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Tree regeneration after fire in a hemiboreal mire in the Nature Reserve "Stiklu purvi" in Latvia

Jolanta Ločmele[1], Inese Silamiķele[2], Guntis Brūmelis[1]*

[1]Department of Ecology, Faculty of Medicine and Life Sciences, University of Latvia, Jelgavas 1, Rīga LV–1004, Latvia
[2]Department of Environmental Science, Faculty of Science and Technology, University of Latvia, Jelgavas 1, Rīga LV–1004, Latvia

*Corresponding author, E-mail: guntis.brumelis@lu.lv

Abstract

Fire is one of the major human-caused and natural disturbances in boreal forests. Ecosystems have adapted to this disturbance, but salvage logging is often employed to hasten the establishment and productivity of new stands. Knowledge of the natural regeneration of the tree layer and its relationship with fire intensity, surviving tree cover, the amount of dead wood and soil factors such as the depth of the organic layer may facilitate the identification of the best post-fire management strategy. Information on tree regeneration is quite copious for dry forest types but insufficient for mire complexes. In 2018, a large fire burned an area of 1353 ha with variable intensity in the protected "Stiklu purvi" mire complex, located in the hemiboreal forest zone in Latvia. The aim of this study was to survey tree regeneration in relation to living and standing dead tree basal areas, log volume, tall shrub density, ground vegetation cover and the depth of the organic layer. It was hypothesized that tree colonization would be greater at sites with deeper peat due to a higher water level and less competition by shading. There was a weak effect of habitat type on tree regeneration, but NMS ordination revealed a positive relationship between birch regeneration and the shallow organic layer. Pine regeneration decreased with increasing basal area of surviving trees, indicating a shading effect. The survival of trees was greater in deeper organic soils.

Key words: dead wood, disturbance, post-fire, tree establishment, vegetation.
Abbreviations: AIC, Akaike information criterion; DBH, diameter at breast height; GLM, generalized linear model.

Introduction

In the Holocene, fires caused by natural and human origins were the foremost disturbance to the boreal landscape at multiple scales (Zackrisson 1977; Berglund, Luuluvainen 2021). The active cultural use of fire in agriculture, which causes a high rate of fires of human origin, was followed by fire suppression in the 20th century (Wallenius 2011; Donis et al. 2017; Kitenberga et al. 2019). The more recent increase in fire risk due to climate change has caused increases in fire frequency and intensity (Burrell et al. 2022). The high-frequency fire-promoting cohort forest structure of Scots pine *Pinus sylvestris* is common in poor dry stands, whereas in mesic stands, low-frequency and stand-replacing fires cause dominance of the shade-tolerant Norway spruce *Picea abies* (Aakala et al. 2023). Fire severity and spread depend on the wind speed, topography, air temperature, amount and type of fuel (litter and wood debris) and moisture (Harris, Taylor 2015). Surface fires, as opposed to crown fires, have been prominent in northern Europe (Kuuluvainen, Aakala 2021), resulting in the survival of some trees and cohort regeneration (Berglund, Kuuluvainen 2021). Light fires can destroy only the moss layer, resulting in rapid regrowth of dwarf shrubs (Schimmel, Granström 1996).

The fire regime is characterized by fire frequency, size and severity, which are highly variable at multiple scales (Bergeron et al. 2002) and depend on human, geographical and ecosystem factors. A longer interval between fires can result in the accumulation of fuel, resulting in greater severity (Braziunas et al. 2023), particularly in uplands (Thompson et al. 2017). Thus, fire creates a patchy mosaic of stand structure resulting from differences in burn severity; lowland areas generally have lower fire frequency and severity, but they are not exempt from fire (Wein 1983; Carlson et al. 2011). On peatlands, afforestation might increase the risk of fire (Davies et al. 2013). Post-fire vegetation succession and the establishment of trees depend on the availability of seeds, abiotic factors, and competition (Lingua et al. 2023).

Pine does not develop a soil seed bank, as seeds do not remain viable after one year (Gunnarsson, Rydin 1998; Kuuluvainen, Rouvinen 2000). Therefore, establishment of pine depends on a seed source, as well as favourable conditions such as exposed soil with an ash layer (Schüle et al. 2023). The germination of pine seeds and their establishment requires sufficient moisture, which can be hindered by a moss and organic layer susceptible to drying (Oleskog, Sahlén 2000) and increased water deficit due to climate change retards post-fire tree regeneration (Stevens-Rumann, Morgan 2019). The germination and establishment of pine are also hindered by litter accumulation and competition from shrubs (Zackrisson et al. 1998) and an organic layer (Johnstone, Chapin 2006) and are most successful in exposed mineral soil and well-lit conditions at the ground level in uplands (Rautio et al. 2023).

In peatlands, fires spatially vary in severity, leaving unburnt patches in a mosaic with sites where above ground biomass and the upper organic layer (Zoltai et al. 1998) along with seeds and roots have been combusted (Parro et al. 2015), particularly in smouldering fires on deep peat (Mickler et al. 2017). In peat soils, while pine seed germination can be high, reaching 70% germination (Gunnarsson, Rydin 1998), especially on *Sphagnum* hummocks, establishment can fail because it is overgrown by *Sphagnum* (Ohlson et al. 2001). Thus, the prediction of post-fire establishment of pine on peatlands requires an understanding of the spatial variability of safe microsites, i.e., the regeneration niche.

Post-fire forest management has focused on salvage logging, especially to extract wood resources, while additionally considering that wood removal improves the success of natural or artificial regeneration sites, but studies have shown that depending on the site type, natural regeneration without wood removal is often superior to natural regeneration after salvage logging (Kitenberga et al. 2020) and to planting after salvage logging (Karkliņa et al. 2020). While many studies have been conducted on the effects of fires on tree regeneration at dry sites, less is known about regeneration patterns in mires. These studies have become important, as climate change is expected to further increase the risk of fire, also in previously wet areas of mires (Turunen et al. 2025). The study of post-fire regeneration is particularly important, as a decrease in landscape production as a result of failure of post-fire regeneration has been predicted, which can be further exacerbated due to increased fire risk under climate warming (Cyr et al. 2022). This type of study should entail determining the spatial and temporal variability of regeneration, as well as the controlling mechanisms (Stevens-Rumann, Morgan 2019).

In 2018, in a hot, dry and windy summer period, a fire broke out in the protected "Stiklu purvi" mire complex Natura area, which burned a total of 1353 ha in an area adjacent to an industrial peat extraction site. Owing to poor regeneration, increased fuel loads, impediments to fighting possible future fires, and hazard risk to humans, salvage logging was recommended by forest management authorities, which was not performed because natural ecosystem development is a priority of the Latvia Nature Conservation Agency (https://www.diena.lv/raksts/videunturisms/dabasdiena/stiklu-mezs-pec-ugunsgreka-14206812; https://retv.lv/raksts/svaru-kausos-daba/).

A survey of the burnt wet forest area was conducted in 2023 and 2024 to assess tree regeneration in relation to living and standing dead tree basal areas, log volume, tall shrub density, ground vegetation cover and depth of the organic layer. It was hypothesized that tree survival would be higher in sites with deeper peat due to a higher water level and that colonization would be greater at sites with less competition by shading.

Materials and methods

Site description

The study was conducted in the Sēmes bog and adjacent forest, which is located in the Natura 2000 protected Nature Reserve "Stiklu purvi". The reserve covers a total area of 7244 ha and is the largest mire complex in northwestern Latvia (Anon. 2021). In 2018, a fire erupted, which affected part of the reserve (Fig. 1).

The Nature Reserve "Stiklu purvi" is located in the coastal climatic subregion and has a climate characterized as moderately warm with a cold and long spring, a cool and wet summer, and a warm and long autumn and moderately warm winter. The mean annual temperature is 5.5 to 5.8 °C, and the mean annual precipitation is 700 mm, with the greater part falling in the second half of summer and autumn (Rēriha 2006). Within the Reserve, the raised bogs are surrounded by forest, forming a forest mosaic of varying fertility and moisture conditions from *Pinus sylvestris* on dry soils to swamp forest. Peat forest dominates, but minerotrophic forest on shallow peat occurs at bog fringes. The water table is generally high (Rēriha 2006).

The study was conducted specifically in the Sēmes bog and adjacent burned forest, which also extends outside of the reserve. Part of the bog is used for peat extraction. The peat thickness in the bog is 4 to 5 m (Anon. 2021). In July 2018, a fire erupted within the peat extraction area of Sēmes Bog, and dry and windy conditions facilitated spread into the reserve, covering an area of 1353 ha and extending into wet areas (Anon. 2021) (Fig. 1).

Field data collection

The 10 × 10 m plots were set up at randomly selected sites at the end of March 2024 (four plots) and the end of August 2024 (20 plots) in the raised bog and forest six years after the burn (Fig. 2). The cover percentage of each species was evaluated, as were the cover percentages of total moss, herb, dwarf shrub, and bare ground.

Seedlings in plots that had obviously regenerated after the fire were counted by species. If the number exceeded 100, then the number was recorded as >100. Additionally,

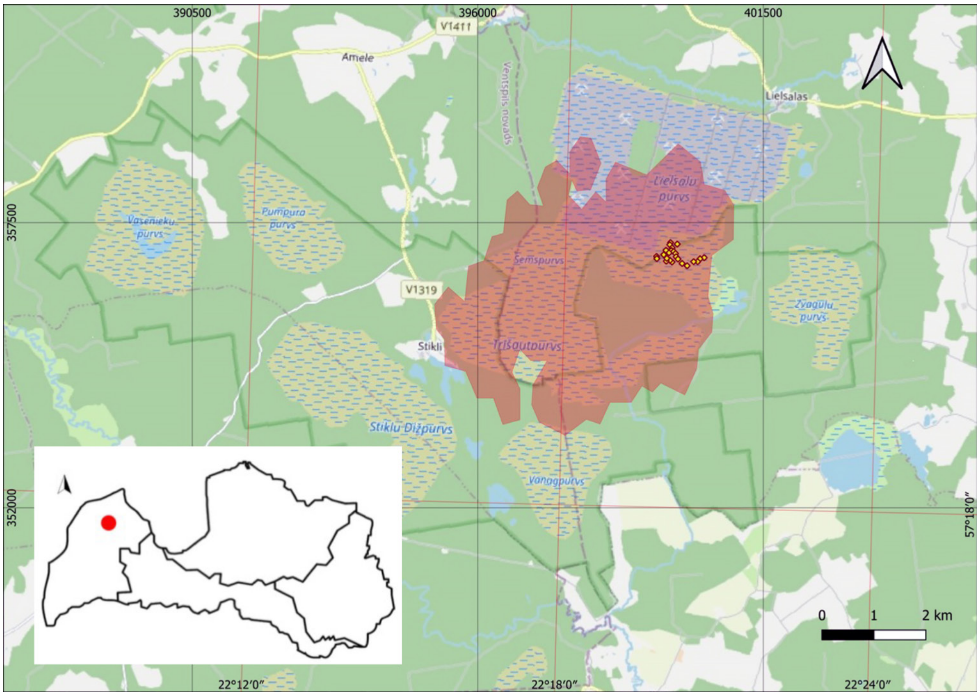

Fig. 1. The area affected by a fire in 2018 in "Stiklu purvi" is shown in red (data from the fire information system Copernicus). The green line denotes the border of the reserve. Yellow dots represent the locations of the study plots. Basemap from OpenStreetmap. The small map shows the location of "Stiklu purvi" in Latvia.

the diameter at breast height (DBH) was measured for all living trees, standing dead trees, snags and logs. The height of the dominant living tree cohort was determined as the mean of three representative living trees with a Suunto clinometer.

A spade or soil auger was used to determine the depth of the organic layer, up to a maximum depth of 120 cm.

Data analysis was conducted using R v. 4.3.1. (R Core Team 2023) unless otherwise specified. The plots were classified into habitat types as raised bogs and for forest plots as treed bogs (*Sphagnosa*), treed swamps (*Caricosa-phragmitosa*), and wet mineral soil forests (*Vaccinio-sphagnosa*) (Fig. 3) on the basis of both the organic layer depth and vegetation, according to the Latvian typology (Liepa et al. 2014), as well as data in the Latvian Forest Register of the State Forest Service.

The relationships between the composition of vegetation and environmental factors (depth of organic layer and basal

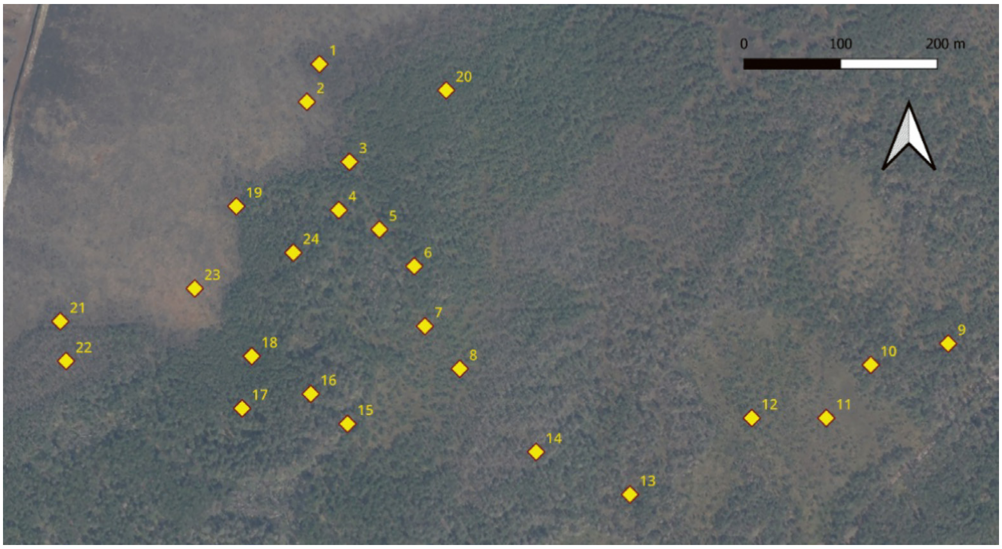

Fig. 2. Locations of the 24 sample plots. The light-colored area at the top left is an open raised bog with scattered small trees. The basemap is from the 8th cycle orthophoto map (Latvian Geospatial Information Agency, 2021 – 2024).

Fig. 3. Study site types in August 2024. A, raised bog; B, treed bog (*Sphagnosa*); C, swamp (*Caricosa-phragmitosa*); D, wet mineral soil forest (*Vaccinio-sphagnosa*).

area of living trees, logs, snags and dead standing trees) were examined via nonmetric multidimensional scaling with the program PC–ORD 7 (McCune, Mefford, 2016). All further analyses were conducted using R (R Core Team, 2023). Owing to nonadherence to a normal distribution, the regeneration of trees (Scots pine *P. sylvestris*, birch *Betula* sp., common aspen *Populus tremula* and Norway spruce *P. abies*) among habitat types was analysed via nonparametric methods. Significant differences were tested via the Kruskal–Wallis test and visualized with box plots. If significant, pairwise tests were performed with the Benjamini–Hochberg procedure.

The effects of the studied environmental factors and dominant understorey species on tree regeneration were tested using a generalized linear model (GLM). Owing to high variance, a negative binomial GLM with a log link was used (glm.nb, MASS package). The parameters were initially checked for multicollinearity via a variable inflation coefficient (car package) to remove parameters with high collinearity (GVIF > 3). The initial model contained all the parameters, and a stepwise approach was used with the Akaike information criterion (AIC) with the stepAIC function to obtain the best model with the lowest AIC. The statistical significance of factors was assessed as $p < 0.05$. Models were developed only for pine and birch because of the low amounts of regeneration of aspen and spruce.

A binomial GLM was used to test the effects of tree diameter and organic layer depth on tree survival (glm function, binomial family). A total of 308 observations of pine (dead or living) were used. Standard model coefficients were expressed as logarithmic log odds to calculate survival probability via the logistic function: $p = \exp(\text{log-odds})/[1 + \exp(\text{log-odds})]$. Statistical significance was defined as $p < 0.05$.

Results

The total number of seedlings in the 10 × 10 m plots ranged from nine to more than 200 (Table 1). A lack of pine regeneration was recorded in two of the 24 plots, whereas the other pine densities were 2 to 35 in plots or 200 to 3500 ha^{-1} (median 800 ha^{-1}). Tree regeneration was dominated by birch, with a mean of 8900 ha^{-1}. Aspen was found in nine plots, with regeneration in a few exceeding 10 000 ha^{-1}. Spruce regeneration was rare.

The mean age of the surviving pines was 74 years (range 25 to 125 years). The mean diameter at 1.3 m height (DBH) for pine, birch and spruce was 12.7, 22.2 and 11.8 cm, respectively. The growth of the trees was low, and even at more than 100 years of age, the DBH was 9 to 37 cm.

The regeneration of trees did not significantly differ (Kruskal–Wallis test) between habitats for pine ($p = 0.729$), aspen ($p = 0.149$) and spruce ($p = 0.084$) (Fig. 4). Habitat type had a significant effect ($\chi^2 = 8.36$, $p = 0.039$) on the regeneration of birch, but there was no significant difference (Wilcoxon rank sum test) between habitat pairs.

The associations between vegetation composition, tree regeneration and surviving and dead tree basal areas, as

Table 1. Stand regenerating and basal trees are the surviving trees. Habitat codes: B, raised bog; TB, treed bog (*Sphagnosa*); TS, treed swamp (*Caricosa-phragmitosa*); WET, wet mineral soil forest (*Vaccinio-sphagnosa*)

Plot	Number of seedlings per hectare					Surviving tree basal area ($m^2\ ha^{-1}$)		Habitat
	Pine	Birch	Spruce	Aspen	Total	Pine	Birch	
1	800	2300	0	8400	11500	0	0	TS
2	300	1100	0	0	1400	0	0	B
3	900	2300	0	6300	9500	11	0	TB
4	1000	> 10000	500	> 10000	21500	3.8	0	WET
5	1200	> 10000	100	2600	13900	6.2	3.8	TS
6	1800	> 10000	0	0	11800	21.3	7.6	WET
7	200	> 10000	0	0	10200	7.2	0.4	TB
8	300	600	0	0	900	11.5	0	TB
9	400	900	400	100	1800	29.4	0	WET
10	200	8900	0	1300	10400	2.1	0	WET
11	1000	> 10000	0	0	11000	4.6	0	TB
12	300	3000	0	0	3300	4.6	0.5	TB
13	600	> 10000	0	0	10600	8.2	0	WET
14	600	> 10000	0	0	10600	0	0	WET
15	500	> 10000	100	> 10000	20600	41.4	0	WET
16	3100	> 10000	300	> 10000	23400	5.3	0	WET
17	200	9200	100	600	10100	47.1	0	TS
18	0	1900	0	0	1900	20.1	0	TS
19	2500	3800	0	0	6300	1.6	0	TB
20	0	1700	0	0	1700	20.3	0	TB
21	3500	3500	0	0	7000	0	0	TB
22	1700	> 10000	0	0	11700	0	0	WET
23	2000	1300	0	0	3300	0	0	B
24	800	> 10000	100	0	10900	20.2	0	WET
Median	800	8900	0	0	10200	5.75	0	

well as organic layer depth, were examined via nonmetric multidimensional scaling (Fig. 5 A and B). The stress level of a 3-dimensional ordination was 11.51, indicating sufficient representation of the data structure. Only the first two axes are shown, as they best explain the associations. A deep organic layer was associated with species typical of bogs such as *Sphagnum* species on the right side of the ordination. Species of mesic forests, such as *Trientalis*

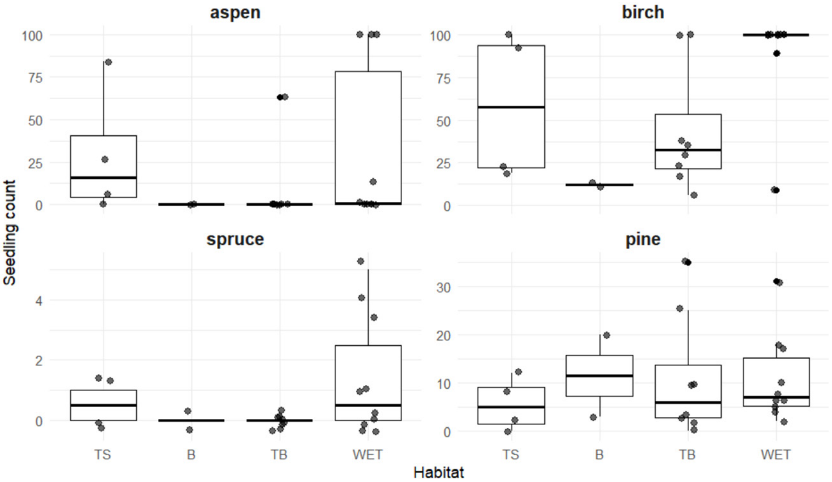

Fig. 4. The number of saplings of each species at each site type is shown as boxplots with medians and interquartile ranges. Habitat codes: B, raised bog; TB, treed bog (*Sphagnosa*); TS, treed swamp (*Caricosa-phragmitosa*); WET, wet mineral soil forest (*Vaccinio-sphagnosa*).

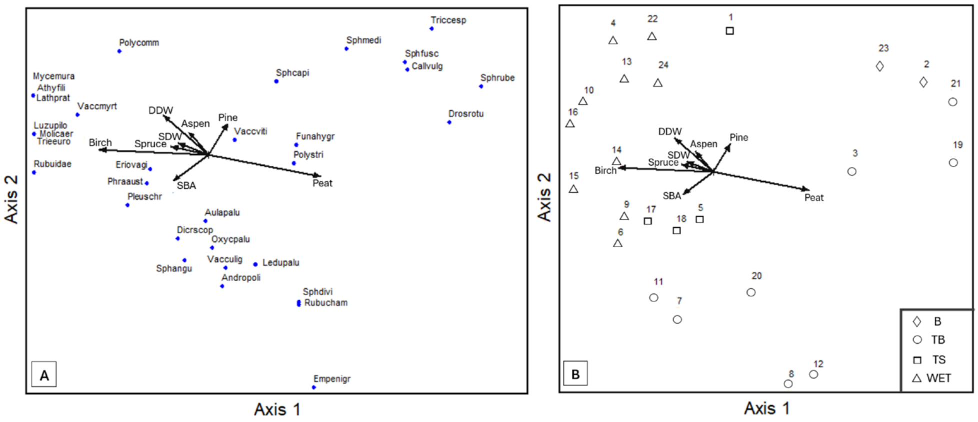

Fig. 5. NMS ordination. A. Species ordination. B. Plot ordination with habitat type. The full names of the species are given in Table S1. DDW, downed dead wood; STD, standing dead wood; SBA, surviving tree basal area; B, raised bog; TB, treed bog (*Sphagnosa*); TS, treed swamp (*Caricosa-phragmitosa*); WET, wet mineral soil forest (*Vaccinio-sphagnosa*). The best predictive GLM for pine regeneration was with the basal area of surviving trees as the only factor (AIC = 162.7), which had a significant negative effect ($p = 0.044$) (Table 2, Fig. 6).

europaea and *Mycelis muralis*, occur on the left side, which is associated with greater birch regeneration. Habitat types formed clusters, from left to right: wet mineral soil, treed swamp, treed bog and raised bog. In the vertical direction, pine was negatively associated with the basal area of living trees, and positively with *Sphagnum* species like *Sphagnum medium*, *Sphagnum capillifolium* and *Sphagnum fuscum*.

GLM showed that pine regeneration was negatively related ($p = 0.044$) to tree basal area (Table 2, Fig. 6). The best GLM for birch regeneration was for the habitat type, showing significantly ($p = 0.006$) lower regeneration in the raised bog habitat (not shown).

Binomial GLM (AIC 370.95) revealed that the survival of pine was significantly positively associated with tree diameter and peat depth ($p < 0.001$) (Table 3, Fig. 7). The estimated probability of survival at the mean DBH (12.7 cm) and organic layer depth (76.6 cm) was approximately 39%.

Discussion

In coniferous forest in Europe, pine and birch are usually the dominant species invading after fire (Schüle et al. 2023). The high amount of birch regeneration can be explained

Table 2. GLM-predicted pine regeneration in relation to the surviving tree basal area. Significance (p) codes: 0, ***; 0.001, **; 0.01, *

Term	Estimate	Std Error	*z* value	*p* value	Significance
Intercept	2.571	0.244	10.553	0	***
Surviving	–2.961	1.471	–2.013	0.044	*

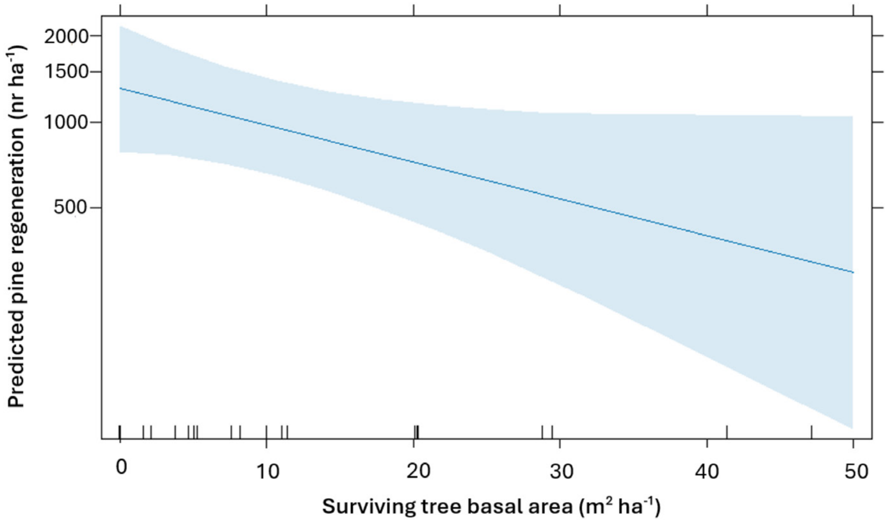

Fig. 6. GLM predicted pine regeneration in relation to the surviving tree basal area (95% CI).

Table 3. Binomial GLM results. Effects of diameter and peat depth on pine survival after fire. Significance (*p*) codes: 0, ***; 0.001, **; 0.01, *

Term	Estimate	Std Error	*z* value	*p* value	Significance
Intercept	−0.434	0.128	−3.402	0	***
Diameter	0.154	0.026	6.017	0	***
Peat depth	0.016	0.003	4.657	0	***

by seed rain from scattered surviving trees and suitable conditions for development due to less shading and removal of competitive vegetation (Dzwonko et al. 2018). The germination and establishment of pine is known to be facilitated by the exposure of mineral soil at dry sites (Rautio et al. 2023) and compact *Sphagnum* hummocks in mires (Brūmelis et al. 2009). In addition to pine and birch regeneration, some establishment of spruce and aspen was observed at the richer sites. However, regeneration was spatially heterogeneous and only partly explained by the studied environmental factors.

Tree regeneration can be affected by competitive vegetation (Sillasoo et al. 2011), soil moisture, the amount of dead wood (Marzano et al. 2013), and distance to the seed source (Schüle et al. 2023). We found a weak habitat effect for birch with birch regeneration, which was associated with the richer habitat in the ordination, but no effect of the studied factors was shown for pine regeneration, perhaps due to interactions between the factors. A negative effect on pine regeneration was observed for the total surviving tree basal area, suggesting an effect of shading on establishment, in contrast with studies showing positive relationship with decreased distance to seed source (Schüle et al. 2023). Thus, while surviving trees supply a seed source, shading can retard establishment (Vacek et al. 2016). The ordination suggested a positive relationship between pine regeneration and cover of *Sphagnum* species that form compact hummocks – *S. medium, S. capillifolium and S. fuscum*. In another mire in Latvia, compact *Sphagnum* hummocks with low dwarf shrub competition were predictive factors for pine establishment (Brūmelis et al. 2009), thus showing interaction of these factors.

However, the organic layer depth and tree DBH had positive effects on pine survival, which is important because these trees act as seed sources (Adámek et al. 2016). The increased survival on deeper organic soils can be explained by wetter conditions that hinder the spread of fire (Grant et al. 2012). Owing to the survival of patches of pine in the mire, as well as tree regeneration, there is no indication of loss of the forest after the fire. In the plots, regeneration was sufficient or greater than that required for regeneration on clearcuts (2000 for pine and 1500 for birch, given in the Cabinet of Ministers regulation 2 May 2012, Nr. 308 “Meža atjaunošanas, meža ieaudzēšanas un plantāciju meža noteikumi”) and/or the basal area was above the minimal level required for a healthy stand and critical basal area that indicates a need for regeneration (Cabinet of Ministers regulation 18 December 2012 Nr. 935 “Noteikumi par koku ciršanu mežā”). For example, for a pine stand with a mean height of 20 m, in normatives, the given minimal basal area is 16 m^2 ha^{-1}, and the critical basal area is 9 m^2 ha^{-1}.

This study has certain limitations, such as low sample size (24 plots), lack of sampling before the burn, and presents only a screenshot of the post-fire succession.

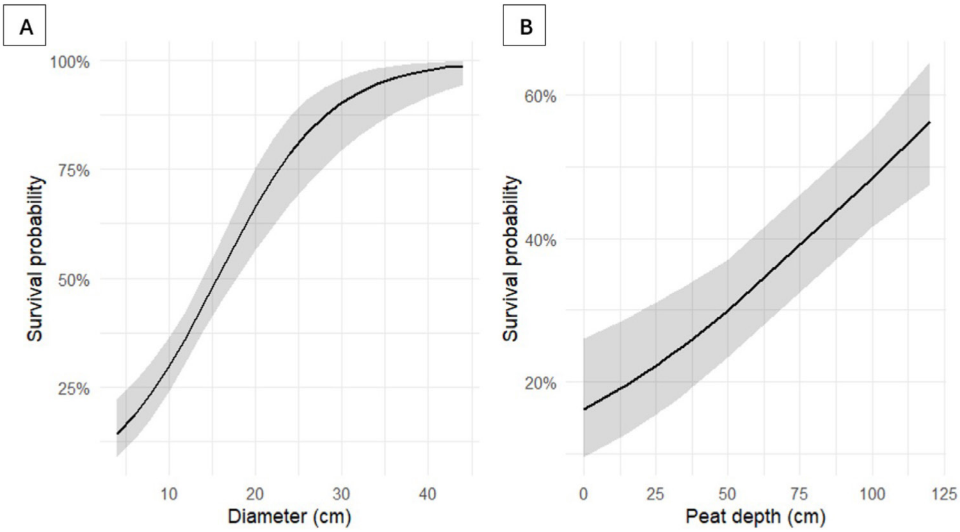

Fig. 7. The GLM predicted pine survival probability depending on tree DBH (A) and organic layer depth (B) with a 95% confidence interval.

However, it is not possible to predict when such a fire will occur to allow planning of such studies. The study does provide baseline data of tree establishment after a fire, and shows that natural tree regeneration was successful, without need for salvage logging and planting. The best type of study in the future would involve the regulation and replication of experimental burns, but the attitude towards human-caused fires as a form of habitat management is extremely negative in Latvia.

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Appendix 1. Full names of the plant species

Species	Code
Herbs and shrubs	
Andromeda polifolia	Andrpoli
Athyrium filix-femina	Atyhfili
Calluna vulgaris	Callvulg
Drosera rotundifolia	Drosrotu
Empetrum nigrum	Empenigr
Eriophorum vaginatum	Eriovagi
Lathyrus pratensis	Lathprat
Ledum palustre	Ledupalu
Luzula pilosa	Luzupilo
Molinia caerulea	Molicaer
Mycelis muralis	Mycemura
Oxycoccus palustris	Oxycpalu
Phragmites australis	Phraaust
Rubus chamaemorus	Rubucham
Rubus idaeus	Rubuidae
Trichophorum cespitosum	Triccesp
Trientalis europaea	Trieeuro
Vaccinium myrtillus	Vaccmyrt
Vaccinium uliginosum	Vacculig
Vaccinium vitis-idaea	Vaccviti
Bryophytes	
Aulacomnium palustre	Aulapalu
Dicranum scoparium	Dicrscop
Funaria hygrometrica	Funahygr
Pleurozium schreberi	Pleuschr
Polytrichum commune	Polycomm
Polytrichum strictum	Polystri
Sphagnum angustifolium	Sphangu
Sphagnum capillifolium	Sphcapi
Sphagnum divinum	Sphdivi
Sphagnum fuscum	Sphfusc
Sphagnum medium	Sphmedi
Sphagnum rubellum	Sphrube

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