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Did long-term fire control the coniferous boreal forest composition of the northern Ural region (Komi Republic, Russia)?

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Abstract

Aim: Documenting past vegetation dynamics and fire-vegetation relationships at a regional scale is necessary to understand the mechanisms that control the functioning of the boreal forest, which is particularly sensitive to climate change. The objective of this study is to document these interactions in the Komi Republic during the Holocene.

Location: Yaksha, Vychegda river basin, Republic of Komi, Russia.

Taxon: Plantae, gymnosperms, angiosperms.

Methods: Two palaeoecological approaches are combined, based (1) on pollen (this study) and charcoal analysis (recomputed from our previous analysis) applied to cores from two peatlands and (2) on a REVEALS model (a part of the Landscape Reconstruction Algorithm "LRA") applied to six regional pollen cores in order to obtain a regional estimate of vegetation cover during the Holocene.

Results: The pollen diagram produced locally from Yaksha was compared with the regional vegetation cover determined by REVEALS. Taxa such as *Abies* sp. and *Pinus* spp. showed differences between the two approaches, but vegetation signals remain qualitatively consistent. From 10,000 to 6,000 cal. yr BP, the forest was mainly a light taiga (composed of *Pinus sylvestris* and *Betula* spp.) and low fire activity was recorded. From 6,000 to 3,500 cal. yr BP, a dark taiga (composed of *Picea* spp., *Abies sibirica* and *Pinus sibirica*) was established due to favourable climatic conditions, despite higher fire activity. From 3,500 cal. yr BP onwards, the continuous increase in fire activity allowed for a gradual return of light taiga, *Betula* spp., likely reinforced by human activities. The dynamics of *Picea* spp. and *Abies* sp. were asynchronous between the sites. For *Picea* spp., the hypothesis of local inter-site expansion distributed along stream corridors is supported by the data. For *Abies* sp., a bias in REVEALS, and in climate cooling may explain disparities between sites.

Main conclusions: We found evidence that in the early and mid-Holocene, vegetation dynamics were probably more influenced by climate, as fire activity was low. During the late Holocene, fire activity and geomorphology, eventually augmented by human activities, increased in influence on vegetation dynamics and led to the predominance of the light taiga forest up to the present.

KEYWORDS

charcoal, disturbances, fire history, palaeoenvironmental reconstruction, pollen, REVEALS model, Russian boreal forest, vegetation-fire interactions

1 | INTRODUCTION

Global warming calls for a better understanding of ecosystem responses to climate and human forcing (Spittlehouse & Stewart, 2003). In the higher latitudes, which are reacting fastest, climate change has been markedly affecting the vegetation dynamics and fire activity in the boreal region (Drobyshev et al., 2017).

Flannigan et al. (2009) suggest that today's forest vegetation dynamics in boreal regions are controlled by both fire regime and climate change. Johnson (1992) and de Groot et al. (2013) relate fire regime to climate (for ignition) and vegetation (for fuel), and more recently by human activities. Furthermore, the climate, fire and vegetation are linked by complex interactions at different temporal and spatial scales (Higuera, Brubaker, Anderson, Hu, & Brown, 2009). At the regional scale, climate is considered to be the main driver of Holocene fire regimes and vegetation, while at the local level, topographic and vegetation factors could interfere with climate forcing (Hellberg, Niklasson, & Granström, 2004). Studies of past fire activity, vegetation and climate dynamics, based on peatland or lake sediments, can document boreal forest dynamics at the ecosystem level or at the regional level of plant biogeography, while providing better insights into the governing ecological mechanisms that govern how they function (Botkin et al., 2007; Peteet, 2000).

In Eurasia, two main types of boreal forests, called taiga, are present (Pflugmacher et al., 2011; Shvidenko & Nilsson, 2000; Syrjänen, Kalliola, Puolasmaa, & Mattsson, 1994; Vygodskaya et al., 2007). They are defined by the presence of some predominant species and by an associated fire regime. Light taiga forests are characterized by *Pinus sylvestris*, *Larix* spp. and *Betula* spp. along with a high-frequency but low-intensity fire regime (mainly surface fires) (Goldammer, 2015; Lapenis, Shvidenko, Shepaschenko, Nilsson, & Aiyyer, 2005; Schulze, Wirth, Mollicone, & Ziegler, 2005; Shorohova, Kuuluvainen, Kangur, & Jögiste, 2009). Dark taiga forests are mainly composed of *Picea* spp., *Abies sibirica* and *Pinus sibirica* and are associated with a high-intensity (crown fires), but low-frequency fire regime (Lapenis et al., 2005; Schulze et al., 2005; Shorohova et al., 2009).

Well-documented past vegetation/fire-related studies of the boreal biome are available from Fennoscandia, North-Western Russia and North America (Clear, Molinari, & Bradshaw, 2014; Girardin et al., 2013; Higuera et al., 2009; Kuosmanen, Fang, Bradshaw, Clear, & Seppä, 2014; Seppä & Birks, 2002; Stivrins et al., 2019). In these regions, boreal biomes are largely dominated by *Picea*, *Pinus*, *Betula* and *Populus* species (Goldammer, 2015) and fire activity is generally associated with crown fires. In the Urals region of Russia, the links

between fire, climate and vegetation during the Holocene have not been investigated, as studies have mainly focused on climate and vegetation dynamics (Antipina, Panova, & Korona, 2014; Panova & Antipina, 2016). West of the Ural mountains, in the Republic of Komi, two studies have documented past vegetation and climate dynamics based on pollen analysis of several sites (Baika, Kalya, Cherny Yar and Syndorsky, Figure 1) during the Holocene (Golubeva, 2008; Sidorchuk, Borisova, & Panin, 2001). They showed that during the beginning of the Holocene (about 11,700 to 10,500 cal. yr BP), a light taiga composed of Scots pine (*Pinus sylvestris*), birche and spruce was established. At the same time, tundra retreated, which was indicated by the disappearance of characteristic species, such as *Artemisia absinthium* (wormwood), Poaceae and herbs (Golubeva, 2008). Subsequently, from 10,500 to 8,800 cal. yr BP, the light taiga remained and *Abies* sp. appeared in the regional vegetation for the first time (Nikiforova, 1979). Then, from 8,800 to 5,300 cal. yr BP, pines and larches successively dominated the light taiga with spruce present. A cool climate was associated with the disappearance of hardwood species. During the mid-late Holocene, from 5,300 to 2,500 cal. yr BP, birch developed and spruce forests decreased, with fir trees reaching their maximum expansion between 4,800 and 3,400 cal. yr BP (Golubeva, 2008; Nikiforova, 1979). The gradual decline of spruce forests reinforced the light taiga which continued to strengthen at the end of the Holocene (from 2,500 cal. yr BP to present; Golubeva, 2008).

Surface fires are currently the most common ecological disturbance for boreal forests of Eurasia. They are frequent, low intensity and usually burn only part of the litter (Goldammer, 2015; Goldammer & Furyaev, 1996; Schulze et al., 2005). This fire regime is clearly associated with the boreal forests, especially the light taiga, which is composed of fire-tolerant species such as *Pinus sylvestris*, and *Larix* spp. (Goldammer & Furyaev, 1996; Schulze et al., 2005). *Pinus sylvestris* for example, is a species that predominates on dry and sandy soils, and is well-adapted to surface fire regimes, with rather high frequencies (a Fire Return Interval (FRI) of up to 20 years) (Drobyshev, Niklasson, Angelstam, & Majewski, 2004a; Goldammer & Furyaev, 1996). Indeed, fires induce pines to release their seeds and stands of trees are generally not damaged as they practice self-pruning of lower limbs, thus preventing fires from spreading up to the canopy, while *Larix* spp. have a thick protective bark (Sannikov & Goldammer, 1996). *Betula* spp. are also frequently found in light taiga because they are a pioneer species that grow quickly after fires, simultaneously with *Pinus sylvestris*, but with faster growth (Schulze et al., 2005). In the boreal forests of Russia, dark taiga forest systems develop in association

investigating taxon biogeography, in particular, *Abies* sp. and *Picea* spp., along with their distribution history.

2 | MATERIALS AND METHODS

2.1 | The study area

The Republic of Komi is a Russian administrative division of 415,900 km², located on the western side of the Ural Mountains (Figure 1a and b). The soils of the region are mainly moraine and surface loams (Zaboeva, 1997; Drobyshev et al., 2004), with podzolic soils and the topography is flat except near the Ural Mountains (Naryshkin, 2003). Currently, the population of the Republic of Komi is about 1.12 million habitants.

In the north, the mean annual temperature is -6°C , while in the south, it is $+1^{\circ}\text{C}$. The annual precipitation varies between 450 and 700 mm (Drobyshev et al., 2004a; Golubeva, 2008). The forest cover consists mainly of spruce (*Picea* spp., from 56% regionally in the Republic of Komi to 13% locally in Yaksha, within a radius of 10 km from the coring site, based on the resolution of Figure 1c), Scots pine (*Pinus sylvestris*, from 25% regionally to 84% locally) and birch (*Betula pendula* and *Betula pubescens*, from 1.4% regionally to 2% locally) (Figure 1). Vegetation maps have therefore opposed the short prevalence of the dark taiga at a regional scale and a clear dominance of a light taiga locally. Ecologically, the young birch trees (Figure 1c and d) follow the hydrographic network, as does *Picea* spp., which favours proximity to small rivers and marshy areas. *Pinus sibirica* and *Abies sibirica* may also occur near wetter areas. Genera which are represented by more than one species in the study area are described with the nomenclature "spp." (such as *Pinus* spp., *Picea* spp., *Betula* spp. and *Larix* spp.). For other genera, which are not known to have several species in the study area, the nomenclature "sp." is used (such as *Abies* sp., as only the single species *Abies sibirica* is known from the Urals).

The study sites are peatlands named Yak2 and Yak3 from the Yaksha area (Figure 1d) (Barhoumi et al., 2019). Two cores were extracted in 2016 using an 8-cm diameter Russian peat corer from

the centre of the *Sphagnum* peatlands, and are named accordingly Yak2-A (168.5 cm) and Yak3-A (350 cm) (Figure 1c and d). Dominating tree species observed were *Pinus sylvestris*, *Betula* spp. and *Picea* spp. stands which could be seen while crossing rivers and streams to access the two peatlands.

2.2 | Dating and chronology of the peat cores

The chronology was based on five radiocarbon measurements from core Yak2-A, and seven radiocarbon measurements from core Yak3-A, that are discussed in detail by Barhoumi et al., (2019) (see Appendix S1, S4, S5 and Figure 2).

2.3 | Pollen analysis

In order to compare pollen and charcoal signals, so as to cover the maximum time extent, a composite sequence was built from cores Yak3-A and Yak2-A. In core Yak3-A, the 0 to 300 cm interval offers the best temporal resolution and its top was preserved (contrary to Yak2-A). Samples were taken every 6–10 cm in Yak3-A. The lower part of core Yak2-A offered access to older time intervals recorded in the organic sediment, although with a lower temporal resolution, where samples were taken every 3 cm. Control samples were taken every 25 cm for the first 100 cm (corresponding to the overlap with core Yak2-A, ensuring the homogeneity of the pollen signal between the two sequences). A 3-cm³ subsample of sediment from the centre of each slice underwent chemical treatment (HCl, KOH, HF, acetolysis) and 500 μm sieving (Moore et al., 1991). The pollen analysis was carried out with a light microscope at a standard magnification of 400x. 39 pollen types were identified using the reference collection at ISEM and photo atlases (e.g. Reille, 1999; Beug, 2004). The two *Pinus* species (i.e. *P. sibirica* and *P. sylvestris*) were identified based on the morphology of pollen bladders, while *Betula* spp. (*B. pendula* and *B. pubescens*) and *Picea* spp. (*P. abies* and *P. obovata*) subspecies were not distinguished. A minimum of 300 pollen grains was counted per sample, and the average sum was 315 pollen grains. Terrestrial pollen percentages were

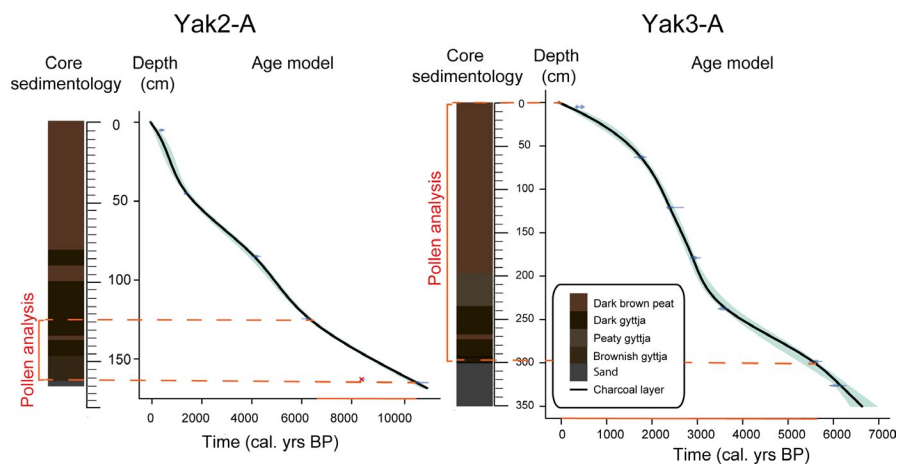


FIGURE 2 Lithology and age-depth model of Yak2-A and Yak3-A cores, in Republic of Komi, based on calibrated radiocarbon ages, modified from Barhoumi et al. (2019). Red star is the age rejected by the age-depth model. The dashed and full orange lines indicate the part of the age model that was used in the pollen analysis

calculated based on the total terrestrial pollen sum; wetland taxa percentages were calculated based on the total wetland taxa (*Sphagnum*, Cyperaceae, *Typha/Sparganium* and *Menyanthes*). Pollen diagram plotting and local pollen assemblage zones were defined using the CONISS function of the Psimpoll program (Bennett, 1992). Pollen data (Yaksha) that support the findings will be available in The European Pollen Database at [<http://www.europeanpollendatabase.net/index.php>].

2.4 | Application of the REVEALS model

To quantify the regional vegetation cover in the study area, the REVEALS model was applied (Sugita, 2007a). The parameters required for REVEALS are basin radius, pollen productivity estimates and the rate of fall of the pollen grains (PPE). As these parameters are not available for the region of the Republic of Komi, the PPE values were obtained from a study conducted in Estonia (Poska, Meltsov, Sugita, & Vassiljev, 2011). This is the closest available dataset from a similar bio-climatic region as the study area. This selection was based on the comparison of metadata of all modern pollen sites using PPE and the bio-climatic world map displayed in QGIS software (Sayre et al., 2014). The same PPE of the genus *Pinus* was assigned for the *Pinus sylvestris* and *Pinus sibirica* species. The REVEALS model tends to correct the regional signal of large-area sites (Sugita, 2007a) and therefore, following Cao et al. (2018), the Yaksha vegetation signal was compared with other signals within a 500 km diameter around the site. Five previously analysed pollen sequences were used from south to north, for which construction of a new age-depth model was necessary (Appendix S6): Baika (Borisova, 2002), Sedkyrkesch (Golubeva, 2008), Kalya (Karmanov, Zaretskaya, Panin, & Chernov, 2011), Cherny Yar (Marchenko-Vagapova & Marieva, 2001) and Syndorsky (Golubeva, 2008) (Figure 1b, Table 1). Combined with the Yaksha record, the six pollen sequences were then homogenized in 23 time-windows from -50 to 10,500 cal. yr BP. The time-spans selected to record general vegetation patterns by REVEALS varied from lengths of 100, 150 and 400 years for the three first time-windows to 500 years for the other 20. The most recent time window was calculated only on the Yaksha values because the other cores do not cover the -50:50 cal. yr BP period (Table 1). For the regional vegetation cover inferred from the REVEALS model (Figure 5), the time-windows were set to 200 years and the diagram was plotted with the R software package 'rioja' (Juggins, 2009). The calculations were performed using the REVEALS 5.0 software and Prentice's model (1985) utilizing the following parameters: 3 m.s⁻¹ wind speed, and each lake's radius (Table 1). The results were plotted with the Psimpoll software (Bennett, 2008) and stratigraphically constrained cluster analysis with the CONISS function.

2.5 | Fire analysis

Sediment treatment and charcoal analysis were carried out by Barhoumi et al. (2019), following the conventional procedures

recommended by Carcaillet et al., (2001) (see Appendix S1). The statistical treatment, and the calculations of computed and temporally smoothed mean Fire Return Interval (mFRI), are based on the four sedimentary cores from the Yaksha study site (see Appendix S1) (Barhoumi et al., 2019; Higuera et al., 2009; Higuera, Gavin, Bartlein, & Hallett, 2011; Mudelsee, Börngen, Tetzlaff, & Grünwald, 2004). Regime shift analysis was performed using the 'changeoint' package (Killick & Eckley, 2014; Killick, Haynes, & Eckley, 2016) with the R program (Team, 2014). The regime shift detection algorithm was used to identify periods of stable mFRI, from R-1 to R-5 (Drobyshev et al., 2016; Rodionov, 2004; Rodionov & Overland, 2005). A significance level of 0.05 was used for all analyses, and to control for the weights of outliers, the Huber's weight parameter was set to 2. A cut-off length of 4,000 years was chosen for the evaluated regime.

3 | RESULTS

From core Yak2-A, 20 samples were counted and four were sterile (no pollen grains preserved, 219-year resolution). From core Yak3-A, 60 samples were counted and 18 were sterile (133-year resolution).

3.1 | Age models

Based on the two age models (Figure 2), the Yak2-A core covers almost the entire Holocene period, from ca. 11,010 to -60 cal. yr BP, with a mean temporal resolution (deposition time) of 65.7 year.cm⁻¹ (standard deviation = 29.3 years). Yak3-A is temporally shorter than Yak2-A, covering the mid-Holocene to the present day (ca. 6,630 cal. yr BP to 50 cal. yr BP, lacking nearly the last 100 years) with a mean temporal resolution of 19.1 year.cm⁻¹ (standard deviation = 9.9 years) (Barhoumi et al., 2019).

3.2 | Pollen and fire analyses at Yaksha

Analysis of the fire activity showed a gradual decrease in FRI during the Holocene, which translates into an increase in fire activity for the entire Yaksha study site (Barhoumi et al., 2019).

The composite sequence for pollen data was analysed from Yak2-A for the early Holocene and subsequently from Yak3-A for the mid- and late Holocene. The bottom sandy part was void of pollen. Terrestrial pollen assemblages from Yaksha (Figure 3) were divided into four pollen zones labelled Z'1, Z'2A, Z'2B and Z'3 (Figure 3). The pollen diagram indicates a forested landscape during the last 10,000 years. From 10,000 cal. yr BP to 6,050 cal. yr BP (Z'-1 in Figure 3 which corresponds to zone Z-1, see Appendix S2), the vegetation was dominated by *Pinus sylvestris* and *Betula* spp. These two taxa are anti-correlated: when *Pinus sylvestris* decreases, *Betula* spp. increases ($r^2 = 0.81$). *Picea* spp. was also recorded and showed close trends to *Pinus sylvestris*, while *Abies* sp. and *Pinus sibirica* were absent during this period. Therefore, this period is consistent with

TABLE 1 Pollen record information for the REVEALS model

Name of the site	Coordinates	Time covered (cal. yr BP)	Lake/peat radius (m)	References
Yaksha	61°43'N, 55°29'E 61°41'N, 55°34'E	-50 to 10,050	265	This study
Baika	61°16'N, 46°44'E	50–8,780	365	Borisova, (2002)
Cherny Yar	62°13'N, 50°17'E	2,880–8,530	300	Marchenko-Vagapova and Marieva, (2001)
Kalya	61°48'N, 51°47'E	0–10,150	300	Karmanov et al. (2011)
Sedkyrleshch	61°43'N, 50°51'E	1,200–4,240	700	Golubeva, (2008)
Syndorsky	62°44'N, 51°51'E	4,730–9,430	10,900	Golubeva, (2008)

the present description of a light taiga system. *Sphagnum* spp. is related to the peatland itself where it develops on the peat surface and wet soils. The percentage of the wetland taxa Cyperaceae, increases between 9,000 and 7,800 cal. yr BP. This coincides with the R-1 and R-2 windows of the mFRI, and therefore indicates two distinct fire regimes: the first from 10,000 cal. yr BP to 7,500 cal. yr BP with a median mFRI of about 400 years, and the second from 7,500 to about 5,800 cal. yr BP, with a median mFRI of 250 years (Figure 3).

The zone Z'-2 extends from 6,050 BP to 100 cal. yr BP and was characterized by an increase of *Picea* spp. and the appearance of *Pinus sibirica*. It was divided into two subparts, Z'-2A from 6,050 to 3,200 cal. yr BP and Z'-2B from 3,200 to 100 cal. yr BP. *Pinus sylvestris* and *Betula* spp. showed different patterns and their relationship was more complex. *Pinus sibirica* appeared in Z'-2A and *Abies* sp. in Z'-2B, signalling the establishment of a dark taiga forest. An increase of Cyperaceae at the beginning and the end of Z'-2A occurred, and during this period, the mFRI was 200 years (R-3). From 3,200 to 100 cal. yr BP (Z'-2-B), the dark taiga decreased slowly and the light taiga reappeared, with an increase of *Pinus sylvestris*. At the same time, the median mFRI fell below 200 years (R-4, 135 years). More recently, there was a strong increase in *Betula* spp., which reached percentages above 65% (Z'3, from 100 cal. yr BP to 0 cal. yr BP), with the mFRI being less than 100 years (R-5).

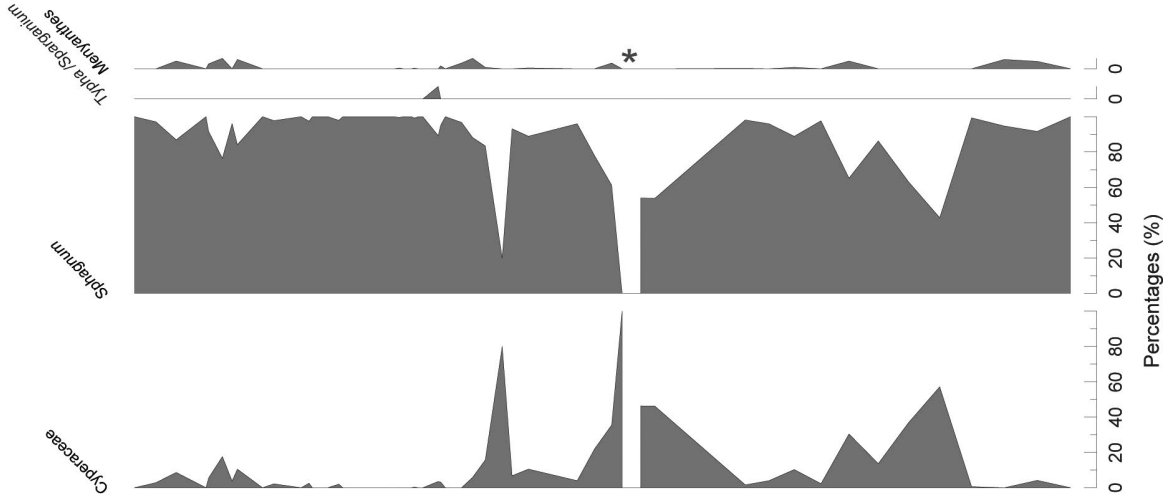
3.3 | REVEALS signals: yaksha vegetation cover versus Komi vegetation cover

REVEALS vegetation cover was divided using CONISS into six zones labelled M-1, M-2, M-3, M-4, M-5 and M-6. In general, the vegetation cover trends at Yaksha were similar to those observed at the regional level in the Republic of Komi (Figure 4). The notable differences were the grasses (Poaceae), which were not well-developed at Yaksha (M-1, M-5 and M-6) and the regional development of *Abies* sp. during the first half of the Holocene (M-2).

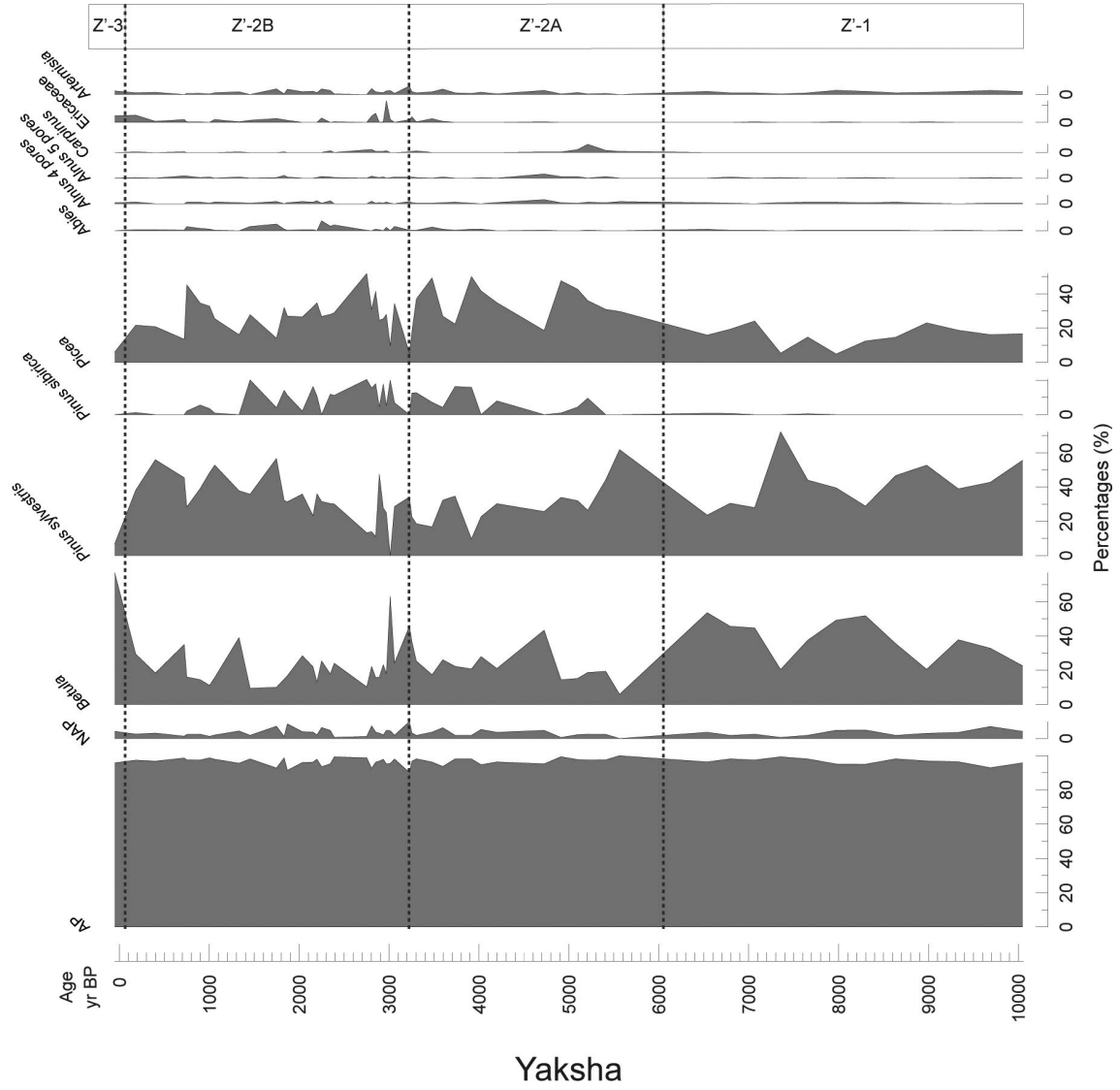
The trends of *Betula* spp., *Picea* spp. and *Pinus sibirica* at Yaksha were similar to those observed at a regional scale (the Republic of Komi). For *Betula* spp., the only notable difference was the lower abundance of *Betula* spp. (< 5%) at Yaksha compared to the regional signal (20%) at 5,500 cal. yr BP. For *Picea* spp., there were few differences in zone M-2, i.e. between 8,500 and 8,000 cal. yr BP, when it was much more represented at Yaksha (30%) than at the regional level (10%) and between 6,500 and 6,000 cal. yr BP, when it was less represented at Yaksha (30%) than at the regional level (60%). For *Pinus sylvestris*, during the first half of the Holocene (M-1, M-2 and M-3), this taxon was more locally represented at Yaksha (generally > 10%–15%) than at the regional level. The signals between the pollen results and REVEALS reached similar levels at 5,000 cal. yr BP (M-3). Finally, *Abies* sp. was the taxon that showed the most differences between the two signals. At the regional level, *Abies* sp. strongly developed from 8,500 cal. yr BP (about 40%, M-2), then gradually decreased to less than 10% at 6,500 cal. yr BP (M-2). In contrast, at Yaksha, its signal was constant but much lower during this period (around 10%). Subsequently, after 6,500 cal. yr BP, the two signals showed more consistency (M-3, M-4 and M-5). Thus, it is more likely that *Abies* sp. developed at Yaksha during its second wave in the Republic of Komi, from 5,000 cal. yr BP (M-3), when the two signals can be corroborated. *Alnus* and Poaceae taxa were poorly represented at the Yaksha site. With the REVEALS model, *Alnus* remained relatively low in the regional representation (maximum 3%, in M-3, around 4,500 cal. yr BP). For Poaceae, high percentages were reconstructed at the beginning of the Holocene in zone M-1, between 10,500 and 10,000 cal. yr BP (30%), though their presence decreased strongly thereafter and remained below 3%, before gradually increasing from 1,000 cal. yr BP, to reach about 8% at 50 cal. yr BP (M-5 and M-6). The dynamics at the regional level were not the same as at the local level at Yaksha, since the presence of Poaceae was only slightly visible between 5,500 and 5,000 cal. yr BP (2%, M-3). In contrast, *Artemisia* percentages were

FIGURE 3 Pollen diagram versus age showing percentages of the main pollen taxa from the Yak2-A and Yak3-A cores, in Republic of Komi, and the mFRI with the Rodionov regime shift zones, modified from Barhoumi et al. (2019). The sample marked with a red star did not contain any wetland taxa. The pollen diagram was divided into four zones with CONISS: Z'-1 from 10,047:6,050 cal. yr BP, Z'-2-A from 6,050:3,200 cal. yr BP, Z'-2-B from 3,200:60 cal. yr BP and Z'3 from 60:-58

Aquatics



Terrestrials



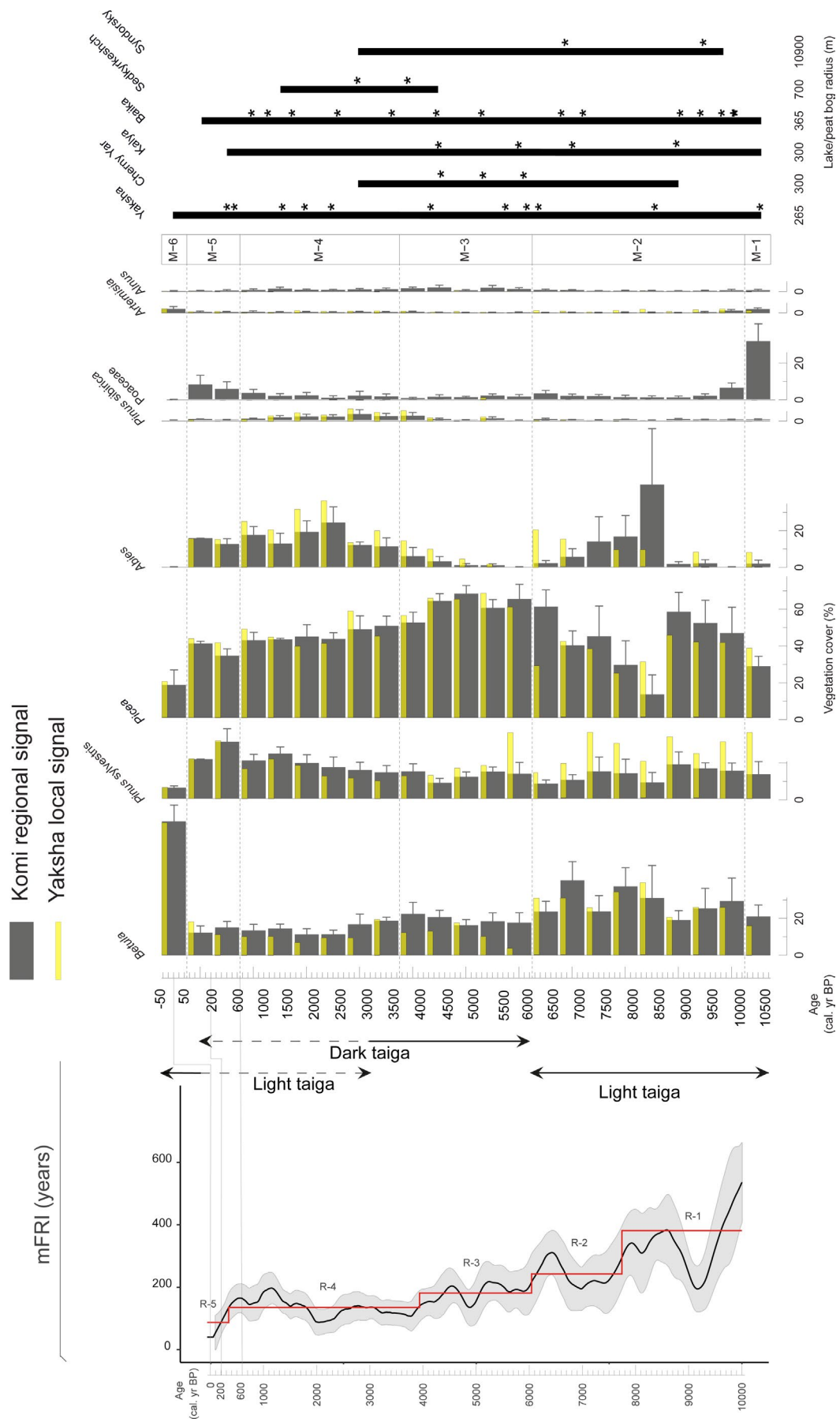


FIGURE 4 Vegetation diagram versus age inferred from the REVEALS model showing percentages of the main forest taxa at the Yaksha site, in Republic of Komi, compared to vegetation at the regional scale. In the histogram, an error bar (± 1 standard deviation) is represented for each estimate made by REVEALS. The contribution of each site to the reconstruction of REVEALS is represented on the left by a bar that indicates the time window over which the site data extend. The radius corresponds to the size of lakes or peat bogs. The black stars to the right of each site correspond to the radiocarbon dates (median cal. yr BP). The mFRI with the Rodionov regime shift zones are represented, modified from Barhouni et al. (2019)

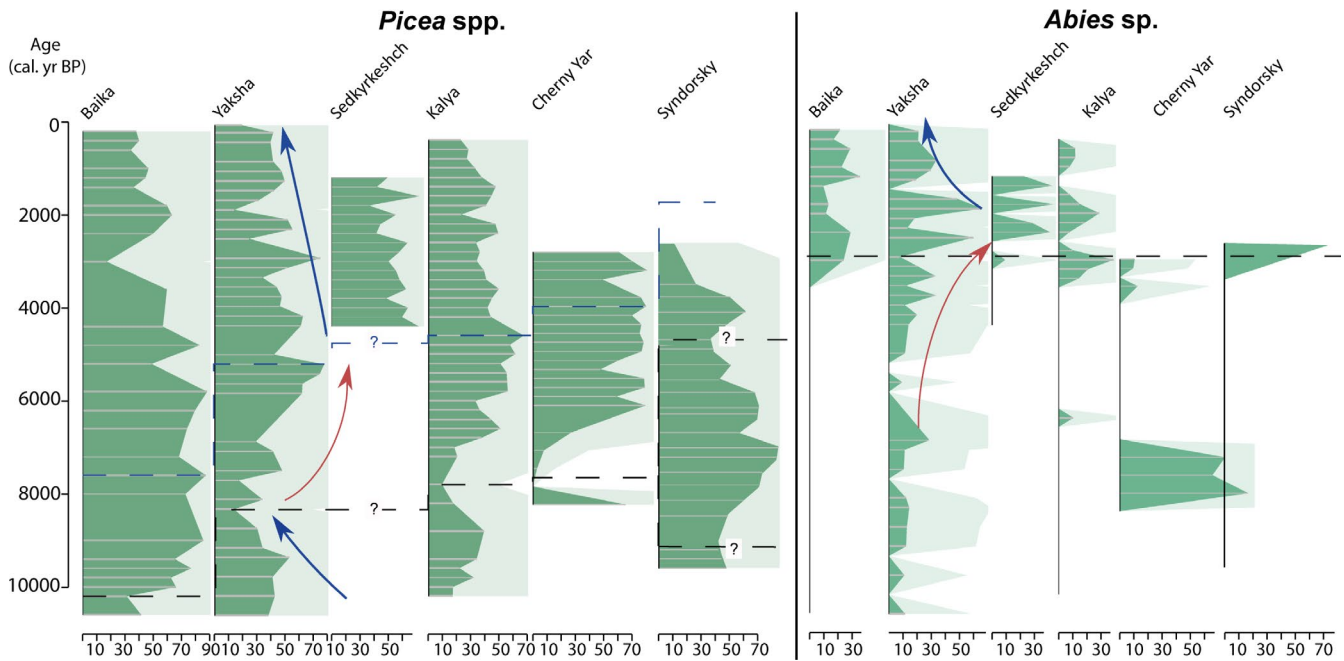


FIGURE 5 Vegetation diagram versus age from the REVEALS model showing the development of *Picea* spp. and *Abies* sp. in Republic of Komi. The sites are ordered according to a south-north gradient

similar at the local and regional spatial scale. Concerning *Pinus sibirica*, results between the Yaksha and Komi regional signals were similar. Percentages were low at the beginning of the Holocene from 10 500 until 4,000 cal. yr BP, and then the signal increased in M-4, reaching about 5% at 2,500 cal. yr BP, after which it decreased again to values close to 0% in the M-6 zone.

4 | DISCUSSION

4.1 | Holocene vegetation dynamic, fire activity and climate

4.1.1 | Republic of Komi

The relatively low fire activity from 10 000 to 6,000 cal. yr BP is associated with light taiga. Increase of *Picea* spp. at 9,000 cal. yr BP led to forest densification. This was most probably caused by more continental and climatic conditions that occurred from 9,600 cal. yr BP with colder temperatures (-3.5°C to -2.5°C in January and -0.5°C in July) and rainfall higher than currently (850 mm per year) up to 9,400 cal. yr BP (Golubeva, 2008; Sidorchuk et al., 2001). Around 8,500 cal. yr BP, increasing temperatures facilitated the appearance

of *Abies* (Golubeva, 2008). These two taxa are indicators of dark taiga, which contrasts with how nuanced the light taiga system is. During phases M-1 and M-2, the forest was mainly light taiga, but dark taiga indicator species were still present. Dark taiga is sensitive to burning (Goldammer & Furyaev, 1996), but mFRI remained high (median R-2 at 250 years) and thus was compatible with the presence of *Picea* spp. and *Abies* sp.

From 6,000 to 3,500 cal. yr BP (M-3), the dark taiga was at its maximum and its development is compatible with reconstructed levels of fire activity with median mFRI at ca. 180 years (R-3) (Gromtsev, 2002; Schulze et al., 2005). Golubeva (2008) observed a warming up to 5,300 cal. yr BP, followed by a cooling up to 5,100 cal. yr BP. Furthermore, Sidorchuk et al. (2001) reported a slight increase in humidity of 700 mm per year around 5,100 cal. yr BP, congruent with the dominance of *Picea* spp. During this period, in the study area, the concomitant increase in Cyperaceae over *Sphagnum* recorded in Yaksha, may attest to a higher water table in the wetlands, and therefore corroborates that moisture may be more important than the influence of fires in shaping the vegetation composition and dynamics.

From 3,500 to 50 cal. yr BP, there was a decrease in the mFRI (at ca. 135 years; R-4), which may have been facilitated by the increase in summer temperatures ($2\text{--}3^{\circ}\text{C}$ more than today) at the beginning

of this period (Golubeva, 2008, Klimanov's method). The decrease in mFRI could be the cause of a reappearance of the light taiga and the reduction in the dark taiga since such values of mFRI are incompatible with this kind of forest according to Goldammer and Furyaev (1996). From 600 to 50 cal. yr BP (M-5), the dominance of the light taiga was re-established, but dark taiga patches remained (presence of *Picea* spp. and *Abies* sp.). The fire activity was high and consistent with this type of forest, despite decreasing temperatures (Goldammer & Furyaev, 1996; Gromtsev, 2002; Hille and Den Ouden, 2004; Golubeva, 2008; de Groot et al., 2013). Indeed, *Pinus sylvestris* has highly flammable needle foliage, but is able to self-prune its lower branches, which reduces the possibility of tree death when a fire event occurs (Schulze et al., 2005). There was also a steady increase in Poaceae at a regional scale (100 cal. yr BP, M-5), which occurred when temperatures increased and rainfall gradually decreased to current values (around 700 mm per year) (Golubeva, 2008; Sidorchuk et al., 2001). This can indicate intensified anthropogenic use of the landscape, generally going hand in hand with the decrease of FRI. Both elements can highlight the relationship between human activities and the increase in fire activity during this period. Furthermore, this is accompanied by increasing temperatures and rainfall gradually decreasing to current values (around 700 mm per year).

The phase M-6 (50 to -50 cal. yr BP) was characterized by a sharp increase in *Betula* spp., probably resulting from increased human impact favouring fires. The climate was the same as it is today (Golubeva, 2008). Indeed, fire activity was the highest of the Holocene (mean mFRI = 81 years), with *Betula* spp. colonizing as a stand-replacing fire species (Schulze et al., 2005). Combined with greater human activities, such as cutting and clearing, these contributed to becoming the main sources of ignition and increasing fire frequency (Drobyshev et al., 2004a; Naryshkin, 2003).

4.1.2 | Boreal biome vegetation-fire interactions

One of the major issues in the functioning of boreal forests is to understand the relative importance of fire and climate drivers. Although Rogers, Soja, Goulden, and Randerson (2015) mentioned that tree species influence differences in boreal fires and climate feedbacks today, the study of past FRI is a useful tool to understand these mechanisms over time. Past FRI analysis has also helped to highlight key periods when fire is the determining factor in vegetation composition, especially when it reaches threshold values, which cannot be determined by current investigations. The most studied boreal forests are from North America where various fire regime changes took place during the Holocene (Ali et al., 2008; Bergeron, 2000; Carcaillet, Richard, Bergeron, Fréchette, & Ali, 2011; Higuera et al., 2009). Unlike the Yaksha study, northern Quebec's forests (*Picea glauca*, *Abies balsamea*) have had an increasing FRI since 800 cal. yr BP (nowadays FRI of about 300 years), in part due to wetter climatic conditions and reduced sunlight (Carcaillet et al., 2011). Forests in southern Quebec (*Abies balsamea*, *Betula papyfera*), on the other hand, have had a decreasing FRI for about 2,200 years with

a current value of about 200 years, similar to those in the Republic of Komi for the R-4 phase. In both cases, Carcaillet et al. (2011) determined that the change in FRI did not significantly affect the composition of the boreal forest, because on the one hand, a high vegetation diversity allowed resilience and on the other hand, the critical threshold values of FRI were not reached. This is similarly the case in the Republic of Komi, during the R-4 phases.

In central Siberia, the forest is a dark taiga, with a dominance of *Picea* spp./*Abies* sp. at the late stage of succession (Schulze et al., 2005). In this ecosystem, disturbances such as fire, wind throws and insects do not affect the nature of the successional stages that occur in this region. However, after a fire-type disturbance, the initial state is restored after about 400 years. Factors such as species ecology (growth/longevity/reproduction) play a major role in the regeneration of the species (Schulze et al., 2005). This can be compared with the R-3/M-3 phases of this study, where dark taiga persists, despite an increasing FRI but not reaching thresholds, which indicate higher fire activity.

Another study in northwest Russia showed that local conditions also play a major role in the composition of boreal forest vegetation (Kuosmanen et al., 2014). Thus, the parallel study of three sites (distances between sites from 800 m to 70 km) showed that in the same region, local conditions have an impact on the fire regime, which was not the same within the three sites. A similar result was observed in a Holocene study of FRI in Northern Europe (Stivrins et al., 2019). At Yaksha, the three study sites did not show the same local recent fire activities when tree ring fire scars were analysed (Barhoumi et al., 2019). In Kuosmanen et al. (2014), the different fire regimes were associated with different kinds of vegetation dynamics. When fires were frequent, the diversity of species was greater and *Picea* spp. was not among the dominant species, while when fires were absent, *Picea* spp. became a dominant species. However, despite different fire histories, the three sites showed a common decline of *Picea* spp. at the end of the Holocene, indicating a stronger impact of regional climate (Kuosmanen et al., 2014).

4.2 | Consideration of REVEALS method

In this study, vegetation dynamics and REVEALS were conducted on a composite core, combining the sequences of Yak2-A and Yak3-A. The investigation has been carried out this way in order to cover the entire Holocene period, and to have access to pollen information at the scale of the Yaksha study area. Since the two sequences do not come from the same peat bog, biases may be included when interpreting the results. However, replicate pollen samples were taken for the common dated periods for both sequences and the pollen percentages were consistent with each other. A similar approach was used for the mFRI study from the Republic of Komi, carried out on a regional level based on four cores (Barhoumi et al., 2019).

The REVEALS method has been tested and validated by several studies of regional vegetation development in Sweden across the Holocene, and especially in correcting the signal from species

with low pollen production, such as *Picea* spp., but also from species that are highly productive in pollen such as *Pinus* spp. and *Betula* spp. (Anderson, Bugmann, Dearing, & Gaillard, 2006; Hellman et al., 2008; Sugita et al., 2010). REVEALS has also been used to estimate vegetation cover in areas other than boreal forests, such as the Tibetan Plateau, for the Holocene period as well (Wang & Herzschuh, 2011). The use of pollen records from multiple small sites, as in this study, instead of from large lakes, has also been tested in Sweden by Trondman et al. (2016). Their study showed that vegetation estimates were well-suited for this kind of data but noted some problems, notably with the estimates of Cyperaceae and *Betula* spp., in bog-type sites.

The data required for the proper use of REVEALS are the size of the lake/peat, the pollen records and the pollen productivity estimates (PPE). However, the PPE, which is related not only to the species, but also to the region where the species are established, is not available for all regions because it has not been estimated everywhere (Bunting & Hjelle, 2010; von Stedingk, Fyfe, & Allard, 2008; Xu et al., 2014) and has not yet been developed in the Republic of Komi (Lisitsyna, Smirnov, & Aleynikov, 2017). Therefore, the selection of PPE from Estonia was chosen because this site has a forest similar to the one studied in the Republic of Komi and is situated at the same latitude (Poska et al., 2011). The climatic conditions are also similar, with total precipitation of approximately 680 mm/year, which is close to the values of the Republic of Komi. Sweden, whose PPE is known, was not chosen as a reference because the vegetation is subject to very different climatic constraints than our study area (Broström et al., 2008; Poska et al., 2011). However, the PPE specific to the Republic of Komi species may be different from the one used and this should be kept in mind when interpreting the results.

Concerning the results of *Abies* sp., the first increase in this taxon in M-1 and M-2 (Figure 4) should be taken with caution, because records show two different patterns when looking at the details from Figure 5b. At Yaksha, the REVEALS model estimates > 10% of *Abies* forest cover from only 1 or 2 pollen grains per sample. This is also the case for the Kalya site, with only two grains of *Abies* sp. pollen counted at 6,347 cal. yr BP. However for the Cherny Yar site, *Abies* sp. increased around 60% with 9 and 39 pollen grains counted during the early Holocene. Indeed, Poska et al. (2011) determined an average value of 6.71 that was used for REVEALS in this investigation. Abraham, Oušková, and Kuneš (2014) also observed unrealistic REVEALS estimates of *Abies* sp. cover in the Czech Republic and attributed them to regionally variable PPE of *Abies* sp. In addition, although *Abies* sp. pollen is heavy and does not transport easily, pollen may still be found in areas where the tree is not present, indicating that it can be transported by other means (Poska & Pidek, 2010). For example, in the high plateaus of Armenia, where firs do not grow, a few *Abies* pollen grains are regularly found throughout Holocene records (Joannin et al., 2014; Leroyer et al., 2016). The pollen transport that occurs in the Komi area must, therefore, be considered as another possible bias, which may affect vegetation estimates made with REVEALS. The Republic of Komi is close to the Ural Mountain Range, which does not necessarily prevent long-distance pollen

transport (Frei, 1997; Rogers & Levetin, 1998; Smith et al., 2008), and several pollen studies have shown that in Northern European Russia, some taxa are over-represented both in relation to pollen production and in relation to long-distance transport (Paus, 2000). The most often over-represented taxa are *Betula* spp., *Pinus* spp. and *Alnus* sp. (Novenko, Mazei, & Kusilman, 2017; Paus, 2000; Siljamo et al., 2008) while the taxa that are likely to come from long-distance transport are *Picea* spp., and *Carpinus* sp. (Latałowa & van der Knaap, 2006; Novenko et al., 2017). Fires themselves may have been a source of long-distance pollen transport by air convection (Pisaric, 2002). Therefore, *Abies* sp. might also be added to the list of over-represented taxa by means of long-distance transported grains that the PPE from Estonia cannot correct for terms of cover estimates. Another caveat is that the REVEALS results from the sites of Yaksha and Kalya should only be taken into account for the second *Abies* sp. rising, which is consistent with the study conducted by Golubeva (2008), indicating the presence of fir trees for the first time from 5,900 cal. yr BP.

Dating errors and the number of dates for each site is also a source of uncertainty for both pollen and REVEALS interpretations. Concerning *Picea* spp. estimates from Figure 5a indicate an acme of *Picea's* spp., centred around 8,000 cal. yr BP in Baika, 7,000 cal. yr BP in Syndorsky, 5,200 cal. yr BP at Yaksha, and around 5,000 cal. yr BP in Kalya and Cherny Yar. The age model of Syndorsky, based only on two ¹⁴C dates, is a source of uncertainty regarding the dynamics of *Picea* spp. and without the Syndorsky site, a south to north expansion gradient (from Baika towards Cherny Yar) could have occurred. This does not correspond to the east-west gradient described by Giesecke and Bennett (2004), but since the Republic of Komi is more continental than their study area, other expansion paths may have occurred. However, the data from the Syndorsky site do not allow for the validation of a clear spread from south to north in the Republic of Komi.

4.3 | Ecology and Holocene plant biogeography of the Republic of Komi

Fire activity has been demonstrated, which is today the primary cause of disturbance of vegetation in boreal forests, to not be the primary driver of vegetation dynamics during the early and mid-Holocene. Instead, long-term climate trends appear to be the major driver in shaping the landscape of the study area. This is particularly important when assuming that ecological processes, such as post-glacial migration and recolonization from refugial zones, are slow for plants in general and for long-living trees in particular. According to Feurdean et al. (2013), *Picea* spp. migration speed in this region is in the order of 60–260 m per year (60–260 km/1000 years). Therefore, linking species distribution and cover estimates against time, site by site, can help to understand taxon biogeography during the Holocene and identify possible time lags. Among the main factors considered for species distribution in palaeoecology, one can cite soil characteristics, seedling competitiveness (Birks & Birks, 2004; Rull, 2005). In

the case of the boreal ecosystem, low diversity allows a close study of individual taxa through time in order to investigate the spread, peak and decline of species. We present this biogeographic analysis for *Picea* spp. and *Abies* sp. (Figure 5). However, *Pinus* spp. were not investigated because the species distinction between *P. sibirica* and *P. sylvestris* had only been carried out at Yaksha, but not at the other sites. Similarly, *Betula* spp. was not selected because it is a pioneer genus, has a short life cycle and has colonized the region since the end of the Late Glacial (Sannikov & Goldammer, 1996).

4.3.1 | Spruce biogeography

Picea spp. was recorded at all sites and was likely present over the 10,500 years in this study. The Baika and Yaksha pollen records, further south, showed an early presence of this taxon at the beginning of the Holocene (10,500 cal. yr BP), as well as at the Kalya site (10,000 cal. yr BP) (Figure 5b). This is consistent with a Late Glacial *Picea* spp. spread as reported in Fennoscandia by Giesecke and Bennett (2004) in their synthesis based on modelling of geographical expansion across the Holocene with pollen percentage thresholds. These authors reported that after an early and rapid Holocene spread, the northern populations remained low or even declined before 8,000 cal. yr BP (Giesecke & Bennett, 2004; Tolonen, 1983), and subsequently a general spread was demonstrated with high population densities moving from east to west around 4,000 cal. yr BP.

The first event observed in the Republic of Komi is a drop of *Picea* spp. at 10,100 cal. yr BP in Baika, 8,500 cal. yr BP in Yaksha, 8,000 cal. yr BP in Kalya, and 7,900 cal. yr BP in Cherny Yar (Figure 5b). To explain the fall in this *Picea* spp. populations, Giesecke and Bennett (2004) listed several hypotheses, such as competition by birch, climate change and genetic diversity. These hypotheses can also be applied to the population in the Republic of Komi. In our study area, REVEALS estimates indicate that *Betula* spp. is increasing when *Picea* spp. decreased. It is also the case with *Abies* sp. (Figure 4), which may indicate that competition has occurred between these taxa. The present study can more clearly state that the fire activity, not hypothesized by Giesecke and Bennett (2004), was not driving this spruce decline which occurred when the median mFRI was at ca. 350 years (R-1).

A study by Väiliranta et al. (2011), based on analyses of pollen, stomata and macrofossils in the Pechora region (including two sites in the north of the Republic of Komi), supports the idea of several small local expansions of tree populations from different isolated patches rather than a broad-scale general movement. This could be one of the causes of the observed discrepancies between the dynamics of *Picea* spp. of the different sites.

Finally, the results of Tollefsrud, Latałowa, van der Knaap, Brochmann, and Sperisen (2015) and Tsuda et al. (2016), based on pollen data and *Picea* spp. DNA, showed that the Urals region was an area of hybridization and introgression between the species *Picea abies* from Fennoscandia and *Picea obovata* from Siberia. The

interbreeding (the precise period is not yet known) between these two species could have had an impact on the fitness of *Picea* spp. populations and also be a source of variability in terms of population dynamics in the Republic of Komi.

4.3.2 | Fir biogeography

The early presence of *Abies* sp. at the site Cherny Yar was not unique in the Republic of Komi, because it was also reported in the region by Nikiforova (1979) with the first appearance of this taxon occurring between 10,300 and 8,800 cal. yr BP, associated with summer temperatures 1°C higher than at present from 10,500 to 9,600 cal. yr BP (Golubeva, 2008). Very high local soil moisture conditions or particularly low fire activity may favour the dynamics of *Abies* sp. development within this particular site and increase its competitiveness against *Picea* spp. between 8,500 and 7,000 cal. yr BP (Furyaev, Wein, & MacLean, 1983).

Subsequently, the regional climatic conditions, such as annual temperature cooling between 7,400 and 6,400 cal. yr BP, could have prevailed over the local conditions of the Cherny Yar site and favoured the expansion of *Picea* spp. over *Abies* sp. from 7,000 cal. yr BP (Golubeva, 2008; Seppä et al., 2009), before a generalized expansion of *Abies* sp. in the Republic of Komi around 3,000 cal. yr BP, as observed in Baika, Yaksha, Sedkyrkesch and Kalya. This is consistent with the study conducted by Nikiforova (1979) about this species in the Republic of Komi, though it occurred later than the maximum expansion observed by Golubeva (2008) between 5,000 and 4,800 cal. yr BP. However, for the Baika site, a revisited age model and REVEALS results show a presence of *Abies* sp. earlier (from 3,800 cal. yr BP) than the study of Sidorchuk et al. (2001) (around 1,400 cal. yr BP).

The decline in *Abies* sp. generally observed around 2000 cal. yr BP was also described by Nikiforova (1979), when the annual climate temperature decreased by 2.5 to 3°C, compared to current values. This temperature decline, in addition to increases in fire activity, led to a deterioration in the growing conditions for *Abies* sp. (Golubeva, 2008). Currently in the Republic of Komi, *Abies* sp. populations are limited to the Ural Mountains.

4.3.3 | Ecosystem biogeography

Presently, at Yaksha, *Picea* spp. are mainly found around peatlands, or often distributed along the head of small streams and on moist soils (Figure 1d), while *Betula* spp. can be observed along eroded riversides (Figure 1d). The first half of the Holocene showed a strong climatic influence on vegetation dynamics. The opposite trends of *Betula* spp./*Picea* spp. were therefore largely controlled by this factor during this period (Figure 3 and Figure 4). From 6,000 cal. yr BP, the hydrographic and peat networks could have become more developed and extensive at Yaksha when the system was filled in by organic sediment accumulation over the Holocene.

Sphagnum peat replaced Cyperaceae mires (Figure 3), and thus, the expansion of humid soils may also have favoured the development of a dark taiga composed first by *Picea* spp. pure stands, and secondly by *Picea* spp. mixing with *Pinus sibirica* and *Abies* sp. Such an hypothesis for the dynamics of soils and river systems was likewise suggested by Zaretskaya, Panin, Golubeva, and Chernov (2014) to explain the chronology of geological events, including the lake dynamics in the Vychegda River Valley of the Republic of Komi. This dark taiga was likely limited spatially to lower areas and stream systems, contrary with the light taiga that was found on slightly higher areas. The local distribution of light and dark taiga growing in the same period also supports the idea of several small local expansions of spruce populations, as suggested by Väiliranta et al. (2011). However, these expansions were not from different isolated patches but rather from ecological corridors distributed along the hydrographic system.

The mixed coniferous dark taiga was first dominated and then suppressed by the fire regime, which took control over climate in the ecology of the boreal forest in the late Holocene. Locally, this ecosystem does not have an equivalent today as only spruce remains. The significant presence of *Betula* spp. found in the late Holocene corresponded to the last sample from Yaksha (dated at -58 cal. yr BP). However, it does not match with the vegetation map (Figure 1c and d), which may be explained by two reasons. The first is that the map was created before the age of the last Yaksha sample (CE 2008) and the second is that the area is currently subject to logging as shown in Appendix S3 where the logging of *Picea* spp. stands occurred in 1984, followed subsequently by rapid colonization of *Betula* spp. at 2016.

The local dynamics of the Yaksha site, provided by the pollen record have been highlighted, with regard to regional vegetation, through the use of REVEALS. The analysis of pollen and charcoal from the sequences Yak3-A and Yak2-A has allowed the landscape dynamics to be determined in the Yaksha area, in the Republic of Komi during the Holocene, revealing the complex patterns between the landscape morphology and the plant species in relation to the climatic context and the nature and frequency of fires. At the beginning of the Holocene, the climatic context of the site was probably the major driver for the establishment of the vegetation, until about 3,500 cal. yr BP. After this period, increasing fire activity played a major role in the disappearance of the dark taiga, in favour of light taiga. Currently, intense fire activity, partly due to human activities, is the dominant factor influencing vegetation dynamics. Fire management efforts should be continued in this area, given current climate change, which has caused the extreme fires that have taken place in Siberia during the summer in recent years. Such extreme events may also be predicted in the study area in the future.

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DATA AVAILABILITY STATEMENT

The data that support the pollen findings are openly available in the European Pollen Database at <http://www.europeanpollendatabase.net/index.php>. The charcoal data concerning the fire analysis from Barhoumi et al. (2019) are available in the Global PaleoFire Database (https://www.paleofire.org/index.php?p=CDA/index&gcd_menu=CDA). The reference codes affiliated to the four sediment cores from Yaksha site used for the macro charcoal analysis are 1,201; 1,202; 1,203 and 1,204.

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BIOSKETCH

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SUPPORTING INFORMATION

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

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