Received: 18 May 2020 | Revised: 6 October 2020 | Accepted: 7 October 2020

DOI: 10.1111/jvs.12966

RESEARCH ARTICLE

Journal of Vegetation Science

IAVS

Burn severity and soil chemistry are weak drivers of early vegetation succession following a boreal mega-fire in a production forest landscape

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Co-ordinating Editor: Rune Halvorsen

Abstract

Questions: Do burn severity and soil chemistry drive species and trait composition on recently burned clear-cuttings? Does the spatial distribution of common, easily dispersed colonizers vary with distance to fire perimeter?

Location: A 13,000 ha production forest landscape in boreal southern Sweden burned in a wildfire in 2014.

Methods: Vascular plants and bryophytes were recorded in permanent plots on clear-cuts two and five years following fire, covering a burn severity gradient. Soil carbon content (reflecting burn severity), pH and nutrients were measured at plot level. Trait data were retrieved from the BIEN and LEDA databases and analyzed using community-weighted mean (CWM) trait values. Statistical analyses included generalized linear mixed models (GLMMs), non-metric multidimensional scaling (NMDS) and multivariate ANOVA.

Results: Low burn severity resulted in higher frequency of legacy species (e.g. *Vaccinium myrtillus*), while high burn severity facilitated colonizing species (e.g. *Senecio sylvaticus*). Vegetation varied with soil chemistry, expressed through pH. Species composition changed between years and deviated from unburned clear-cuts. After five years the most common taxa on burned plots were the vascular plants *Chamaenerion angustifolium*, *Betula* spp. and *Populus tremula* and the bryophytes *Ceratodon purpureus* and *Polytrichum juniperinum*. CWM specific leaf area (SLA) decreased markedly with time and root buds increased with total carbon content in the soil (i.e., toward less severely burned plots), while soil pH was not associated with any studied trait. *Chamaenerion angustifolium* decreased with distance to the fire perimeter, while *Ceratodon purpureus* increased.

Conclusions: Burn severity and soil pH weakly drive vegetation dynamics in the early phase following fire on clear-cuts, indicating a large influence of stochastic processes. Deciduous trees are common already after five years and their further expansion will affect light and nutrient availability. To understand future vegetation trajectories on

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burned clear-cuts, studies need to incorporate the light factor and links between tree species' identity and soil nutrient availability.

KEYWORDS

bryophyte, *Chamaenerion angustifolium*, clear-cut, disturbance, fire, production forest, *Senecio sylvaticus*, succession, Sweden, traits, *Vaccinium*, vascular plant, vegetation

1 | INTRODUCTION

Fire is a main disturbance agent in boreal forests, giving rise to large variations in disturbance extent and severity, depending on site conditions and the landscape context (Kuuluvainen, 2009; Shorohova et al., 2011). Forest species are adapted to the pulse and intensity of disturbance events and processes that follow them, and insight into disturbance dynamics is essential for the understanding of species patterns in time and space (Pickett & White, 1985). Ground vegetation is an important part of forest ecosystems that controls tree regeneration and nutrient cycling. Nevertheless, post-fire successional trajectories in boreal forests are still poorly understood, particularly in managed forests. Studies on post-fire succession have mainly been performed in North America (e.g. Turner et al., 1999; Donato et al., 2009; Romme et al., 2016), while only a handful have been conducted in north Europe (e.g. Uggla, 1958; Uotila & Kouki, 2005), of which all are chronosequence studies (i.e., using space-for-time substitution). A knowledge gap for boreal Europe is also evident regarding the links between post-fire ground vegetation and soil chemistry. Here we present a post-fire vegetation time series from Sweden across a boreal production forest landscape to investigate the early succession phase after fire.

Fire is an important driver of natural selection and plant adaptations to fire including traits related to dispersal, regeneration and growth are widespread in fire-prone ecosystems (Pausas & Keeley, 2019). Plants with specific traits may be selected by fires of different severity. As a result, burn severity becomes an important modulator of vegetation succession (Turner et al., 1997). For instance, the temperature at which rhizomes and other tissues are harmed is lower compared that for seeds in the seed bank (Granström & Schimmel, 1993). Very hard burns may cause local extincitons of practically all species, also in the seed bank (Schimmel & Granström, 1996), with the implication that species colonizing the site (seeds, spores and other diaspores) will determine the successional trajectory. Schimmel and Granström (1996) provide a conceptual trait model, suggesting that pioneer species will increase and rhizomatous species will decrease with consumption of organic material while seed bank species will have a unimodal response, promoted by intermediate disturbance severity. Life-form response to burn severity was also evident in a Finnish restoration experiment in which evergreen dwarf shrubs and forest mosses decreased, and pioneer mosses increased with burn severity while intermediate severity promoted herbs and grasses (Hekkala et al., 2014). These studies suggest that examination of species' traits related to dispersal (e.g. seed weight) and regeneration (root buds, seed bank) may assist our understanding of post-fire recolonization patterns under variable fire severity.

Fires often drastically alter the chemical, physical and biological properties of the surface soil (Certini, 2005). Combustion of the organic layer is the most obvious effect and burn severity determines the degree of change. The formation of ash and charcoal causes a strong basic reaction and a sharp increase in pH, occasionally up to 2–3 units (Viro, 1974; Úbeda et al., 2005). The concentration of inorganic N, the most prominent nutrient for plant growth in boreal forests, often increases considerably, as do P and base cations (Certini, 2005). The pulse of water-soluble ions such as nitrate is transient and their concentrations successively return to background levels (e.g. Antos et al, 2003). Although few studies deal with links between vegetation and soil chemistry following forest fire, variations of soil pH and nitrogen have been found to affect post-fire community composition including individual species (e.g. Driscoll et al., 1999; Hollingsworth et al., 2013).

A mega-fire (sensu Stephens et al., 2014) hit south-central Sweden in 2014. It was the largest fire in Sweden for at least one hundred years, covering about 13,000 ha, in parts with very high burn severity (above-ground and below-ground organic matter consumption from fire; Keeley, 2009). About half of the affected area has been set aside as a nature reserve, offering an unusual opportunity in boreal Europe to study natural vegetation succession over a large area that covers the gradient in burn severity (Figure 1). Before the fire, the area was a typical production forest landscape of Fennoscandia, dominated by even-aged stands of *Pinus sylvestris* regenerated after clear-cutting (Gustafsson et al., 2019). Here we focus on burned clear-cuts to exclude the influence of light, a strong driver of vegetation dynamics (Tilman, 1985; Penone et al., 2019), varying markedly after fire due to differences in the size and density of standing dead trees. Furthermore, clear-cutting minimize the risk that trees fall and harm study plots, and guarantee long-term accessibility to plots, which enables vegetation surveys to be performed over decades.

Our overall aim is to increase the knowledge on vegetation dynamics following fire in boreal production forests shaped by clear-cutting. We report on vegetation dynamics the first five years after a large and intense fire, focusing on links to burn severity and soil chemistry (e.g. pH). The summer after the fire, we established permanent plots that covered a burn severity gradient, and recorded vegetation the second and fifth year after the fire. Our predictions are: (i) that in this early phase, burn severity and soil chemistry are the most important drivers of vegetation dynamics; (ii) that on severely burned soils, species with traits associated with rapid

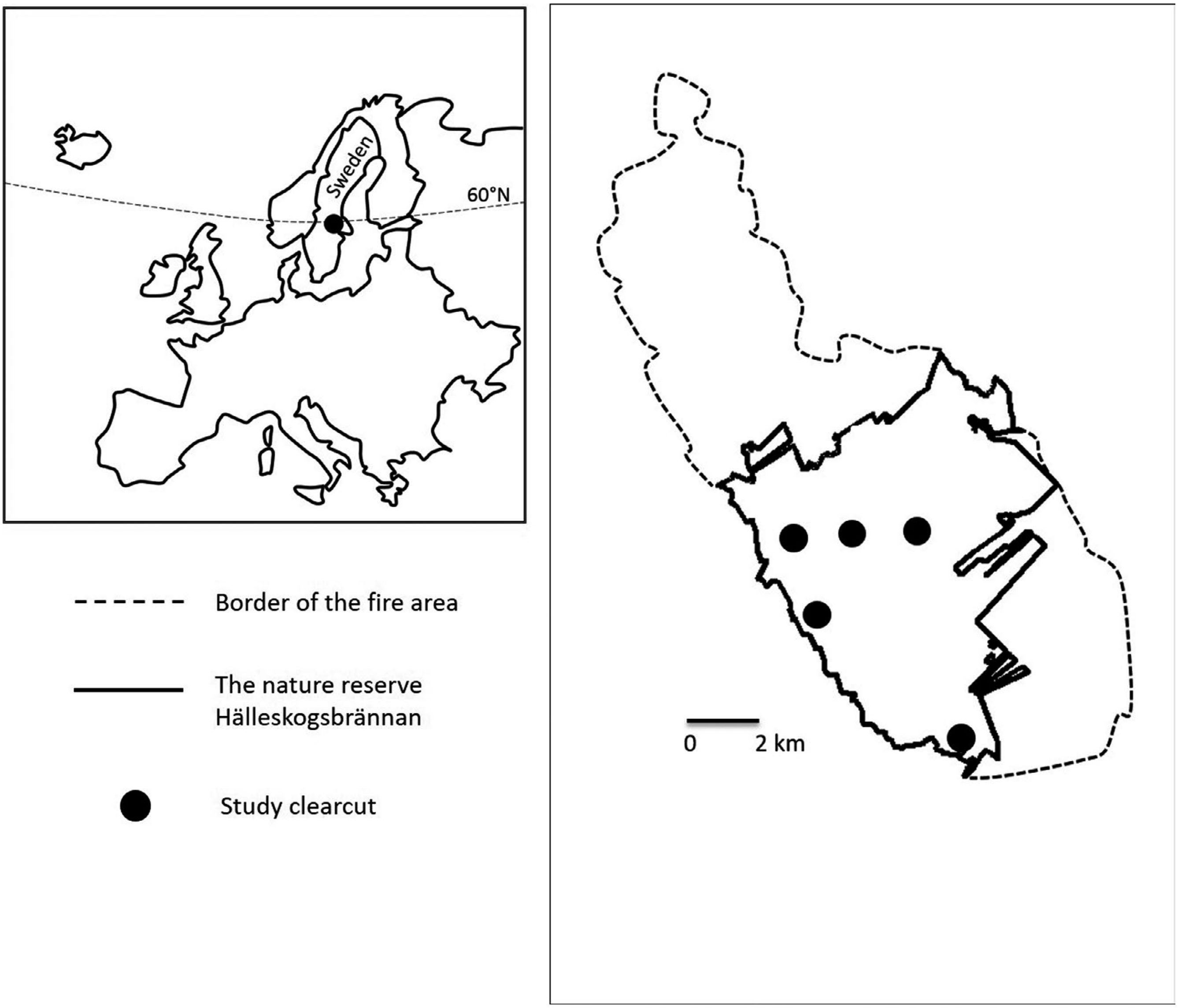

FIGURE 1 Geographic position and geometry of the Västmanland fire area, the nature reserve in which the study was conducted, and location of the studied clear-cuts

dispersal and fast growth will prevail, while on lighter burns species surviving below-ground will dominate; (iii) that soil chemistry has a detectable effect mainly through availability of easily accessible nutrients; and (iv) that easily dispersed colonizers will have an even distribution over the fire-affected area because of a homogenous seed rain, regardless of distance to the fire border.

2 | METHODS

2.1 | Study area

The fire area is located at the border between the hemi-boreal and south boreal regions (Ahti et al., 1968), in the county of Västmanland (59.8° N, 16.1° E), south-central Sweden (Figures 1, 2). Here the large wildfire occurred in late July–early August 2014. Remote-sensing analyses show that > 90% of the soil cover was affected by the fire, that crown fire occurred in 21% of the area, and that tree crowns with > 50% damage occurred on about half of the area (Nilsson et al., 2014). Even-aged production forests dominated by *Pinus sylvestris* covered 75% of the area before the fire (information from forestry company databases). These forests were managed through clear-cutting forestry with a rotation time of 80–100 years. In this part of Sweden, forests have been intensively used for centuries, originally to supply charcoal for the iron industry but since the 19th century gradually for forest industry purposes (Brynte, 2002). The landscape also contains mires, lakes, roads and a few small nature reserves (Gustafsson et al., 2019). The mean annual temperature in the area was 6°C for the period 1987–2016, and the mean annual precipitation in this period was 687 mm (http://luftwebb.smhi.se/). The elevation ranges between 60 m and 180 m. The geology is representative of most

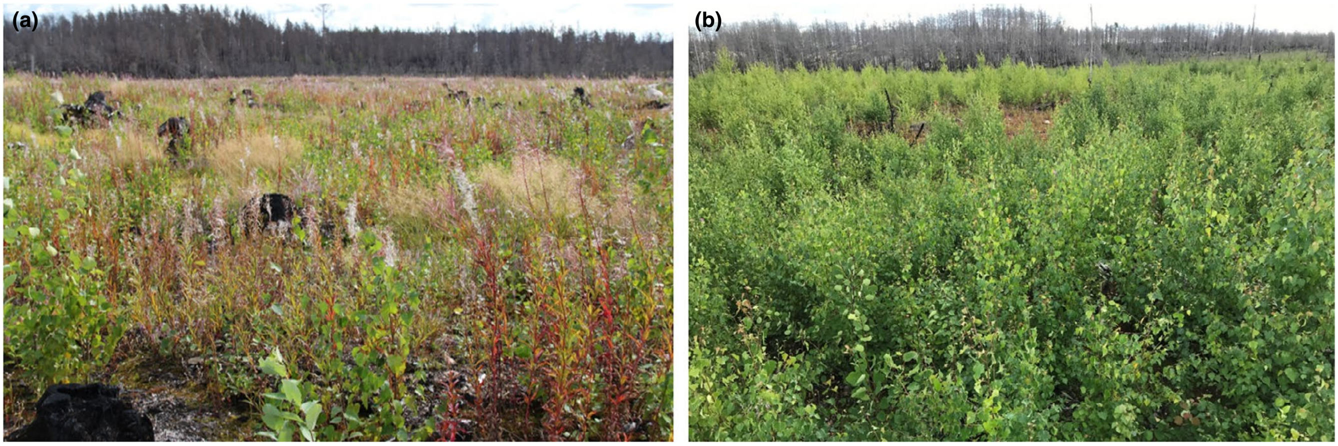

FIGURE 2 One of the studied clear-cuts. (a) In year 2016, two years after the fire, with *Chamaenerion angustifolium* and *Senecio sylvaticus* as dominant species. (b) In year 2019, with rapid regeneration of deciduous trees, mostlywith *Betula* spp. and *Populus tremula*. Photos: Lena Gustafsson

of boreal Sweden, with bedrock dominated by granite and pegmatite, quaternary deposits dominated by moraine interspersed with peat and shallow soil cover on rock, with podzol soils prevailing (https://www.sgu.se/en; Jansson, 2011). The study took place within Hälleskogsbrännan, a nature reserve covering 6,500 ha, established by the government following the fire (Figure 1).

2.2 | Selection of stands

Potential stands were selected from databases of the forestry companies Sveaskog, Bergvik and Karl Hedin AB using the following criteria: (a) <6 years between clear-cutting and the fire; (b) an intermediate productivity index (T20–T26), which is the most common pine forest site condition in Sweden as well as in the county of Västmanland (Swedish Forest Agency, 2014); (c) >1 ha in size; and (d) >50 m from unburned forest. Additional criteria for stand selection after field inspection were: (e) high fire-induced mortality of above-ground vegetation; and (f) within-stand variation in burn severity, from very severe with all humus combusted, exposing ash-covered mineral soil, to low severity with only the uppermost part of the humus layer combusted. Five stands were identified fulfilling all criteria, varying in size between 8.1 and 22.2 ha, with a mean of 13.7 ha. The closest distance between each plot and the fire perimeter polygon was estimated by use of georeferenced data in QGIS 10.3.1 (QGIS Development Team, 2019). The plot-level distances were averaged to obtain the stand-scale distance.

2.3 | Selection of study plots

In each stand, we established 16 permanent plots (50 cm × 50 cm) covering a gradient of burn severity, i.e., 80 plots in total in the five stands. The selection was a random subset from a large number of potential plot locations (>100 for each stand) fulfilling the following criteria: (a) >90% ash cover; (b) >10 m from forest with tree height > 10 m; (c) no boulder >50 cm high within a 2-m radius; (d) no dead standing trees >10 m tall within 5 m in direction SE–S–SW; (e) flat ground with mesic soil; (f) ground not affected by soil scarification; (g) mineral soil depth on average >2 cm (measured at five spots in the plot with a thin measuring rod); and (h) >5 m to the closest-situated plot. Criterion (a) was applied to avoid fire refugia, criteria (b–d) ensured that shade effects were avoided (although clear-cuts were used these could contain dead seed trees as well as dead trees retained for biodiversity conservation purposes); criterion (e) minimized site-driven variation in species composition; criterion (f) was enacted to avoid effects of the removal of the organic layer by forestry machines; criterion (g) ensured that rocky surfaces with very shallow soil were not included, and criterion (h) minimized spatial dependence between plots. Measurement of carbon content (cf the subsequent soil analysis) provided quantitative estimates of burn severity for each plot. The within-stand maximum distance between plots ranged between 148 m and 525 m, and the mean distance between plots ranged between 42 m and 242 m, for the five study stands.

2.4 | Vegetation surveys

Each study plot was divided into 16 equally sized sub-plots (12.5 cm × 12.5 cm), in each of which the occurrence of all species of vascular plants and bryophytes was recorded. Subplot frequency on a 0—16 scale was used as a measure of species abundance in plots. Total plant cover (in %) in each plot was registered for vascular plants and bryophytes, respectively, using a scale with levels 0, 0%–1%; 1%–5%; 5%–10%; 10%–20%…and in intervals of 10% up to >90%. Vegetation was recorded in July and August 2016 and July 2019. Nomenclature for vascular plants follows Krok et al. (2013) and for bryophytes Hallingbäck (2016). The term "species" is used throughout although some species were aggregated to higher taxa, e.g. *Betula* spp. which includes *Betula pendula* and *Betula pubescens*.

2.5 | Soil chemistry

Soil sampling was performed in September 2016, i.e., two years after the fire, to avoid strong peaks in pH and soluble-ion concentrations commonly occurring directly following fire. For each vegetation plot, one bulk soil sample was obtained by merging 12 cores (diameter = 6 cm, depth = 5 cm), taken 30 cm–40 cm outside plot edges; three cores outside each of the four edges. We sampled the top 5 cm because roots of ground vegetation are concentrated in this soil layer (Persson & Stadenberg, 2009), and, accordingly, the chemical conditions in this layer are considered as most decisive for plant re-establishment.

Bulk soil samples were kept cool in a refrigerator (+2°C) awaiting further handling, then weighed, sieved through a 4-mm mesh, and thoroughly mixed. Samples dried at room temperature were used for measurement of organic C and N using a Leco TruMac CN analyzer (Leco Nordic AB, Leco corporation, Täby, Sweden). Refrigerator-stored samples were used tor determine: (a) dry weight (105°C); (b) pH (1:5 fresh soil:water by volume); (c) Na, K, Ca, Mg, P extracted with 1 M ammonium lactate (pH 3.75), analyzed using a Perkin Elmer Avio 200 (LAB Analytical Nordic AB, Farsta, Sweden); and (d) NH_4^+ and NO_3^- using 1 M KCl extraction, and analyzed colorimetrically on a Seal Analytical AA500 autoanalyzer (Seal Scandinavia AB, Älvsjö, Sweden).

Due to strong correlations among soil chemistry variables (Appendix S2), we selected two only weakly correlated variables ($r = -0.24$) for all further analyses: total carbon content (soil total C) as a measure of burn severity, and pH, a major correlate of plant community composition (Pärtel, 2002).

2.6 | Plant traits

Species' trait values for vascular plants were extracted from the trait databases BIEN (Enquist et al., 2009), using the R package BIEN (Maitner, 2020), and from the LEDA database (Kleyer et al., 2008). The following species traits were extracted: diaspore mass (mg), specific leaf area (SLA, $m^2\ kg^{-1}$), bud vertical distribution (here we selected root buds, which is the number of buds 0 cm–10 cm above- and 10 cm–0 cm below-ground), and seed longevity (three-level index). Diaspore mass is related to long-distance dispersal ability (seeds with lower mass have higher probability to spread longer), number of root buds indicates the ability to regenerate vegetatively after fire, seed longevity is related to potential presence in the seed bank (re-establishment by germination), and SLA is associated with nutrient acquisition and growth rate in a post-disturbance setting (high SLA means high growth rate). For diaspore mass and SLA, we extracted trait values from the BIEN database, complemented with traits for a few species that were only found in the LEDA database. For root buds and seed longevity the LEDA database was used. Species names were cross-checked (including checking for synonyms), and the trait data were closely examined for our most common species, i.e., species with high weight in our analyses, to ensure that they were based on a high number of studies of which the most influential were made in a relevant geographical area. Finally, species trait means were calculated by averaging over all studies in the database. For a few species, the genus-level mean was used for diaspore mass and SLA. The two species of ferns were not included in the diaspore trait analyses as their spore weights are several orders of magnitude lower than weights of the diaspores of other plants.

2.7 | Statistical analyses

To test if species diversity (species richness and Shannon diversity index) differed between years we used generalized linear models (GLMs; Bolker et al., 2009) with year as explanatory variable. For species richness, we used a Poisson error distribution (GLM with a log-link function) and for the Shannon diversity index we used a normal error distribution (GLM with identity-link function). We tested if the two diversity measures were explained by soil total C, pH and distance to the fire perimeter using the same modeling approach.

To describe the general plant species composition and changes over time we performed a global non-metric multidimensional scaling (GNMDS) ordination on plant frequency data (0–16). To facilitate visual interpretation we only included species recorded in >7 plots and we obtained a two-dimensional NMDS solution. The NMDS was performed using the metaMDS function in the R package vegan (Oksanen et al., 2013) using the Bray–Curtis dissimilarity index. The convergence criterion (sfgrmin parameter) was set at default (10–7) and we ran multiple starting configurations to convergence (maxit = 1,000, trymax = 1,000). Relationships between species composition (as summarized by the two-dimensional NMDS) and explanatory variables — soil total C (burn severity), pH, distance from fire area border, and year — were assessed with multivariate ANOVA (function adonis in vegan). To test if the beta diversity increased between 2016 and 2019 we also performed a permutation test of homogeneity of multivariate dispersion (function betadisper; Anderson, 2006). To test if the same explanatory variables were associated with the occurrence of the dominant species (recorded in >14 plots) we fitted GLMs. Separate models were fitted for each year with a negative binomial error distribution to account for over-dispersion. To test the relationship between plant traits and the explanatory variables (year, soil total C, pH and distance) we calculated community-weighted mean (CWM, Sonnier et al., 2010) trait values for each trait, plot and year (i.e., plot-level trait values weighted by species occurrence frequency). We then regressed CWM values against our explanatory variables using generalized linear mixed models (GLMMs) with a normal error distribution and to account for temporal intra-plot dependence resulting from plots sampled two times (two years) we included plot id as a random effect. To facilitate interpretation of our GLMM results we present the model with the lowest Akaike information criterion (AIC).

We used NMDS and multivariate ANOVA (see above) to compare burned and unburned clear-cuts. Data on unburned clear-cuts, taken from Johansson et al. (2020), see also Appendix S1, comprised

TABLE 1 Vascular plants, bryophytes and vegetation cover

	2016		2019	
	Subplot occupancy	Plot occupancy	Subplot occupancy	Plot occupancy
Vascular plants				
Agrostis capillaris	0.00	0.00	0.01	0.04
Betula spp.	0.03	0.13	0.16	0.31
Calamagrostis arundinacea	<0.01	0.01	0.02	0.06
Calluna vulgaris	0.03	0.08	0.06	0.11
Carex leporina	<0.01	0.01	<0.01	0.01
Carex pilulifera coll	0.03	0.14	0.03	0.09
Chamaenerion angustifolium	0.43	0.94	0.27	0.81
Cirsium vulgare	<0.01	0.01	<0.01	0.01
Deschampsia flexuosa	0.04	0.14	0.14	0.28
Luzula pilosa	0.01	0.08	0.01	0.05
Maianthemum bifolium	<0.01	0.01	<0.01	0.01
Melampyrum sp.	0.00	0.00	<0.01	0.01
Picea abies	0.00	0.00	<0.01	0.01
Pilosella cymosa	0.00	0.00	<0.01	0.01
Pinus sylvestris	0.02	0.08	0.04	0.16
Populus tremula	0.01	0.08	0.10	0.30
Pteridium aquilinum	0.00	0.00	<0.01	0.01
Rubus idaeus	0.04	0.13	0.04	0.15
Rumex acetosella	0.01	0.01	0.01	0.03
Salix caprea	<0.01	0.04	0.02	0.08
Senecio sylvaticus	0.13	0.59	<0.01	0.03
Taraxacum vulgare	0.00	0.00	<0.01	0.01
Vaccinium myrtillus	0.06	0.21	0.06	0.16
Vaccinium vitis-idaea	<0.01	0.01	0.03	0.09
Veronica officinalis	<0.01	0.01	0.00	0.00
Bryophytes				
Ceratodon purpureus	0.48	0.75	0.71	0.94
Marchantia polymorpha	0.02	0.08	0.00	0.00
Polytrichum juniperinum	0.13	0.49	0.43	0.73
Mean cover (%)				
Vascular plants	23.59	18.91		
Bryophytes	27.44	41.14		

Proportion of occupied subplots and plots of species recorded in the survey years 2016 and 2019. A total of 80 plots and 1,280 subplots were surveyed each year. Mean percentages per year are given for estimated cover at plot level of vascular plants and bryophytes as groups, respectively.

vegetation recorded in 15 unburned reference clear-cuts adjacent to the burned area (27 plots per clear-cut, $N = 405$). As the plot size used in Johansson et al. (2020) was larger (radius = 3 m) and species abundance was recorded as total cover (%), we chose to exclude rare species (occurring in less than 10% of the plots in each data set) and ran the analyses on presence/absence data. A two-dimensional NMDS was obtained using the same options and settings for these options as above, and the multivariate ANOVA only included treatment (burned or unburned) as explanatory variable. To identify which species contributed most to the differences in species composition between burned and unburned clear-cuts we performed an indicator species analysis (Dufrêne & Legendre, 1997) using the indval function in R package labdsv (Roberts, 2019).

3 | RESULTS

3.1 | Species diversity, dominant species and vegetation cover

Two years after the fire (2016), we found 19 vascular plant species and three bryophyte species; after five years (2019) 24 vascular plant species and two bryophyte species were found. A total of 25 vascular plant species and three bryophyte species were recorded. *Veronica officinalis* and *Marchantia polymorpha* occurred in 2016 only, and *Agrostis capillaris*, *Melampyrum* sp., *Picea abies*, *Pilosella cymosa*, *Pteridium aquilinum* and *Taraxacum* sp. occurred in 2019 only (Table 1). Neither species richness nor Shannon diversity were explained by year or by any of the recorded environmental variables. The most common vascular plant species in 2016 were *Chamaenerion angustifolium* (average plot frequency 0.94) and *Senecio sylvaticus* (0.59), in 2019 *Chamaenerion angustifolium* (0.81), *Betula* spp. (0.31) and *Populus tremula* (0.30). The bryophytes *Ceratodon purpureus* and *Polytrichum juniperinum* dominated both survey years with plot frequencies in 2019 of >0.9 and >0.7, respectively. The largest recorded between-year changes for vascular plants were plot frequency increases of 0.22 for *Populus tremula*, 0.18 for *Betula* spp. and 0.14 for *Deschampsia flexuosa*, while the largest decreases were −0.56 for *Senecio sylvaticus* and −0.13 for *Chamaenerion angustifolium*. The cover of vascular plants decreased somewhat between the first and the second survey year (from 24% to 19%) while bryophyte cover increased (from 27% to 41%). None of these cover changes were, however, significant.

3.2 | Soil chemistry

Soil chemistry varied considerably among plots. Total C ranged from nearly 50%, approaching the content of unburned organic material, to 2%, indicating almost complete combustion of the organic soil layer. Soil pH varied from 4 to just above 7. Many plots had high concentrations of inorganic N (Table 2). Several soil chemistry variables were strongly correlated, e.g. pH with base cations ($r = 0.45$), P ($r = 0.76$) and NO_3^- N ($r = 0.46$) (Appendix S2).

3.3 | Environmental drivers of community composition and dominant species

NMDS results revealed a significant change in community composition of vascular plants between 2016 and 2019. The permutation test of homogeneity of multivariate dispersion ($F = 31.3$, $p < 0.001$) revealed increasing among-site heterogeneity (i.e., beta diversity) with time (Table 3, Figure 3). Community composition was weakly explained by pH and soil total C (Table 3). Among species occurring in at least 15 plots (outlined in Table 1), *Vaccinium myrtillus* increased with soil total C in 2016 and *Chamaenerion angustifolium* in 2019, while *Senecio sylvaticus* decreased with soil total C in 2016. *Senecio sylvaticus* increased with pH, and *Polytrichum juniperinum* decreased with pH, in 2016 (Table 4).

TABLE 2 Summary statistics of soil chemical variables based on samples at plot level ($N = 80$)

Variable	Mean	Minimum	Maximum
Total C, %	12.7	1.82	48.7
Total N, %	0.40	0.06	1.41
C/N	30.2	16.8	54.8
Density, kg/m^2 (5 cm depth)	34.0	10.1	60.6
pH	4.94	4.43	7.13
Base cations, meq/100 g	4.72	0.70	37.3
P, mg/100 g	6.00	0.70	60.2
NH_4^+ N, mg/kg	44.8	1.20	449
NO_3^- N, mg/kg	16.2	0.14	157

TABLE 3 Relationship between vascular plant composition and explanatory variables (soil total C reflecting burn severity, pH, distance from fire area border, year), estimated with multivariate ANOVA (adonis test)

Variable	*F*	*R*^{2}	*p*-value
log(soil total C)	5.62	0.031	<0.001
pH	2.57	0.014	<0.001
log(distance)	2.55	0.014	<0.001
Year	12.91	0.072	<0.001

3.4 | Traits

Community-weighted mean values of diaspore mass increased with soil total C (i.e., higher diaspore mass was recorded in plots burned at lower severities), and also increased from year 2 to year 5 post-fire (Table 5). However, only the increase with time remained significant if *Vaccinium myrtillus* (a common plant with heavy diaspores) was removed from the data. We also found an effect of year on seed longevity, which decreased over time (i.e., increasing cover of plants with short-lived seed banks with time). However, this effect was completely driven by the disappearance of *Senecio sylvaticus* in 2019 and no difference between years was detected when this species was removed from the data ($p = 0.96$). CWM values of root buds were higher for less severely burned plots, although this relationship was less clear if *Vaccinium myrtillus* was excluded from the analyses (a change from $p < 0.007$ to $p = 0.07$). A more robust result was found for SLA, the marked

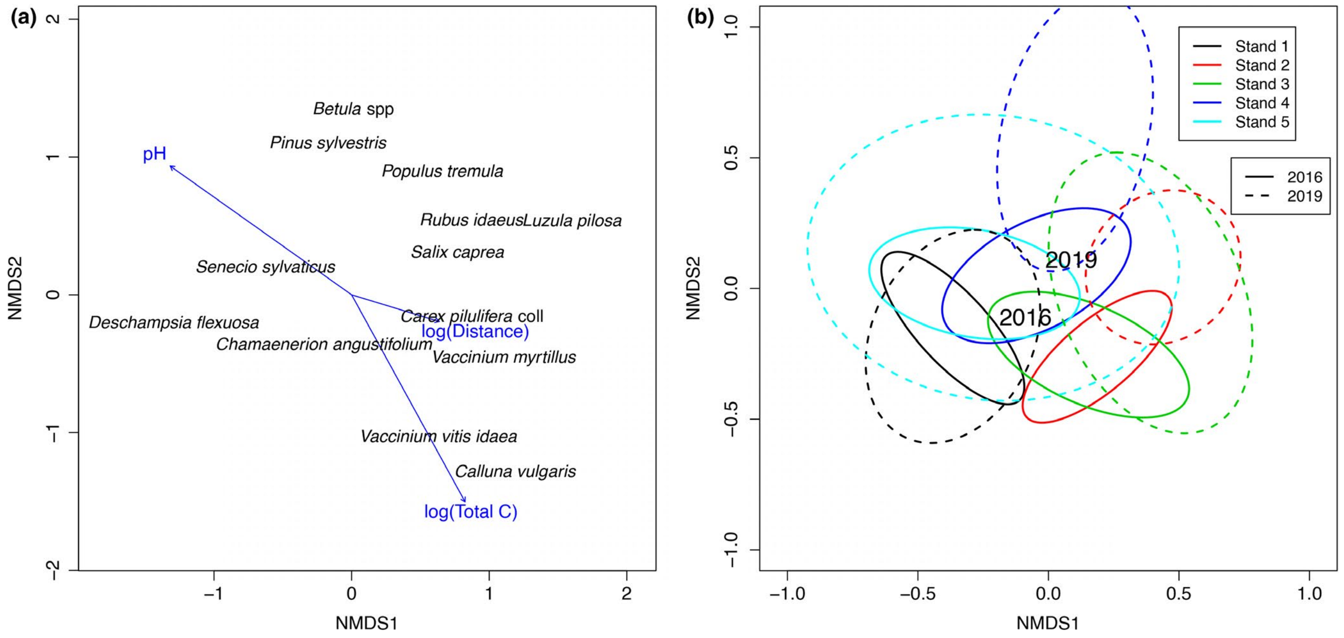

FIGURE 3 Ordination by non-metric multidimensional scaling (NMDS) of vascular plant species in burned clear-cuts showing vectors pointing in the direction of maximum increase of significant explanatory variables (pH, soil total C, distance to perimeter). Data for both survey years (2016 and 2019) were used. Stress = 0.20. Only species recorded in ≥8 plots any year are included

decrease of which over time remained strong and significant even if common species were excluded from the analysis. Variation in soil pH was not associated with any trait.

3.5 | Distance to fire perimeter

The distance between individual plots and the fire perimeter varied between 73 m and 3,957 m with a mean of 1,321 m. Community composition was significantly explained by distance to fire perimeter (Table 3). The abundances of *Vaccinium myrtillus* and *Ceratodon purpureus* increased with distance in 2016, while a decrease with distance was observed for *Chamaenerion angustifolium* in 2019 (Table 4). CWM values of diaspore mass decreased with distance to the fire perimeter but only at the survey made two years after the fire (Table 5).

3.6 | Species composition compared to unburned sites

There was a difference in community composition between our burned clear-cuts and unburned reference clear-cuts (Figure 4; multivariate ANOVA; $R^2 = 0.30$, $F = 209.1$, $p < 0.001$). Twelve of the 15 most common species in the burned plots also occurred on unburned clear-cuts (Appendix S1). Indicator species analysis revealed that *Chamaenerion angustifolium* and *Senecio sylvaticus* were associated with burned clear-cuts while *Betula* spp., *Deschampsia flexuosa*, *Picea abies*, *Vaccinium myrtillus* and *Vaccinium vitis-idaea* were associated with unburned clear-cuts (Appendix S1).

4 | DISCUSSION

The results from this study contribute to improve our understanding of post-fire vegetation dynamics of boreal production forests shaped by clear-cutting, and fills the gap of missing time series observations following fire in boreal Europe. Results confirm our predictions of burn severity as well as soil chemistry (reflected in pH) as drivers of the early vegetation succession but also indicate the strong influence of stochastic processes. Distribution patterns of two colonizing species are related to distance to the perimeter of the burned area.

Overall, community-level species and trait composition were poorly explained by the environmental variables (Tables 3 and 5, Figure 3) suggesting a large influence of stochasticity early in the succession. This accords with results of other studies (e.g. Del Moral, 2009; Måren et al., 2018). The observed increase in beta diversity over time (Figure 3b) supports the prediction that the impacts of stochastic processes, such as “chance colonizations”, on spatial compositional heterogeneity (i.e., beta diversity) can amplify over time via priority effects (Chase, 2003; Fukami, 2015). Since stochastic variation is typically larger at fine spatial scales (e.g. Li et al., 2016), the small size of our plots (50 cm × 50 cm) may contribute to the weak habitat-filtering signal. Still, a clear pattern is found: common immigrants (e.g. the herb *Chamaenerion angustifolium*) abound on severely burned soil and legacy species (e.g. the dwarf-shrub *Vaccinium myrtillus*) thrive on less severely burned soil. Similar distributions of plants in relation to burn severity are found in other studies on early fire succession (e.g. Hollingsworth et al., 2013; Abella & Fornwalt, 2015), and burn severity effects are evident also for other organisms such as ectomycorrhizal macrofungi (Salo & Kouki, 2018) and soil microarthropods (Malmström,

TABLE 4 Relationship between occurrence of dominant species (recorded in > 14 plots) and explanatory variables

	2016				2019				
Species	**Soil total C**	**Distance**	**pH**	**ED, N**	**Soil total C**	**(Soil total C)^2**	**Distance**	**pH**	**ED, N**
Betula spp.	NA	NA	NA	NA	3.61^{***} (1.68)	-4.58^{***} (1.76)	–	$-0.77°$ (0.40)-	14%, 25
Chamaenerion angustifolium	–	–	–	0%, 75	0.28^{***} (0.10)	–	-0.37^{***} (0.10)	–	20%, 65
Deschampsia flexuosa	NA	NA	NA	NA	–	–	–	–	0%, 22
Populus tremula	NA	NA	NA	NA	–	–	–	–	0%, 24
Senecio sylvaticus	-0.34^{***} (0.15)	–	0.40^{***} (0.14)	15%, 47	NA	NA	NA	NA	NA
Vaccinium myrtillus	1.30^{***} (0.35)	0.66^{***} (0.31)	–	28%, 17	NA	NA	NA	NA	NA
Ceratodon purpureus	–	0.35^{***} (0.13)	–	7%, 60	–	–	–	–	0%, 75
Polytrichum juniperinum	–	–	-0.83^{***} (0.30)	9%, 39	–	–	–	–	0%, 58

Parameter estimates (with *SE*) for species-specific models of abundance in relation to soil total C (and its squared term), pH, and distance from fire perimeter.

Abbreviations: *ED*, Explained deviance (0% if no variables improve the model); *N*, number of occupied sample plots; NA, occurrence in < 15 plots. Total C and distance were log-transformed before analysis.

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{°}p < 0.1$.

2010). The early dominance of colonizing species followed by a later recovery of residual species coincides with findings of the only other detailed vegetation study of succession after wildfire on clear-cuts that we are aware of, by Dyrness (1973). The large variation of soil total C confirms that our study included a wide range of variation along the burn severity gradient, from almost pure mineral soil to soil barely affected by the fire. Since our study plot location criteria were set to assure homogenous pre-fire conditions in soil fertility and moisture, the variations in soil conditions revealed by the post-fire sampling (Table 2) are most likely an effect of variation in fire severity as such.

Our trait analyses supported the prediction that the plant community contained more root buds in lightly burned plots, illustrating how species can survive a fire and rapidly resprout. In contrast, we did not find support for the prediction that fast-growing species (with high SLA) and species with light diaspores were favored by higher burn severity. There was stronger evidence for changes in trait composition over time, with a clear decrease in SLA with time indicating that the phase of dominance by early fast-growing species is very short. Furthermore, the late-successional communities are characterized by species with heavier diaspores and more short-lived seeds, supporting an overall pattern that earlier-successional, short-lived species form a more abundant seed bank while later-successional species are generally long-lived and contribute relatively less to the seed bank (Rees, 1994). We find it quite remarkable that the temporal trends, which accord with predictions from longer successional studies in other systems (e.g. 45 years; Vile et al., 2006), could be detected already two to five years post-fire.

The higher abundance of *Vaccinium myrtillus* on less severely burned plots accords with expectations. It is a common species in unburned clear-cuts in the region (Appendix S1), and experiments corroborate that this rhizomatous species survives vegetatively in light burns but is strongly reduced by severe fires (Schimmel & Granström, 1996). The negative relationship between the abundance of the grass *Deschampsia flexuosa* and soil total C, does not, however, comply with our expectations since severe burns have been shown to kill rhizomes of this species while light burns stimulate its vegetative growth (Schimmel & Granström, 1996). The doubling of plot occupancy of *Deschampsia flexuosa* from two to five years post-fire may be explained by seed dispersal from the surroundings as the seeds of this species are known to germinate well in burned soil (Schimmel & Granström, 1996).

The early pioneer species *Chamaenerion angustifolium* dominates after the fire, being recorded in > 90% of the plots in 2016 and still being common in 2019 (>80% plot occupancy). This species does not occur in the seed bank (Granström, 1987) and establishes from seeds originating in the surroundings (Granström & Schimmel, 1993). Rhizomes enable local persistence, although for long-term survival additional disturbance that creates bare soil and open spaces is necessary (Broderick, 1990). The positive relationship with soil carbon content remains to be explained, since it conflicts with earlier studies that show a clear increase in germination of *Chamaenerion angustifolium* with higher burn severity (Schimmel & Granström, 1996).

TABLE 5 Relationship between plant traits and explanatory variables (year, soil total C, pH and distance from fire perimeter)

Trait	Tot C	Distance	Distance×year	Year
Diaspore mass	0.26^{***} (0.14)	0.21^{***} (0.098)	-0.18^{***} (0.087)	1.36^{***} (0.56)
SLA				-4.75^{***} (0.48)
Root buds	0.45^{***}(0.16)			
Seed longevity				-0.06^{***} (0.015)

Parameter estimates (with *SE*) for models of community weighted trait means (CWD) in relation to soil total C, distance and year.

$^{***}p < 0.001$; $^{**}p < 0.01$; $^{*}p < 0.05$; $^{°}p < 0.1$.

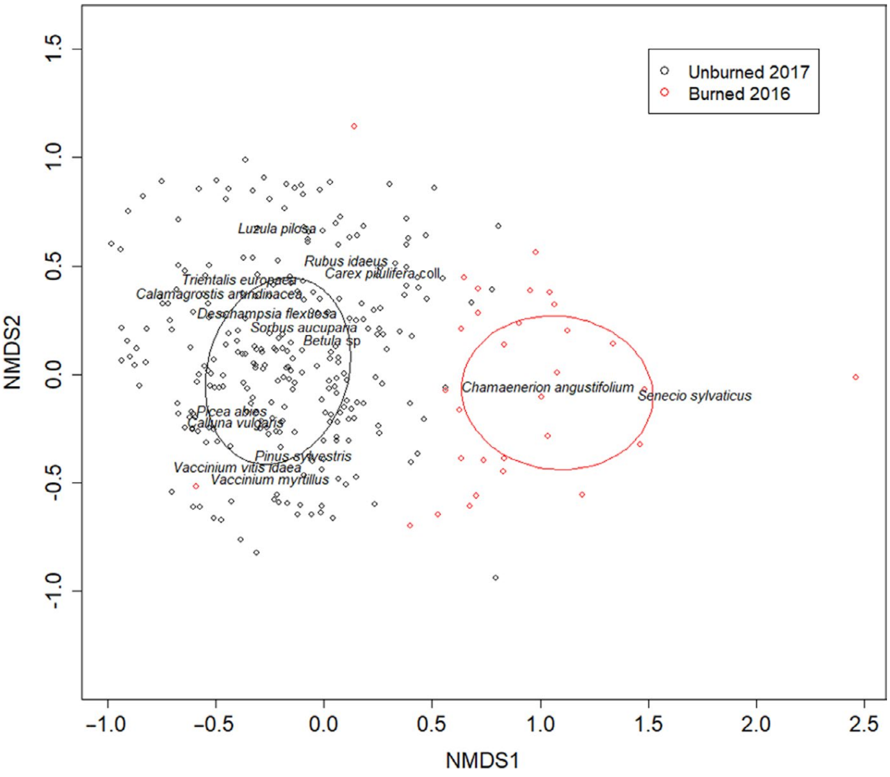

FIGURE 4 Ordination by non-metric multidimensional scaling (NMDS) of the species composition in the fire area in 2016 (80 plots), and in unburned clear-cuts of similar age in the surroundings of the fire area in 2017 (405 plots). Stress = 0.17

The positive effect of burn severity on the abundance of *Senecio sylvaticus* agrees with expectations since burning promotes germination of this pioneer, annual species (West & Chilcote, 1968). The strong decline of this species, with a drop in plot occupancy of almost 95% between 2016 (two years after the fire) and 2019, corresponds to observations from the USA, where the species peaked two years post-fire (Dyrness, 1973; Halpern, 1988). The large size of this species, typically reaching a height of > 70 cm (Mossberg et al., 1992), is the main reason for the 5% reduction in total cover of vascular plants from 2016 to 2019, more than outweighing the increase in several other species' cover.

The significant but weak effect of pH on community composition (Table 3) agrees with a study of early succession after fire in Alaska (Hollingsworth et al., 2013), in which pH is recognized as the second most important factor, next to burn severity. West and Chilcote (1968) find increasing abundance of *Senecio sylvaticus* with increasing soil fertility in slash-burned clear-cuts in Oregon, in accordance with our observations. The negative relationship of the bryophyte *Ceratodon purpureus* to high pH does not accord with the observation of Dyrness and Norum (1983) that this species colonizes ash.

Chamaenerion angustifolium, which decreases significantly with distance to the perimeter of the fire area, has light airborne seeds (Solbreck and Andersson, 1986) and occurs on unburned clear-cuts close to the fire area, with a plot occupancy of 20% in our reference data (Appendix 1). Since a considerable fraction of the production forests in the county of Västmanland where the fire study area is situated consists of clear-cuts (Skogsdata, 2019), the landscape seed pool of *Chamaenerion aangustifolium* should be substantial but the species seems nonetheless dispersal-limited.

The opposite pattern is shown by the bryophyte *Ceratodon purpureus*, which increases towards the center of the fire area. This species is known to characterize areas affected by high-severity fire (Richardson, 1981) and it seems unlikely that habitat suitability was higher in the central parts since fire severity was relatively homogenously distributed over the fire area (Gustafsson et al., 2019). A more likely explanation is that this perennial bryophyte reproduced and colonized repeatedly in the fire area after the initial colonization, a process that can cause local peaks in population size at central parts, since the margin contains fewer neighbors that may act as propagule sources (Bahn et al., 2006).

All common plant species on unburned clear-cuts in the surroundings also occurred on the burned clear-cuts studied by us (Appendix S1), demonstrating a large resilience of clear-cut vegetation to fire (i.e., tendency to return to prefire conditions; Abella & Fornwalt, 2015). Burned as well as unburned clear-cuts contain a mixture of more or less the same pioneer species, remnant grasses and dwarf shrubs, which differ in abundance. This explains the difference observed in the NMDS (Figure 4). The similarity between burned and unburned clear-cuts, both dominated by early-successional species, is likely to be larger than between burned and unburned old forests which represent widely different successional stages. No study seems to have documented this so far.

We found a rapid increase in abundance of deciduous trees, mainly *Betula* spp. and *Populus tremula*, both having a plot occupancy of ca. 30% five years after fire, agreeing with early-successional trajectories after fire in natural boreal European forests (Hytteborn et al., 2005). Deciduous trees comprised only 7% of the pre-fire forest volume in the area (Gustafsson et al., 2019), and thus most regeneration must have been from seeds although *Betula* spp. (especially *B. pubescens*) as well as *Populus tremula* have resprouting abilities (Engelmark & Hytteborn, 1999). *Pinus sylvestris*, with a pre-fire volume proportion of about 55% (Gustafsson et al., 2019), also established rapidly but increased more slowly than the deciduous trees. The abundance of *Pinus sylvestris* is likely to increase towards later successional stages due to the species' adaptation to the relatively dry, nutrient-poor and shallow soils found in the study area, and its long lifespan. The shade-tolerant conifer *Picea abies*, with a pre-fire volume of 18% (Gustafsson et al., 2019), is also likely to increase but this species will not become as dominant because it prefers more nutrient-rich, mesic moist soils.

The openness that characterizes clear-cuts resembles the conditions faced by early successional stages following stand-replacing fires in natural forest landscapes (e.g. Romme et al., 2016). Still, the trajectories of compositional change in forest-floor plant species on burned clear-cuts may differ from those of fire-induced successions in natural forests, since the latter leave behind large amounts of coarse woody debris (e.g. Pedlar et al., 2002; Tatsumi et al., 2020), and have effects on the light environment, soil nutrient dynamics and associated processes (Harmon et al., 1986; Leverkus et al., 2016). Coarse woody debris is also one of the most important habitats for forest species (Stokland et al., 2012). Ideally, future studies should include comparisons with intensively burned unmanaged forest landscapes, but such are virtually lacking in boreal Europe outside Russia due to the long history of industrial forestry and effective fire suppression.

Our study provides evidence that burn severity as well as soil chemistry affect vegetation succession on clear-cuts following fire, although to a limited extent, suggesting a strong influence of stochastic processes at this early stage of succession. The species composition in plots diverged over time, indicating an important role of priority effects. Expanding tree growth will be important for the development of forest-floor vegetation in coming years through shading effects and litter production affecting soil nutrient availability in ways that vary between tree species (Barbier et al., 2008). To disentangle processes connected to the abiotic (e.g. nutrients) and biotic (e.g. tree layer) drivers, future observations of species compositional shifts in permanent plots should be supplemented with measurements of light and repeated soil chemistry analyses.

ACKNOWLEDGEMENTS

We thank two referees for constructive and valuable comments on our manuscript. We are grateful to Anders Jonshagen who conducted the soil sampling.

AUTHOR CONTRIBUTIONS

LG conceived of the research idea with input from GG, VJ, AL and HN; LG, GG and HN collected data; VJ performed statistical analyses with contribution from GG; LG wrote the paper with contribution of all authors, who discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

Data are stored at Zenodo, Gustafsson et al. (2020), http://doi.org/10.5281/zenodo.4014320.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

Appendix S1. Comparison of vegetation on burned and on unburned clear-cutts

Appendix S2. Correlation between soil chemistry data

How to cite this article: Gustafsson L, Granath G, Nohrstedt H-Ö, Leverkus AB, Johansson V. Burn severity and soil chemistry are weak drivers of early vegetation succession following a boreal mega-fire in a production forest landscape. *J Veg Sci.* 2021;32:e12966. https://doi.org/10.1111/jvs.12966