and wider synchronized trajectories through spatial and temporal co-occurrence patterns could substantially enhance the predictability of future forest composition and have important implications in many post-disturbance contexts. It is essential for setting realistic expectations of the structural and compositional forest recovery through ecological processes across the forested landscape. It is also vital for guiding active restorations, such as tree planting, so that habitat suitability for these efforts can be aligned with an appropriate species composition that follows synchronized post-fire pathways.

Our study highlights the importance of environmental context for post-fire forest recovery in topographically complex regions where tree species' regenerative strategies and establishment success are challenged along wide environmental gradients. Given that sandstone rocky landscapes with *P. sylvestris* forests are currently and historically among the most fire-prone in Central Europe, it is crucial for land managers to thoroughly recognize the key environmental drivers of structural and compositional post-fire recovery in these areas to adapt the most ecological and cost-effective restoration strategies.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42408-025-00374-3>.

Supplementary Material 1

Acknowledgements

The authors thank the many students and colleagues who contributed to the field work, as well as the Administration of the Bohemian Switzerland National Park for their open and helpful support of our long-term research activities. This work was supported by the Ministry of Education, Youth and Sports of the Czech Republic through the e-INFRA CZ (ID:90254).

Authors' contributions

JH, DJ, PŠ, LH, and KK designed the study and collected the data. JH and DJ analyzed the data. JH drafted the manuscript. JH, DJ, PŠ, LH, and KK interpreted the data and provided comments on the manuscript.

Funding

This research was funded by the Technology Agency of the Czech Republic (Grant/Award Number: DivLand SS02030018).

Data availability

The data that support the findings of this study are available from the corresponding author upon 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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Received: 3 December 2024 Accepted: 17 April 2025

Published online: 12 May 2025

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