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RESEARCH ARTICLE

Climatic and vegetational controls of Holocene wildfire regimes in the boreal forest of northern Fennoscandia

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Abstract

1. Climate change is expected to increase wildfire activity in boreal ecosystems, thus threatening the carbon stocks of these forests, which are currently the largest terrestrial carbon sink in the world. Describing the ecological processes involved in fire regimes in terms of frequency, size, type (surface vs. crown) and severity (biomass burned) would allow better anticipation of the impact of climate change on these forests. In Fennoscandia, this objective is currently difficult to achieve due to the lack of knowledge of long-term (centuries to millennia) relationships between climate, fire and vegetation.
2. We investigated the causes and consequences of changes in fire regimes during the Holocene (last ~11,000 years) on vegetation trajectories in the boreal forest of northern Finland. We reconstructed fire histories from sedimentary charcoal at three sites, as well as vegetation dynamics from pollen, moisture changes from *Sphagnum* spore abundance at two sites, and complemented these analyses with published regional chironomid-inferred July temperature reconstructions.
3. Low-frequency, large fires were recorded during the warm and dry mid-Holocene period (8500–4500 cal. year BP), whereas high-frequency, small fires were more characteristic of the cool and wet Neoglacial period (4500 cal. year BP onward). A higher proportion of charcoal particles with a woody aspect—characterizing crown fires—was recorded at one of the two sites at times of significant climatic and vegetational changes, when the abundance of *Picea abies* was higher.
4. *Synthesis*. Our results show both a direct and an indirect effect of climate on fire regimes in northern Fennoscandia. Warm and dry periods are conducive to large surface fires, whereas cool and moist periods are associated with small fires, either crown or surface. Climate-induced shifts in forest composition also affect fire regimes. Climatic instability can alter vegetation composition and structure

and lead to fuel accumulation favouring stand-replacing crown fires. Considering the ongoing climate warming and the projected increase in extreme climatic events, Fennoscandian forests could experience a return to a regime of large surface fires, but stand-replacing crown fires will likely remain a key ecosystem process in areas affected by climatic and/or vegetational instability.

KEYWORDS
boreal forest, charcoal, climate change, crown fire, pollen, spruce, surface fire

1 | INTRODUCTION

The rise in temperature during the 21st century is expected to increase tree growth in high-latitude boreal forests more than in southern boreal forests (Kellomäki et al., 2018; Ruiz-Pérez & Vico, 2020). However, there is evidence that climate change also increases the probability of occurrence of extreme natural disturbance events such as large and severe wildfires, leading to increased tree mortality (Bright et al., 2014; Gaboriau et al., 2020; Kuuluvainen et al., 2017). The vulnerability of high-latitude boreal forests to future disturbance regimes could cancel out the positive effects of higher temperatures on tree growth (Timoney et al., 2019).

Recent large and severe wildfire events around the world, such as in the summers of 2014 in the Northwest Territories (Canada), 2018 in Scandinavia, 2019 in Australia, and 2020 in Siberia, were linked to exceptionally dry conditions (Ponomarev et al., 2021; Pyne, 2021; Stephens et al., 2014). In boreal forests, the balance between temperature (annual and summer) and precipitation is the main factor that controls fire activity. Global change will likely favour the development of dry spells leading to anomalous fire events, as increased precipitation will not compensate for increased evapotranspiration due to higher temperature (Ruosteenoja et al., 2018). This scenario is particularly alarming for the boreal biome where wildfire is omnipresent and plays a key role in ecosystem dynamics and vegetation composition (Goldammer & Furyaev, 2013; Young et al., 2017). As the boreal biome holds the largest terrestrial carbon stocks in the world, it could transform into a carbon source due to increased wildfire activity (Bowman et al., 2020; Bradshaw & Warkentin, 2015). However, our understanding of the interactions between fire, vegetation and climate in Eurasian boreal forests is hampered by the short time spans covered by historical records. Palaeoecological investigations can improve our understanding of the effect of past climate on fire activity and provide key information for modelling-based fire predictions (Marlon, 2020; McMahon et al., 2010; Whitlock et al., 2010).

The boreal forest of northern Fennoscandia (Northern Finland, Sweden, Norway and the Kola Peninsula in Russia) is dominated by *Pinus sylvestris* (Scots pine) and *Betula pubescens* (downy birch), as well as *Betula pubescens* ssp. *tortuosa* (mountain birch) at higher elevations. *Pinus sylvestris* dominates forests on well-drained poor soils and on forested nutrient-poor bogs, while *Betula pubescens* is found on more productive mesic upland sites and on mires (Kuuluvainen et al., 2017). *Picea abies* (Norway spruce) has a more southerly distribution compared to *Pinus sylvestris* or *Betula* spp., but in those parts of the region where it is present, it dominates late-successional stands on mesic upland soils and on forested mires (Heiskanen & Mäkitalo, 2002).

In northern Fennoscandia, fires in the past millennium have been less frequent but more severe in forests dominated by *Picea abies* than in those dominated by *Pinus sylvestris* (Pitkänen et al., 2003; Wallenius et al., 2010). However, knowledge of fire history and its interactions with climate and vegetation is limited at longer time-scales. Based on the concentration of charcoal fragments in lake sediments, a previous study suggested that maximum fire frequencies were recorded between 7500 and 5000 calibrated years before present (hereafter, cal. year BP) and after 2500 cal. year BP in northern Sweden (Carcaillet et al., 2007). Increased temperature and dryness induced by orbital forcing during the early- to mid-Holocene (before 4500 cal. year BP) caused higher fire activity and facilitated the migration and expansion of *Pinus sylvestris* (Bjune et al., 2004; Carcaillet et al., 2007; Seppä et al., 2002). From approximately 5500 cal. year BP, pollen records show the spread of *Picea abies* (Giesecke & Bennett, 2004; Seppä, Alenius, Bradshaw, et al., 2009). Cooler and moister conditions during the Neoglacial period (after 4500 cal. year BP), as well as lower fire frequency between 5000 and 2500 cal. year BP, could have favoured *Picea abies* over *Pinus sylvestris* or *Betula pubescens* as shown further south in the boreal forest (Clear et al., 2015; Kuosmanen et al., 2014). Although Carcaillet et al. (2007) suggested that drier conditions, more conducive to fire occurrence, prevailed after 2500 cal. year BP, *Picea abies* remained abundant in the landscape until today (Kremenetski et al., 1999; Reinikainen & Hyvärinen, 1997; Soloviena & Jones, 2002). Hence, the causes of the persistence of *Picea abies* are unknown, especially considering that the species is adapted to cool and humid climates and sensitive to high fire frequencies (Ohlson et al., 2011).

Studies on contemporary vegetation dynamics in response to changes in fire regimes have shown that *Pinus sylvestris* benefits from frequent low-severity surface fires, whereas *Picea abies* replaces *Betula* after infrequent severe (stand-replacing) crown fires (Gromtsev, 2002; Rogers et al., 2015). Thus, a regime shift from frequent surface fires in the early- to mid-Holocene, to infrequent crown fires in the late Holocene could explain the persistence of *Picea abies* in northern Fennoscandia.

To better understand the interactions among climate, fire and vegetation during the Holocene (last ~11,000 years) in northern Finland, we performed palaeoenvironmental reconstructions based on proxies sampled in lake sediments in Finnish Lapland. To reconstruct fire history, vegetation dynamics and moisture, we analysed charcoal particles, pollen grains and *Sphagnum* spp. spores, respectively. To define past fire regimes, we reconstructed biomass burned, fire frequency, area burned and fire type (surface versus crown) inferred from charcoal morphology. We used temperature reconstructions from chironomid analyses performed by Luoto et al. (2014) and Seppä et al. (2002). Based on previous studies conducted in northern Fennoscandia, we hypothesized (1) that *Pinus sylvestris* expansion was favoured by warm and dry climate conditions in the early- and mid-Holocene (before ~4500 cal. year BP), which were conducive to high-frequency, large, low-severity surface fires; and (2a) that the spread and persistence of *Picea abies* were favoured by cooler and moister climate conditions during the Neoglacial period (after 4500 cal. year BP) and/or (2b) by a regime shift to low-frequency, small, high-severity crown fires.

2 | MATERIALS AND METHODS

2.1 | Study sites

We sampled sediments at lakes Charly, Rosalia (unofficial names) and Pikku Härkäjärvi (official name, hereafter 'Pikku'), located near Nellim, at the southeast of Lake Inari (Figure 1; Table S1). The sampling was done with a permission from Metsähallitus Forestry Ltd. Deglaciation of the area occurred between 12,500 and 10,700 cal. year BP (Cuzzone et al., 2016; Stroeven et al., 2016). According to the Köppen-Geiger classification (Peel et al., 2007), the current climate is subarctic, with long cold winters and short mild summers. The current average temperatures of the warmest (July) and coldest (January) months are 14.2°C and −12.1°C, respectively. Mean annual precipitation is about 474 mm, with snow falling from November to April (Inari Nellim station, Finnish Meteorological Institute, 1990–2020 data). The vegetation surrounding the studied lakes is dominated by *Pinus sylvestris* L. with some stands of *Betula pubescens* Ehrh. and rare stands of *Picea abies* (L.) H. Karst. The understorey is dominated by lichens (mostly *Cladonia* spp.), mosses (mostly *Pleurozium* spp.) and several shrub species such as *Betula nana* L., *Empetrum nigrum* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L. and *Juniperus communis* L. In terms of geology, the studied lakes are located at the transition between the Lapland Granulite Belt (in the south) and the Inari craton (in the north) (Rasilainen et al., 2008). Thus, the watersheds of Lakes Charly and Pikku are mainly on tills derived from acid granulite, whereas the watershed of Lake Rosalia is characterized by gneiss rocks. Lakes Pikku and Charly are surrounded by coarse rocky and well-drained soils, while lake Rosalia is surrounded by peat and more humid soils.

2.2 | Sediment sampling and chronology building

We used a Russian corer to sample sediment sequences from the three lakes in July 2017. These lakes were chosen due to their small

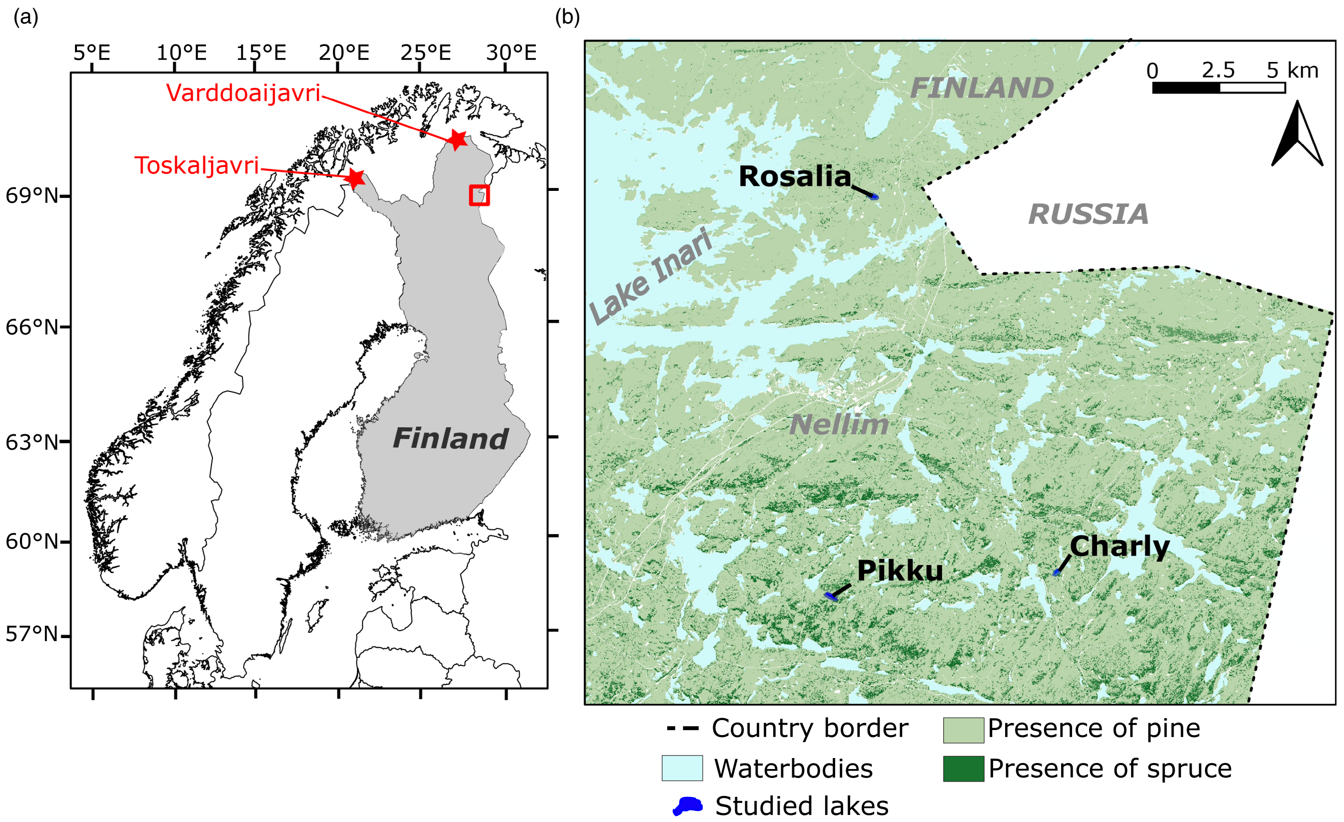

FIGURE 1 Location of the study area (a) and sampled lakes (b). Source: National Resources Institute Finland (The Multi-source National Forest Inventory Raster Maps of 2019).

surface area (<4 ha), relatively deep water column (>5 m) and absence of inlet or outlet. To collect the water–sediment interface, we used a Kajak-Brinkhurst gravity corer (Glew et al., 2001). The sediment sequences were sliced into contiguous 0.5-cm-thick subsamples to obtain fine-scale time resolution for analysis. The different cores composing the sediment sequences at each site were sampled so that there was a certain overlap from core to core. Then, in the laboratory, the alignment of the different cores was verified by comparing the synchronicity of the charcoal signatures.

Because the sediments were poor in plant macroremains, the core chronologies were realized from radiocarbon dating of bulk gyttja samples by ^{14}C accelerator mass spectrometry (Table S2). Dates from bulk sediments can be affected by a carbon-reservoir effect (Björck et al., 1998; Grimm et al., 2009). However, this effect is not systematic (i.e. it does not occur in all lakes and not at all sediment depths within a single lake). Furthermore, the studied watersheds did not have clay mineral or carbonate deposits that could increase the risk of dating error (Ojala et al., 2019; Strunk et al., 2020). We used the Bchron v.4.7.6 R package (Parnell et al., 2008) to reconstruct Bayesian sediment accumulation histories and calibrate age-depth models (Figure S1). We used the IntCal20 calibration curve for terrestrial northern hemisphere material (Reimer et al., 2020). Ages were interpolated at contiguous 0.5-cm depth intervals and all dates are expressed in calibrated years before present (cal. year BP).

2.3 | Pollen analysis and reconstruction of vegetation dynamics

A total of 248 subsamples were extracted from the Pikku sediment sequence, and 284 subsamples from the Rosalia sediment sequence for palynological analysis. Prior to chemical treatment, one *Lycopodium* spore tablet was added to each sub-sample (batch No. 1031 with 20848 spores per tablet or batch No. 124961 with 12542 spores per tablet) to estimate the concentration of microscopic objects per cm^3 (Stockmarr, 1971) and pollen accumulation rates (PARs; pollen grains cm^{-2} $year^{-1}$). Sub-samples of 0.25 cm^3 and 1-cm thickness were treated using the standard pollen preparation procedure (10% HCl; 10% KOH for 10 min in a hot water bath). We used the acetolysis method in a hot water bath for 3 min (Berglund & Ralska-Jasiewiczowa, 1986) to remove polysaccharides. The prepared samples were stored in glycerine. At least 500 terrestrial pollen grains per sample were counted to the lowest possible taxonomic level using published pollen keys and the reference collection of the Department of Geography at the University of Latvia. The percentage of taxa was estimated using arboreal and non-arboreal pollen sums. The pollen zones were established through constrained incremental sums of squares (CONISS) cluster analysis of the relative abundance of pollen taxa (Grimm, 1987) using the Rioja R v.0.9–26 package (Juggins, 2017). The rate of change was computed at each level using the RRatepol R v.0.6.1 package (Mottl et al., 2021) with an age-weighted average smoothing method applied for each species. The PAR was used as a proxy of changes in tree biomass and density, with higher PAR reflecting denser tree populations (Bennett et al., 1986; Davis et al., 1964; Seppä, Alenius, Muukkonen, et al., 2009).

2.4 | Fire regime reconstructions

To reconstruct fire regimes at the three study sites (Pikku, Rosalia and Charly), we first took a 1-cm^3 subsample from each 0.5 cm-thick slice of sediment and shook it for 24 h in an aqueous solution of 5% sodium hexametaphosphate ($Na_6O_{18}P_6$), 5% KOH and 10% NaCl to facilitate deflocculation and to differentiate black charcoal from bleached organic matter (Bamber, 1982; Schlachter & Horn, 2010). The solution was then passed through a sieve to collect charcoal particles larger than 160 μm, assumed to originate from fire events having occurred up to 30 km away from the lakeshores (Higuera et al., 2007; Oris et al., 2014). Charcoal particles were measured and counted using an image analysis software (WinSEEDLE, Regent Instruments Inc.), allowing to calculate charcoal concentration (pieces cm^{-2}).

We reconstructed an index representing past biomass burning (hereafter *BB*; no unit) at each study site based on charcoal accumulation rates (hereafter CHAR, i.e. pieces cm^{-2} $year^{-1}$), using sediment accumulation rates obtained from the age-depth models. To remove bias induced by variations in sedimentation rate at the site level, we interpolated individual CHAR series using a constant time resolution corresponding to the median sample resolution of each lake (between 19 and 25 years). We pooled and smoothed the series (using a 500-year window) by (1) rescaling initial CHAR values using min-max transformation, (2) homogenizing the variance using Box-Cox transformation and (3) rescaling the values to *Z*-scores (Power et al., 2008) using the paleofire R package v.1.2.3 (Blarquez et al., 2014). The average of individual *BB* series is interpreted as the pooled regional biomass burned (hereafter *RegBB*; unitless).

We used the CharAnalysis v.1.1 software (Higuera et al., 2010; available at https://github.com/phiguera/CharAnalysis) to detect past fire events for each interpolated individual CHAR series. We estimated and removed background noise, corresponding to charcoal particles resulting from re-deposition processes, sampling bias or extra-regional transport (Figure S2; Higuera et al., 2007; Remy et al., 2018). We considered that our charcoal reconstructions in each of the three lakes did not necessarily detect all fires, and that charcoal peaks could have represented one or several fire events (Higuera et al., 2010; Magne et al., 2020). We minimized this bias by using the Signal-to-noise index to evaluate the effectiveness of the discrimination between fires (Figure S2; Brossier et al., 2014; Kelly et al., 2011). We calculated the fire frequency (hereafter *FF*; fire.$year^{-1}$) at each site with a kernel density estimation procedure based on a 500-year smoothing bandwidth (Ali et al., 2012). The pooled regional fire frequency (hereafter *RegFF*; fire.$year^{-1}$) was constructed by averaging the *FF* series.

We used the ratio between *BB* and *FF* as well as between *RegBB* and *RegFF* to assess fluctuations in fire size through time for individual and regional records (hereafter *FS index* and *RegFS index*; Ali et al., 2012). *BB* and *RegBB* values are correlated with long-term changes in area burned inferred from fire histories (Higuera et al., 2010; Kelly et al., 2013). Fire size is related to the temporal trajectory of mean biomass burned per fire, reflecting part of the loss of organic matter (*BB* and *RegBB*), and modulated by the number of fires through time (*FF* and *RegFF*). High values of *FS index* and *RegFS index* are indicative of a high mean area burned per fire, whereas low *FS index* values reflect a low mean area burned per fire (Ali et al., 2012; Remy et al., 2017).

2.5 | Charcoal morphology

We analysed charcoal morphology for the Rosalia and Pikku samples, the two sites for which we also carried out vegetation reconstructions, to compare the two types of records at the site scale. We calculated the aspect ratio L/W with L the longest axis and W the shortest axis for each charcoal particle to qualify their plant source, that is elongated graminoid charcoal particles with high aspect ratios vs more cubic tree and shrub (wood and leaves) charcoal particles with low aspect ratios (Feurdean, 2021; Vachula et al., 2021). We used the thresholds established by Vachula et al. (2021) from data collected worldwide and the ones estimated for the Siberian taiga by Feurdean (2021) to discriminate non-woody fuel types ($L/W > 3.5$), characterizing surface fires, and woody fuel types ($L/W < 2.5$), characterizing crown fires, the charcoal particles having a L/W between 3.5 and 2.5 do not allow to determine fuel type.

2.6 | July temperature data

We used chironomid-based reconstructions of mean July air temperature already published for lake Toskaljavri (latitude 69°12′N, longitude 21°28′E; Seppä et al., 2002) and lake Varddoaijavri (latitude 69°53′N, longitude 26°31′E; Luoto et al., 2014), whose locations are shown in Figure 1a. The chironomid-based mean inferred July temperature was 9.62°C with a root mean square error of prediction (RMSEP) of 0.73°C, and 11.06°C with a RMSEP of 0.84°C, for Toskaljavri and Varddoaijavri lakes, respectively (Figure S3). July air temperature records were averaged over a 136-year time step corresponding to the average time resolution of sediment samples from lakes Toskaljavri and Varddoaijavri and smoothed over a 500-year moving-window for comparison with the reconstructed fire histories.

2.7 | Statistical analyses of the interactions between climate, fire and vegetation

We used Pearson's correlation analyses to assess relationships between vegetation changes (inferred from pollen data) and temperature variability (chironomid-inferred July temperature in °C) as well as fire activity (charcoal-inferred biomass burned and fire frequency reconstructed from each sediment sequence, and fire size averaged for the three sequences) and fire type (inferred from the proportion of charcoal particles with a woody aspect, averaged by time unit). We computed the distributions of correlation coefficients using bootstrap resampling with 999 iterations (von Storch & Zwiers, 2002). We conducted the correlation analyses on the period from 8000 cal. year BP to the present to avoid bias due to lower sample size and higher climatic and vegetational instability in the early Holocene (Barker et al., 2019; Panizzo et al., 2008). For each iteration, we used half of the non-interpolated pollen records (randomly sampled) and the corresponding interpolated values for temperature and fire activity (i.e. 110 values for Rosalia and 108 values for Pikku). For the correlations with the proportion of charcoal particles with a woody aspect, we removed the samples without recorded charcoal particles (i.e. 84 samples for Rosalia and 92 samples for Pikku). All numerical analyses were performed with R (v.4.0.3, R Core Team, 2021).

3 | RESULTS

3.1 | Chronologies

The age-depth models indicate 7600 years of sedimentation at Charly, 9500 years at Pikku and 11,000 years at Rosalia (Figure S1). Mean sedimentation rates are comparable, with Charly having the highest at 0.0318 cm per year, followed by Rosalia at 0.0148 cm per year, and Pikku at 0.0145 cm per year (Table S1). The age-depth models exhibit episodes with higher sedimentation rates between 2400 and 1800 cal. year BP at Charly and between 7800 and 6500 cal. year BP at Rosalia. As the time span covered by individual sediment records is unequal, caution must be exercised when interpreting the period before 7600 cal. year BP.

3.2 | Fire histories and climate variability

While the sedimentation process started around 11,000 cal. year BP at Rosalia, we analysed proxies only from 9000 cal. year BP to present for direct comparison with Pikku. The number of fires detected per sediment record during the last 9000 years ranged from 36 to 49 (Figure S2). Regional biomass burned (*RegBB*) increased drastically between 9000 and 6500 cal. year BP, before stabilizing until 3000 cal. year BP. Then, *RegBB* decreased until 1500 cal. year BP and remained low thereafter, at a level comparable to the one before 7500 cal. year BP (Figure 2). Regional fire frequency (*RegFF*) tended to increase from about 1 fire every 280 years around 9000 years BP to reach 1 fire every 180 years around 4000 years BP and then stabilize over the last 4000 years (Figure 2). During the last 500 years, *RegFF* decreased to about 1 fire per 250 years. Fire size (*RegFS index*) followed the opposite trend to *RegFF* and was higher during the early and mid-Holocene, from 9000 to 4000 cal. year BP, than during the late Holocene, from 4000 to the present (Figure 2).

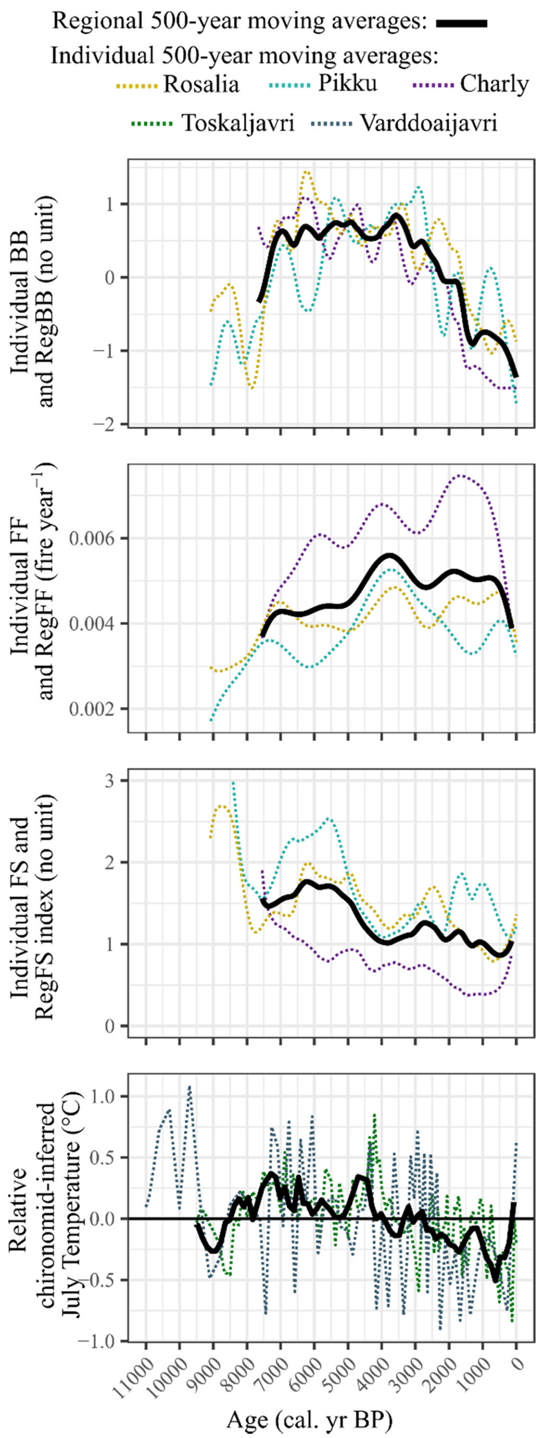

FIGURE 2 Individual and regional fire histories reconstructed from charcoal particles retrieved from the sediments of Lakes Rosalia, Pikku and Charly, and relative (i.e. the average July air temperature over the whole period was subtracted from all observations for each site) mean July air temperature reconstructed from chironomid remains retrieved from sediments of Lakes Toskaljavri and Varddoaijavri.

The mean July air temperature was higher between 8500 and 4000 cal. year BP than before and after (Figure 2). The highest mean temperatures occurred between 7500 and 6000 cal. year BP, and between 4500 and 4000 cal. year BP, whereas the lowest mean temperatures occurred between 9500 and 8500 cal. year BP and during the last 2500 years.

3.3 | Vegetation dynamics

The landscapes were initially dominated by *Betula* with some *Alnus*, and *Juniperus*, along with Poaceae in the understorey (Figure 3). Then, afforestation began around 7800 cal. year BP at Rosalia (Zone R-4) and 8700 cal. year BP at Pikku (Zones P-6 and P-5) with a sharp increase in *Pinus* to the detriment of *Betula* and Poaceae. This period was characterized by a high rate of change at both sites. Forest composition remained dominated by *Pinus* and *Betula* until the arrival/expansion of *Picea* around 6500 cal. year BP at Rosalia (Zone R-3) and 5000 cal. year BP at Pikku (Zone P-4), the two periods with highest mean July air temperature on record. At Rosalia, this period was marked by a high rate of change. Between 6000 and 4000 cal. year BP, *Alnus* decreased, whereas Ericaceae and *Sphagnum* increased (Zones R-2 and P-3). At Pikku, PAR (as a proxy of tree density) was 2.5 times higher, and the rate of change increased between 4000 and 2000 cal. year BP, compared to before and after (Zone P-2). Forest composition remained stable until 1000 cal. year BP, when *Picea* increased at Rosalia (Zone R-1) and decreased at Pikku concurrent with a high rate of change (Zone P-1).

3.4 | Individual fire histories and variations in fuel types

The same trends in fire histories are recorded at Rosalia and Pikku, with higher biomass burned between 7500 and 2000 cal. year BP, peaks in fire frequency around 7000, 4000 and 500 cal. year BP, and larger fire size before 8000 cal. year BP and between 6500 and 4500 cal. year BP (Figure 4). There are two episodes when biomass burned and fire frequency were lower at Pikku than at Rosalia, and fire size larger (around 6500 cal. year BP and around 2000 cal. year BP).

General trends of charcoal aspect indicate mostly non-woody fuel types throughout the Holocene at both sites, although there was a tendency toward aspect values indicative of woody fuel types at Pikku between 5500 cal. year BP and 2500 cal. year BP (Figure 4).

3.5 | Correlation between climate, vegetation and fire parameters

Overall, the correlations between vegetation variables, fire regime variables and July temperature followed the same trends at both sites, except for *Pinus* which increased at Rosalia and decreased at Pikku during periods of high fire frequency (Figure 5). The correlations between fire size and vegetation variables were generally higher at Pikku than at Rosalia, with more *Pinus*, *Betula* and *Alnus* and less *Picea* when large fires occurred. The PAR and the rate of change

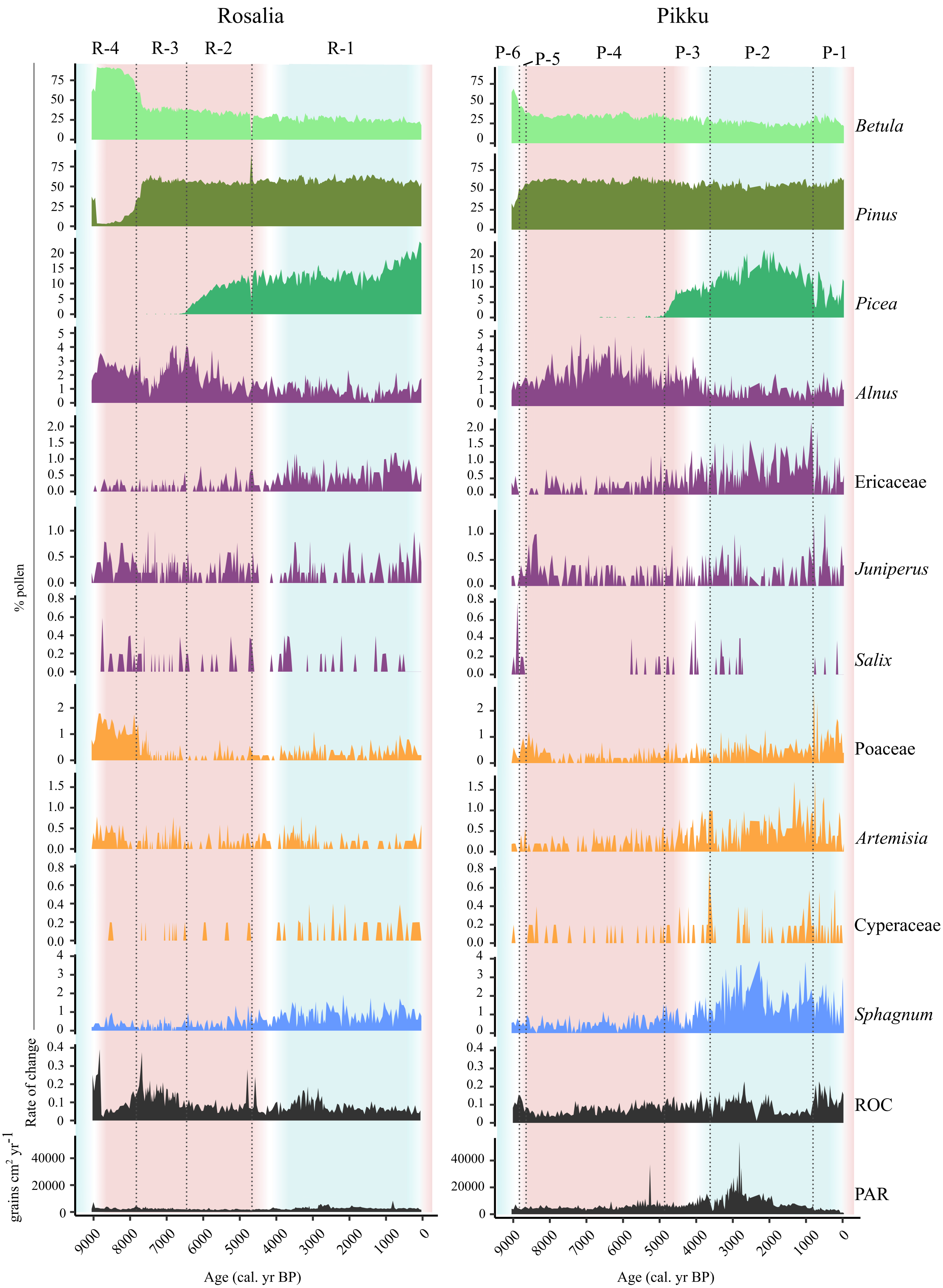

FIGURE 3 Pollen percentages (taxa with summed percentage >10% through the entire period), rate of change (ROC) and pollen accumulation rate (PAR) for lakes Rosalia and Pikku. Dotted lines demarcate the zonation based on cluster analysis (see Figure S3). Background colours differentiate warm (red) and cool (blue) periods.

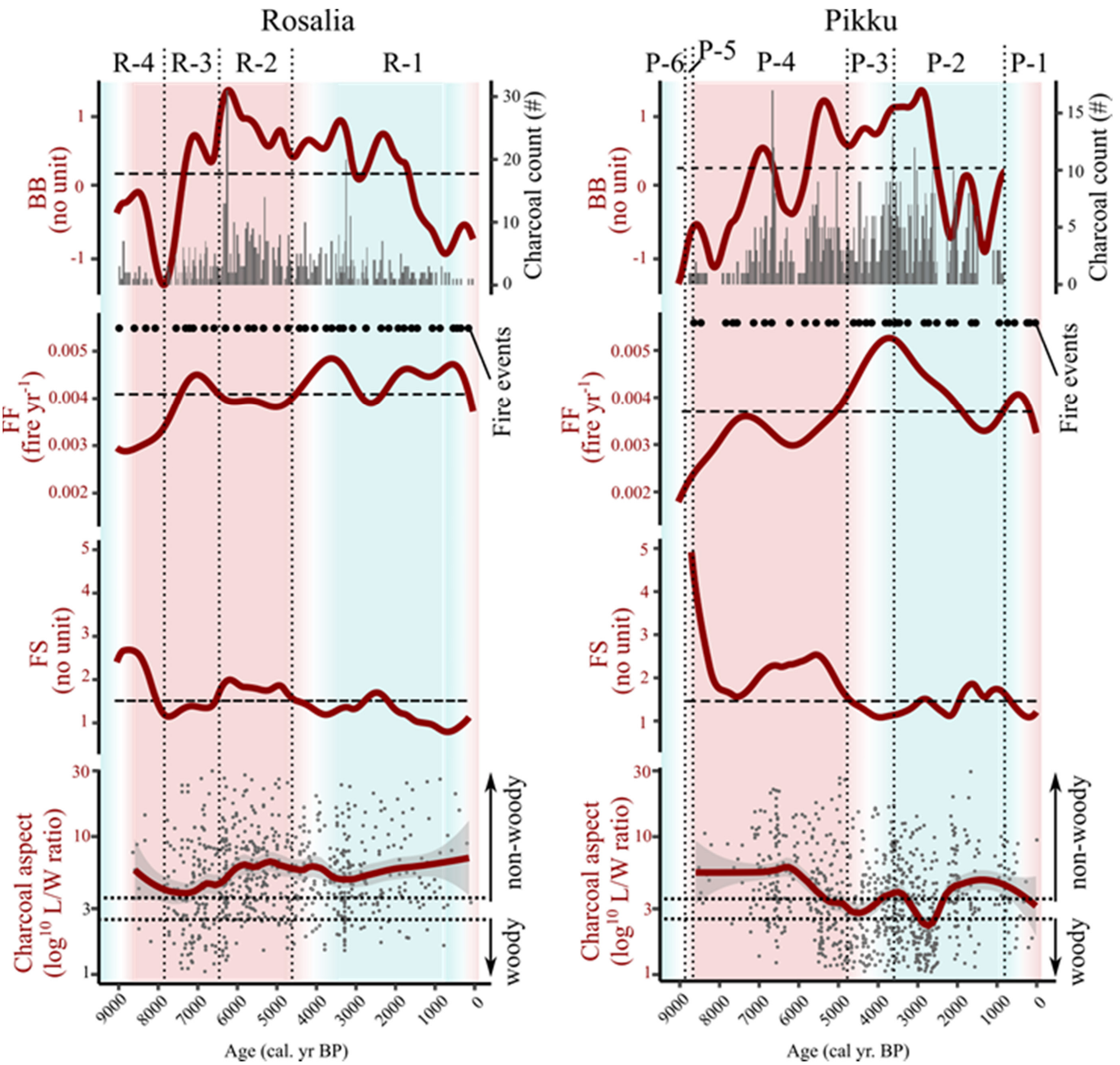

FIGURE 4 Charcoal count, biomass burned (BB), fire frequency (FF), fire size (FS) and charcoal aspect reconstructed from charcoal particles retrieved from sediments of Lakes Rosalia and Pikku. The thick red lines are moving averages (500-year window) from Figure 2 for BB, FF and FS, and from loess smoothing for charcoal aspect (span at 30% with grey areas corresponding to confidence intervals). Black dots correspond to fire events. Grey dots correspond to charcoal aspect for individual samples. Horizontal dashed lines show the mean for the entire period by site. Horizontal dotted lines show the thresholds used to discriminate charcoal particles from woody and non-woody fuel types. Vertical dotted lines show the pollen zones (see Figure 3). Background colours differentiate warm (red) and cool (blue) periods.

increased with biomass burned and fire frequency and decreased with fire size at Pikku, while they tended to be less correlated with the fire regime variables at Rosalia. Overall, warm periods were associated with higher abundance of *Betula* and *Alnus* and lower abundance of *Picea*, Ericaceae, Poaceae and *Spagnum*.

Correlations between the proportion of charcoal particles with a woody aspect and fire regime variables were higher at Pikku than at Rosalia (Figure 6). The proportion of charcoal with a woody aspect increased with biomass burned and fire frequency and decreased with fire size. The correlation of the proportion of charcoal particles with a woody aspect and July temperature was negative at Pikku and positive at Rosalia. Similarly, the correlation between the proportion of charcoal particles with a woody aspect and vegetation variables showed mostly opposite trends at Pikku and Rosalia. Correlations were positive with *Picea*, *Salix*, Ericaceae, Poaceae, *Sphagnum* and PAR at Pikku, compared to *Pinus*, *Betula* and *Alnus* at Rosalia. The rate of change was positively correlated to the proportion of charcoal with a woody aspect at both sites.

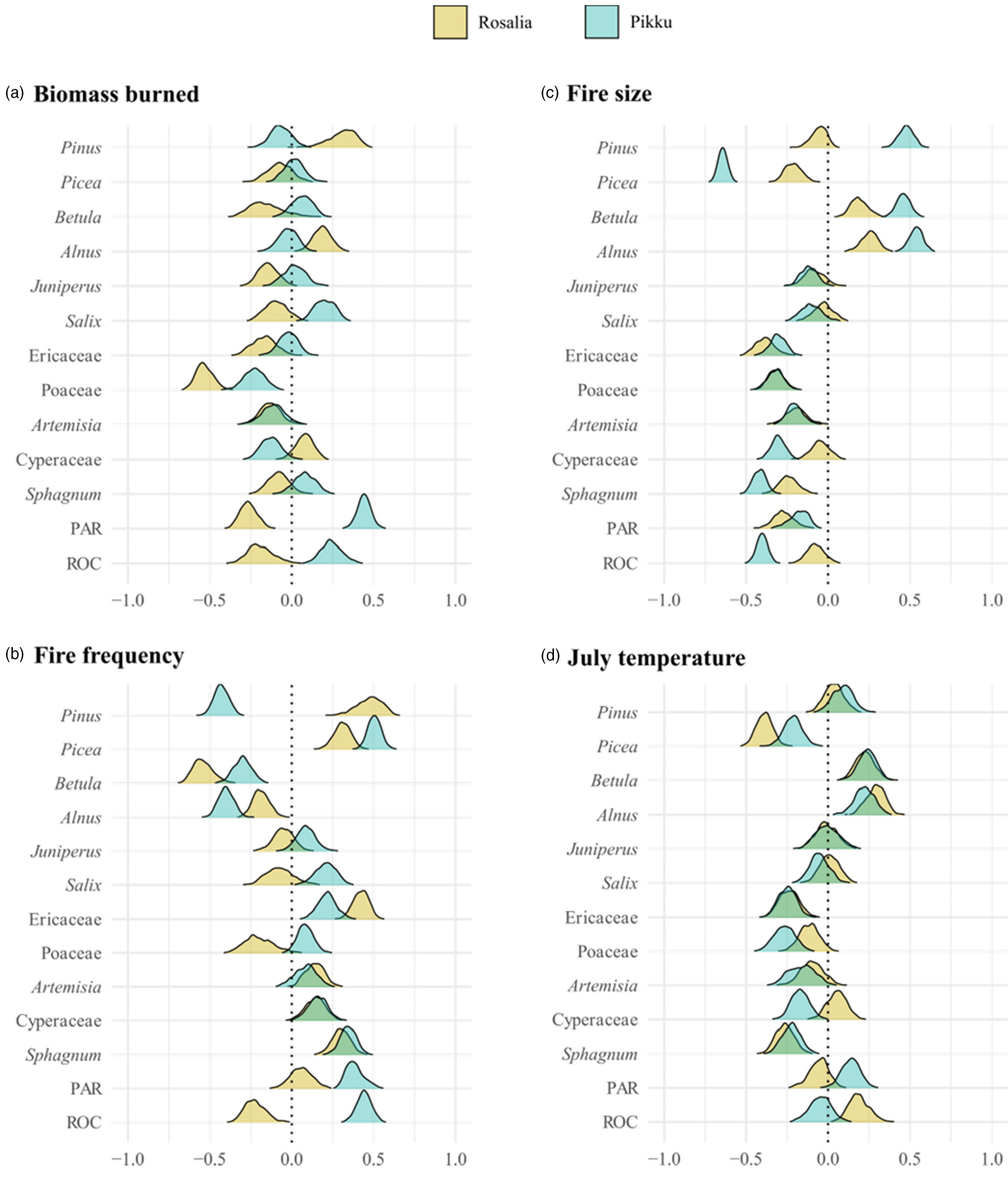

FIGURE 5 Density distributions of the 999 Pearson correlation iterations between vegetation (pollen) variables, fire regime variables (biomass burned (a), fire frequency (b) and fire size (c) from Rosalia and Pikku); and average chironomid-inferred mean July air temperature (d) throughout the Holocene for lakes Rosalia and Pikku.

4 | DISCUSSION

Our analyses of pollen and charcoal from lake sediments in northern Finland allowed us to reconstruct Holocene vegetation dynamics and fire regimes and to discuss their links with environmental processes. Our results partially support our first hypothesis, as warmer and drier climatic conditions promoted *Pinus sylvestris* expansion. However, this occurred under a regime

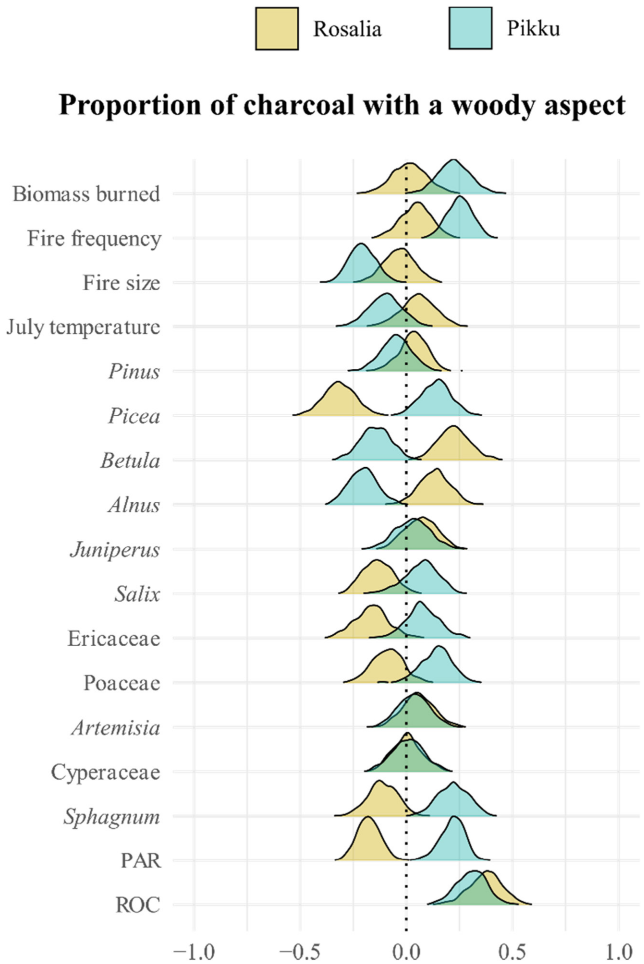

FIGURE 6 Density distributions of the 999 Pearson correlation iterations between environmental variables (fire, climate and vegetation) and average proportion of charcoal with a woody aspect for Lakes Rosalia and Pikku.

characterized by lower fire frequencies than expected, with medium-large surface fires since the beginning of the Holocene and more so during the Holocene Thermal Maximum (between 8500 and 4500 cal. year BP). Then, regarding the spread of *Picea abies* and its persistence until current times, our two alternative (but not mutually exclusive) hypotheses were not fully supported. The first—related to climate—was partially supported. *Picea abies* was more abundant under cooler mean July temperatures, and the species' establishment coincided with the beginning of the cool and moist Neoglacial period (after 4500 cal. year BP) at Pikku. The earlier arrival of *Picea abies* at Rosalia, at the middle of the Holocene Thermal Maximum, could be explained by a moister microclimate. The second alternative hypothesis—related to fire—was also partially supported, as the expansion and persistence of *Picea abies* at Pikku were associated with crown fires, and highest *Picea abies* abundances were recorded when fires were smaller at both sites, but at mid-high rather than low frequencies, contrary to what was expected. The shift in fire regime from mid to late Holocene was not solely climate related, but involved feedback loops among vegetation, fire and climate.

4.1 | Early Holocene

Following deglaciation of the region in the early Holocene, the landscapes were dominated by *Betula*, shrubs and grasses (Hyvärinen, 1975; Seppä, 1996). This vegetation composition resulted from humid and cool climate conditions from 9500 to 8500 cal. year BP (Davis et al., 2003; Korhola et al., 2002; Luoto et al., 2014; Seppä et al., 2002; Shala et al., 2017), likely more pronounced at Rosalia than at Pikku. Fire frequency was very low, because of moist conditions and/or low vegetation flammability (Cumming, 2001; Hoecker et al., 2020).

4.2 | Transition to Mid-Holocene: Establishment of *Pinus sylvestris*

A shift in vegetation composition occurred around 8700 cal. year BP at Pikku and 7800 cal. year BP at Rosalia, leading to dominance of *Pinus sylvestris* (Figure 3). This vegetation change has been noted in other regional-scale Holocene vegetation reconstructions across northern Fennoscandia (Reinikainen & Hyvärinen, 1997; Seppä et al., 2004; Soloviena & Jones, 2002), and is explained by warmer and drier conditions during the period known as the Holocene Thermal Maximum (Barnekow, 2000; Bjune et al., 2004; Donner et al., 1978; Heikkilä et al., 2010; Korhola, 1995; Korhola et al., 2005; Luoto et al., 2014; Seppä & Birks, 2001; Seppä & Hammarlund, 2000). The later increase in *Pinus sylvestris* at Rosalia might be explained by wetter conditions due to the proximity of the large Lake Inari and more basic soils due to bedrock composition, considering the preference of *Pinus sylvestris* for drier, acid and nutrient-poor habitats (Heiskanen & Mäkitalo, 2002; MacDonald et al., 2000; Richardson, 2000; Sutinen et al., 2002; Sutinen & Middleton, 2020). However, the timing difference could also be the consequence of a reservoir effect on radiocarbon dates (Björck et al., 1998; Grimm et al., 2009) having differentially affected the Rosalia and Pikku chronologies. Indeed, the pollen grains of *Pinus sylvestris* and *Betula* spp. are dispersed over long distances and should display a common regional signal (Prentice, 1985). Following *Pinus sylvestris* establishment, fire frequency gradually increased in response to warmer and drier conditions but remained relatively low (Figure 2). The fire return interval was approximately 250 years, a result in line with other reconstructions in Fennoscandia (Carcaillet et al., 2007; Clear et al., 2015). It is reasonable to assume that surface fires were the main fire type, as the self-pruning ability of *Pinus sylvestris* decreases the probability of crown fire occurrence by hampering vertical fire spread to the canopy for lack of ladder fuel (low-lying branches; de Groot et al., 2013; Johnston et al., 2015; Schwilk & Ackerly, 2001).

4.3 | Mid- to late-Holocene: Establishment of *Picea abies*

Large fires were recorded during the culmination of the Holocene Thermal Maximum (6500–4700 cal. year BP) at both sites, a period characterized by high temperature and low humidity in northern Fennoscandia (Hyvärinen & Alhonen, 1994; Korhola et al., 2005; Seppä, Alenius, Bradshaw, et al., 2009). At Pikku, severe fires occurred, as suggested by the increase in the proportion of charcoal particles with a woody aspect around 5500 cal. year BP. However, such severe fires remained relatively infrequent until about 4800 cal. year BP. The moist microclimate at Rosalia might have prevented crown fire occurrence, as evidenced by the continuous predominance of non-woody fuel charcoal types in the sediment record (Feurdean, 2021; Vachula et al., 2021).

At Pikku, the spread and persistence of *Picea abies* were recorded around the beginning of the Neoglacial period (ca. 4500 cal. year BP), in line with our hypothesis and other reconstructions in northeastern Fennoscandia and northwestern Russia (Kremenetski et al., 1999; Reinikainen & Hyvärinen, 1997; Seppä et al., 2004; Soloviena & Jones, 2002). *Picea abies* is known to be favoured by cool and moist environments (Carcaillet et al., 2007; Clear et al., 2015; Kuosmanen et al., 2016). It is also known as a fire-sensitive species favoured by low-frequency stand-replacing fires creating forest gaps allowing its establishment (Giesecke & Bennett, 2004; Seppä et al., 2004).

At Rosalia the expansion of *Picea abies* occurred earlier, between 6500 and 4700 cal. year BP. This result is counterintuitive considering the species' climatic preferences. However, early arrival of *Picea abies* has also been recorded in other lakes and bogs in Karelia, to the southeast of our study area (Babeshko et al., 2021; Soloviena & Jones, 2002). The difference in timing could also be the consequence of a reservoir effect on radiocarbon dates (Björck et al., 1998; Grimm et al., 2009). However, the presence of a reservoir effect at this period is unlikely for two reasons: (i) the temporal coincidence of the largest charcoal peak (around 6500 cal. year BP) at both sites and (ii) trace abundance of *Picea abies* pollen at Pikku between 6500 and 5000 cal. year BP, indicating that regional populations established at the same time at both sites, although local expansion occurred later at Pikku (Figure S5). Thus, our interpretation is that the arrival of *Picea abies* occurred around 6500 cal. year BP at both sites, but that earlier expansion at Rosalia could be attributed to the proximity of Lake Inari and to the type of bedrock, leading to moister, less acidic and more nutrient-rich habitat conditions (Henne et al., 2011; Miller et al., 2008; Sutinen & Middleton, 2020).

Between 4500 and 2500 cal. year BP, the fire regime shifted towards smaller but more frequent events, as was observed in other regional-scale reconstructions (Matthews & Seppälä, 2014; Pitkänen et al., 2003). Previous studies in north European and northwestern Russian boreal forests suggest that increased fire frequency during the Neoglacial period could have resulted from changes in the inter-annual precipitation pattern controlled by the North Atlantic sea surface temperature, leading to more lightning strikes and/or periodic summer droughts (Barhoumi et al., 2019; Brown & Giesecke, 2014; Drobyshev et al., 2016; Pitkänen et al., 2003). Smaller fires were likely due to higher annual precipitation (inferred by increased *Sphagnum* abundance; Heikkilä et al., 2010; Korhola et al., 2005) preventing fire spread. The cooler and moister Neoglacial climatic conditions were favourable to *Picea* arrival at Pikku and persistence at Rosalia. Increased *Sphagnum* abundance and PAR during the Neoglacial period can be attributed to the expansion of peat deposits and to densification of the forest cover, respectively (Barnekow et al., 2008). An increase in crown fire occurrence was recorded at Pikku, especially between 3000 and 2500 cal. year BP, as shown by the large proportion of charcoal particles with a woody aspect. Denser forest stands, together with the high proportion of *Picea abies* (with high vertical fuel continuity) likely increased ecosystem vulnerability to stand-replacing fires during severe episodic dry periods (Rogers et al., 2015; Van Wagner, 1977; Weise et al., 2018).

A shift towards reduced *Picea abies* abundance was recorded at Pikku during the last 2000 years, likely due to reduced humidity as expressed by decreasing *Sphagnum* abundance. Lower woody fuel charcoal type and lower fire activity were also recorded, indicating a return to a regime consisting mainly of surface fires, except around 900–600 cal. year BP when crown fires likely occurred during the Medieval Warm Period (1150–650 cal. year BP; Ljungqvist, 2010), which opened the landscape and favoured *Betula*. Despite this change in vegetation composition, fire severity did not increase, probably because fuel levels remained too low to sustain crown fires. At Rosalia, *Picea abies* abundance remained high until today, probably due to moister habitat conditions than at Pikku (Pitkänen et al., 2003; Tryterud, 2003; Wallenius et al., 2010).

Our results show that climate can directly affect fire regimes in northern Fennoscandia, as warm and dry periods were more associated to low-frequency, large surface fires, whereas cool and wet periods were more associated with high fire frequency. However, an indirect effect of climate on fire regimes is also caused by a feedback loop with vegetation depending on local abiotic conditions. Indeed, higher *Picea abies* abundance together with denser forest stands can cause fuel accumulation favouring small crown fires, which, in turn, favour *Picea abies* and so on. Therefore, as noted in other boreal ecosystems (Gaboriau et al., 2022), understanding fire regimes necessitates to consider not only the interactions between climate and fire, but also with vegetation.

4.4 | Perspectives for future northern Fennoscandian boreal forests

Despite the possibility of increased annual precipitation in the future, higher temperature will increase evapotranspiration, leading to decreased moisture in the soil surface layer during the more frequent anomalously dry climatic events (Ruosteenoja et al., 2018). Our results indicate that, under future warmer and drier conditions, forests in northern Fennoscandia could experience a return to a fire regime characterized by large surface fires favouring *Pinus sylvestris* and *Betula*, as observed during the Holocene Thermal Optimum. However, greater climatic instability could alter vegetation succession patterns by locally increasing *Picea abies* abundance, resulting in denser forest stands, higher fuel abundance and increased ecosystem vulnerability to episodic small stand-replacing crown fires. A more in-depth understanding of the impact of climatic instability on the composition and structure of forest stands according to soil types would make it possible to better anticipate fire regimes at the local scale in boreal Fennoscandia.

AUTHOR CONTRIBUTIONS

Cécile C. Remy, Gwenaël Magne and Adam Ali developed the framework used in this study. Gwenaël Magne, Normunds Stivrins, Tuomas Aakala, Hugo Asselin, Heikki Seppä and Adam A. Ali performed the fieldwork. Gwenaël Magne, Normunds Stivrins and Nauris Jasiunas collected the pollen and charcoal data. Tomi Luoto and Heikki Seppä provided and analysed the reconstructed mean July temperature data. Cécile Remy performed the analyses. All authors contributed to the drafting of the manuscript and gave final approval for publication.

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CONFLICT OF INTEREST

The authors declare no conflict of interest associated with this work.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data sources and codes are freely available on Zenodo at https://zenodo.org/badge/latestdoi/521305132 (Remy et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Main characteristics of the sampled lakes. Mean sediment accumulation rates and median time resolutions of each individual core were derived from their respective age-depth models.

Table S2. AMS ^{14}C dates.

Figure S1. Age-depth models for each lake sediment profile.

Figure S2. Charcoal accumulation rates (CHAR) series from the studied lake sediment cores. CHAR series were interpolated to median sample resolution and were decomposed into a background component and a peak component. The background component results from long-distance burning and/or redeposition processes of charcoal particles that are unrelated to watershed fire occurrences. It was estimated by applying the LOWESS-smoothing technique robust to outliers, and removed by subtracting the charcoal values lower than the LOWESS-smoothing function from the interpolated CHAR series to isolate the peak component (Higuera et al., 2007).

Figure S3. Chironomid-based reconstructions of mean July air temperature from lakes Toskaljavri (Seppä et al. 2002) and Varddoaijavri (Luoto et al. 2014).

Figure S4. Broken stick model used to find the appropriate number of groups in CONISS. The changes in total sum-of-squares indicates 4 groups for the Lake Rosalia and 6 groups for the Lake Pikku.

Figure S5. Pollen percentage of *Picea abies* at Pikku before local expansion (see Fig.3).

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