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Vegetation dynamics and fire history at the southern boundary of forest vegetation zone in European Russia during the Mid- and Late Holocene

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Abstract

Climate and human activity affected significantly the Eurasian on the forest vegetation zone through the Holocene. This paper presents new multi-proxy records of environmental changes at the southern boundary of the mixed coniferous-broadleaf forest zone in the east-central part of the East European Plain during the middle and late Holocene. Palaeoecological analyses of a peat core for pollen, charcoal, peat humification, plant macrofossils and testate amoebae with dating using radiocarbon have shown that climate appears to have been a dominant control on vegetation. There is strong evidence for a reduced precipitation-evapotranspiration ratio and high fire frequency during the Holocene thermal maximum (6.9–5.3 ka BP), leading to dominance of *Betula-Pinus* forests. By contrast subsequent climatic cooling led to the expansion of broadleaf forests and establishment of *Picea*. Human activities influenced vegetation from the Neolithic onwards but played a role which was secondary to climate until the recent past. Over the last century human impacts considerably increased due to harvesting of broadleaf trees and contributed to the formation of the current mixed coniferous-broadleaf forests.

Keywords: peatlands, pollen, plant macrofossils, testate amoebae, fire free interval, Mordovia State Natural Reserve

Introduction

The ecotones between biomes are often particularly sensitive to environmental change with regional and global changes locally amplified. Some of the best evidence for contemporary climate change impacts on vegetation comes from changes at ecotones (Allen and Breshears, 1998) and such locations have long been attractive for palaeoecological reconstructions. The importance of addressing long-term change at ecotones is amplified because the availability of diverse resources within a confined area has frequently made these areas attractive locations for human settlement (Stehberg and Dillehay, 1988). Palaeoecological studies at ecotones offer the possibility to simultaneously investigate both broad-scale environmental change and the consequences of this for human activity and use of the landscape. While the Holocene dynamics of some ecotones are well-studied (e.g. the boreal treeline (Seppä and Birks, 2001), others are much less understood. An example of this is the transition from forest to steppe biomes across southern Eurasia.

The focus of this paper is the southern boundary of the forest vegetation zone in European Russia. Although many palaeoecological studies have been undertaken in this general region, most of these have focused on the north-western and central parts of the East European Plain, Fennoscandia and eastern Baltic region (Khotinsky and Klimanov, 1997; Krementski et al., 2000, Seppä and Birks, 2001; Seppä and Poska, 2004; Saarse et al., 2010) with many fewer at the southern margin and little explicit consideration of the dynamics of the forest-steppe ecotone (Novenko et al., 2015). At this ecotone there is evidence for a long history of human occupation which has driven change in vegetation in concert with climate (Marquer et al., 2014). Fire, livestock grazing and agriculture have been detected during the late Holocene in a number of studies (Behre 1981; Kalis et al., 2003; Bradley et al., 2013; Kunes et al., 2015) and are suggested to have had a substantial impact on vegetation (Feurdean et al., 2015). These direct human impacts can potentially both demonstrate the human consequences of climate change and complicate interpretation of vegetation change in strictly climatic terms. For instance, Novenko et al., (2015) demonstrated that increasing abundance of *Picea* at the southern boundary of its range during the last several centuries was due to reduced competition following logging of *Quercus*-dominated broadleaf forest rather than being driven by climate.

This paper focuses specifically on ecotonal changes at the southern boundary of forest vegetation zone of European Russia in the P.G. Smidovich Mordovia State Natural Reserve (MSNR). This area is challenging for palaeoenvironmental studies due to its location at the margin of the forest and forest-steppe zone, the availability of peat deposits suitable for palaeoecological reconstruction and because this region has been scarcely investigated by palaeoecologists. The reserve is a protected area, which has protected palaeoenvironmental archives from direct human disturbance (Vargot, 2016). Eighty years of observations demonstrate that natural and human-induced forest fires are a particularly important disturbance factor in the region. For instance, during the severe summer drought of 2010 approximately one third of the total area of the reserve (12000 Ha) was burnt. However, the longer-term history of burning is less well understood. Reconstructing the long-term fire history may provide information on burn frequency and intensity and the links between burning and changes in vegetation, climate and human activity and thereby inform practical environmental management (Whitlock et al., 2010). The aim of this paper is to reconstruct vegetation dynamics at the forest-steppe ecotone in European Russia and to identify the main environmental and anthropogenic drivers basing on a multi-proxy paleoecological study.

Study area

The MSNR is located in the central part of the East European Plain (the Republic of Mordovia, Russia) (Fig. 1). The reserve occupies the northern portion of the Moksha River basin and the catchment of the Oka River. The area is situated at the boundary between the forest landscape of the Meschera Lowlands and the forest-steppe Volga Upland region (Mil’kov and Gvozdetsky 1986). The study area includes the floodplain of the Moksha River with elevations ranging between 103 and 110 m a.s.l. and an undulating plain with moraine and fluvio-glacial deposits (110-132 a.s.l.). Scattered ridges of relict Aeolian material occur across the region. Quaternary deposits are 1-26 m deep with Early-Middle Pleistocene till of the Don Glacial complex, Middle Pleistocene fluvio-glacial sediments and Late Pleistocene – Holocene alluvial deposits of the Moksha River (Bayanov, 2015). Pre-Quaternary deposits of Upper Carboniferous and Lower Jura limestones lie close to the surface. Numerous mires are situated in small depressions formed by thermokarst processes during Late Pleistocene Glaciations and in deeper sinkholes (Grishutkin, 2012).

The climate of the study area is temperate and moderately continental with relatively cold winters and warm summers. Based on meteorological observations in the town of Temnikov (20 km southwest of the study site, since 1886) the mean July temperature is +20.3°C, the mean January temperature is -10.5°C and mean annual temperature is +4.7°C (http://www.ecad.eu).

Annual precipitation is around 520 mm with more than half of this falling as rain in the summer-autumn period with the rest falling as snow during winter and spring. The vegetation of the study area is dominated by mixed pine-deciduous forests with *Pinus sylvestris* L., *Quercus robur* L. and *Tilia cordata* Mill. *Picea abies* L., *UImus glabra* Huds., *Acer platanoides* L. and *Fraxinus excelsior* L. are present as an admixture in forest stands (Tereshkin and Tereshkina, 2006). Oak-lime forests mainly occur in habitats with fertile soils on moraine and limestone deposits. Secondary forests of *Betula pendula* Roth. and *Populus tremula* L. are abundant in areas of former clear-cutting. *Alnus glutinosa* (L.) Gaertn. is common in wet areas of floodplains.

The coring site for this study is a mesotrophic peatland Klukvennoe (‘Cranberry Mire’) at N 54.77724, E 043.44663. The site is located in a depression (3.6 ha) between aeolian-fluvio-glacial ridges with 250 cm of peat deposits underlain by fluvioglacial sands. Vegetation of the peatland is relatively homogenous and currently consists mainly of *Betula* sp*.*, *Eriophorum vaginatum* L. and Ericaceae (*Ledum palustre* L*.*, *Chamaedaphne calyculata* (L.) Moench*.*, *Vaccinium uliginosum* L*.*, *Oxycoccus macrocarpus* (Aiton) Pursh.) with a dense cover of *Sphagnum* sp. and sedges *(Carex pseudocyperus* L.). *Pinus sylvestis* occurs sporadically across the mire.

Materials and methods

Coring and sediment description were carried out during the summer of 2013. A core was extracted using a Russian peat corer (inner chamber length of 50 cm and diameter of 5 cm). We applied a number of palaeoenviornmental proxies to the core including pollen analysis as an indicator of regional and local vegetation, plant macrofossil analysis as an indicator of local vegetation, colorimetric peat humification analysis as an indicator of peat decomposition and testate amoeba analysis as an indicator of surface wetness. Cores were sub-sampled at 2-3 cm for all of these proxies with the exception of plant macrofossil analysis (5 cm) where larger sample volumes were required.

The chronology of the core was established using radiometric radiocarbon dating of 6 bulk peat samples (Table 1). Radiocarbon dating was performed in the Radiocarbon Laboratory of the Institute of Geography of the Russian Academy of Science (Moscow, Russia) using Liquid Scintillation Counting. The ^{14}C dates were calibrated with Calib 13.0 and the Intcal13 calibration dataset (Reimer et al., 2013). Age-depth models were developed using the Clam 2.2 package (“classical” age-depth modelling; Blaauw, 2010) in R (R Core Team, 2014).

Samples for plant macrofossil analysis (5-10 cm³ per sample) were disaggregated with water and washed through a 0.25 mm mesh sieve. The plant remains were identified using a binocular microscope at 200x magnification following Katz et al. (1977).

LOI was determined following the procedures outlined by Dean (1974) by combusting dried 50 g samples at 550 °C. Peat humification was determined using the alkali-extraction and colorimetry method (Caseldine et al., 2000; Chambers et al., 2010/11).

Samples for pollen analysis were prepared following Moore et al., (1991) by heating the sub-samples for 10 min in 10% KOH to remove humic material followed by acetolysis in a water bath for 5 min to dissolve cellulose. A minimum of 500 pollen grains per sample were identified and counted using a Motic BA210 microscope at ×400 magnification following Beug (2004). To determine pollen and charcoal concentrations, *Lycopodium* tablets were added to each sample (Stockmarr, 1971). Microscopic charcoal concentrations were assessed using the point-count methodology (Clark, 1982).

Samples for testate amoeba analysis were prepared using a water-based preparation method similar to that of Hendon and Charman (1997). Samples were soaked in distilled water for 24 h, agitated on a flask shaker for 5 min, sieved through a 500 µm mesh to remove coarse material and left to settle for 24 h. The supernatant was decanted off and the samples were mixed with neutralized formaldehyde. Two millilitres of the concentrated sample were placed in a Petri dish (5 cm diameter) and inspected at ×160 magnification. All tests were identified and counted in 200 microscopic fields. Pollen, plant macrofossil and testate amoeba diagrams were constructed using Tilia 2.0.2 and TGView (Grimm, 1990).

The long-term fire history of the study area was reconstructed based on studies of visible charcoal bands in the peat core (Pitkänen et al., 2001; Ohlson et al., 2006). We propose that charcoal layers in our core from the centre of the peatland indicate local burning which affected the peatland directly rather than simply the surrounding forest (Novenko et al., 2016). The core was described and photographed immediately after extraction and the depths of visible layers recorded. The age of charcoal layers were determined using the age-depth model and fire-free intervals calculated (Whitlock et al., 2010).

Tree cover was reconstructed based on pollen data using the extended Best Modern Analogue (BMA) technique (Overpeck et al., 1985; Nakagawa et al., 2002) following the example of previous studies in European Russia (Novenko et al., 2014). Modern analogues for the reconstruction were based on 950 pollen samples originating from a wide variety of landscapes in Europe and Siberia. Woodland coverage was estimated over a radius of 20 km around each site from the reference dataset of modern pollen assemblages using MODIS satellite images. BMA calculations were performed using Polygon 2.2.4 (http://polsystems.rits-palaeo.com).

Results

Chronology and peat accumulation

Radiocarbon dating (Fig. 2, Table 1) shows that the accumulation of peat in the mire began in the mid-Holocene at 7.0-6.6 ka BP. Peat accumulation rates were initially relatively rapid (1.16 mm yr^{-1} during 6.6-5.6 ka BP) with considerable mineral input but subsequently slowed to more typical peatland rates of 0.30 to 0.46 mm yr^{-1} (5.6-2.7 ka BP). Through the late Holocene (2.7-0.1 ka yr. BP) peat accumulation slowed further to 0.15 mm yr^{-1}, however, a part of peat deposits could be lost as a result of fires. The uppermost layer of peat (depth 35-0 cm) was formed during the last 100 years, but true accumulation rate of this layer is likely to be overestimated due to a high amount of undecomposed plant remains.

Plant macrofossil, peat humification and organic matter content

Plant macrofossil analysis shows that the peat deposits can be divided into four macrofossil assemblage zones (MAZ) (Fig. 3).

MAZ 1 (250-75 cm, about 7.0-2.8 ka BP). Eutrophic peat with remains of *Calamagrostis sp., Carex sp., Menyanthes trifoliata* and other herbs. Remains of *Pinus sylvestris* were identified consistently but in low quantities. Subzone MAZ 1a (250-190 cm) was characterized by relatively high amount of *Sphagnum* remains with *S. obtusum* initially abundant but subsequently replaced by *S. palustre*. Subzone MAZ 1b (190-150 cm), *Sphagnum* declined with herbs consistently abundant. The subzone MAZ 1c (150-130 cm), the abundance of brown mosses increased. *Scirpus* and *Sphagnum palustre* are also more abundant.

MAZ 2 (75-55 cm, 2.8-1.4 ka BP). Eutrophic peat composed by *Menyanthes trifoliata* (up to 50%) and *Typha latifolia* (20%). *Sphagnum* was virtually absent and there was a marked reduction in the abundance of sedges and herbs which were abundant in MAZ 1.

MAZ 3 (55-20 cm, 1.4 – ~ 0.1 ka BP). Eutrophic peat with remains of *Calamagrostis* and other herbs. *Sphagnum* became more abundant (*Sphagnum obtusum, S.* sect Cuspidata). Macrofossils of tree species are at their highest abundance of the core in this zone with these primarily of *Pinus sylvestris*, but also *Betula* and *Salix*.

The uppermost peat horizon (MAZ 4, 20-0 cm, approximately the last 100 years) was separated from the underlying peat by a distinct charcoal layer that might suggest an accumulation hiatus (although our age-depth model does not have the resolution to confirm this). MAZ 4 was composed of poorly humified mesotrophic *Sphagnum* peat mainly formed from section Cuspidata (*Sphagnum angustifolium/fallax*) and *Sphagnum flexuosum*. The proportion of *Carex* sp. and *Eriophorum* increased and *Oxycoccus* appeared. Wood remains were much rarer than the preceding zone.

Organic matter content sharply increased from 35 to 79% in the transition zone from clastic sediments to peat at the bottom of the core. LOI was high (96-98%) throughout the majority of the core (230 - 75 cm) with frequent fluctuations in the range of 1-2% in the interval 230-150 cm. Between 75 and 40 cm organic matter content gradually declined and at 40-30 cm LOI dropped to 85%. In the upper 20 cm LOI increased to 93-95%, almost regaining levels in the lower half of the core. The base of the core (250-235 cm, 7.0-6.8 ka BP) was characterized by peat with low absorbance, which may relate to the high inorganic content. The majority of the core was characterized by moderate absorbance values (235-115 cm, 6.8-3.8 ka BP) which indicated a presence of moderately humified peat deposits. Above 115 cm the absorbance values increased and remain relatively stable (115-53 cm, 3.8-1.3 ka BP), suggesting an accumulation of well decomposed peat layers. Absorbance subsequently declined and remained low for almost 600 years from 53-45 cm (1.3-0.8 ka BP). Towards the surface the absorbance further decreased (45-0 cm, 0.8 ka – present), revealing a poorly humified peat horizon.

Testate amoebae

Samples were prepared for testate amoeba analysis from throughout the core but concentrations were found to be very low below 47 cm depth and the resulting record is fragmentary. In the lower samples only a few individual tests could be identified. In total fifty one testate amoeba taxa were identified with the majority of taxa generalists and the assemblage composition typical of minerotrophic peatlands (Payne 2011). The testate amoeba (TA) assemblages were subdivided into four zones, but in only one of these were test concentrations sufficient to draw robust conclusions (TA4) (Fig. 4). Zone TA1 at the base of the core (250-195 cm, 7.0-6.1 ka BP) was characterized by very low abundance of testate amoebae with the occurrence of *Difflugia* and *Archerella* spp. In zone TA 2 (195-100 cm, 6.1-3.4 ka BP), the abundance of testate amoebae remained low and occurrence inconsistent, taxa identified were more xerophilous. In zone TA 3 (100-50 cm, 3.4-1.1 ka BP), testate amoebae were entirely absent. However, zone TA 4 (50-0 cm; 1.1 ka BP - present) was characterized by comparatively diverse and abundant testate amoeba assemblages with species composition typical for biotopes with moderate surface moisture.

Pollen and micro-charcoal analyses of peat samples

The pollen proportion (Fig. 5) and accumulation rate diagrams (Fig. 6) were divided into four pollen assemblage zones (PAZ), corresponding to the main phases of vegetation development.

PAZ 1 (250-160 cm, 7.0-5.3 ka BP) was dominated by *Betula* (60–70%) and *Pinus* (20-40%) with a small proportion of broad-leaved trees (*Tilia, Ulmus, Quercus, Fraxinus*) and *Picea* (2-3%). Pollen accumulation rates (PAR) were relatively high. The proportion of NAP was less than 10% with most of this was represented by Poaceae*, Artemisia,* Chenopodiaceae, Rosaceae, Ranunculaceae and other herbs. Pollen of *Centaurea cyanus, Plantago, Rumex, Convolvulus* and *Ranunculus acris* and rare pollen grains of Cerealia were found. Micro charcoal particles were registered in each sample but CHAR (Charcoal accumulation rates) was low.

PAZ 2 (160-115 cm, 5.3–3.8 ka BP). Pollen values of *Quercus* (6-8%), *Tilia, Ulmus, Alnus* and *Corylus* increased. The proportion of *Betula* and *Pinus* remained relatively high (30-40%), but PAR of these taxa reduced.

PAZ 3 (115–35 cm, 3.8 – about 0.1 ka BP). PAZ was characterized by the greatest proportion of *Quercus* (15-25%), *Tilia*, *Ulmus* (10-15%) and *Alnus* (15-20%) and highest PAR of these species (up to 3500 pollen grains cm^{-2} yr^{-1}). *Corylus* was also relatively abundant in the upper part of the zone (70-35 cm, 10-12%). *Picea* pollen values varied from 0.5 to 4% and a few grains of *Carpinus* pollen were identified. The share of NAP (mainly Poaceae, Rosaceae, *Artemisia, Rumex* and Chenopodiaceae) did not exceed 10%. The CHAR increased significantly reaching a peak (2770 particles cm^{-2} yr^{-1}) at 45 cm depth.

PAZ 4 (35-0 cm, the last century). AP values decreased to 75%, *Tilia* and *Ulmus* disappeared completely, *Quercus, Alnus* and *Corylus* reduced considerably, while *Pinus* and *Betula* maintained their high proportions. The share of *Picea* pollen increased to 7-10%, PAR of *Picea* increased significantly reaching 500 pollen grains cm^{-2} yr^{-1}. Within the NAP and spores, *Artemisia*, Poaceae, and Chenopodiaceae increased along with Cyperaceae and Sphagnum. The pollen of cultivated cereals (5-7%), *Fagopyrum, Cannabis* and ruderal plants (*Plantago major/media, Rumex, Centaurea cyanus, Ranunculus acris* –type) became more abundant.

Fire free interval

Field recording of charcoal bands in the peat core demonstrates that the largest proportion of charcoal bands (16) was deposited between 6850 and 5600 cal yr BP. The fire free interval did not exceed 100 years and was frequently in the range 10-20 years (Fig. 7). In the period from 5600 to 3000 cal yr BP fire frequencies decreased (fire free interval reached 300-500 years) and later only one charcoal layer was observed in the period between 3000 and 1500 cal yr BP. Several fire episodes were detected at about 1000 cal yr BP. During the last millennium fire return period reduced to 150-200 years. Two charcoal layers were formed during the last century; the fire free interval was estimated as 30 years.

Woodland coverage

The reconstructed total woodland coverage in a 20 km radius around the Klukvennoye peatland (Fig. 7) showed a considerable short-term (150-200 years) variability (40-60%) during the period 7000-5000 cal yr BP. Subsequently, an expansion of woodland coverage (60-70%) occurred which persisted until 4000 cal yr BP. A series of fluctuations in the forest cover from 50 to 70% were detected between 4000 and 2400 cal yr BP and were followed by a reduction in the total woodland coverage (30-40%) during the periods 2400-1500 cal yr BP and 1200-1170 cal yr BP. An expansion of tree cover (60-70%) was reconstructed during 1500-1200 cal yr BP and at 1100 cal yr BP. Total woodland coverage has declined 30-40% since 1000 cal yr BP up to the beginning of the 20th centaury AD. During the last 100 years woodland cover has recovered, clearly as result of conservation within the Mordovia Reserve.

Discussion

The results of the study allow us to reconstruct the development of the peatland and the wider landscape and relate it to climate changes, fire regime and human activities in the eastern part of the Meshchera Lowlands during the Mid and Late Holocene (Fig. 7). For discussion we subdivide the proxy records into five periods: 7.0-5.0 ka BP, 5.0-2.3 ka BP, 2.3-1.5 ka BP, 1.5 ka BP-17th/18th centuries AD and the last 100 years.

The Holocene Thermal Maximum (7.0-5.0 ka BP)

Peat accumulation at the site began at about 7.0 ka BP. This is slightly later than the early Holocene peak of northern peatland initiation (9.0-8.0 ka BP) but still broadly typical of peat initiation date across large areas of the Northern Hemisphere (Yu et al., 2010). The peatland developed due to paludification, initially as a meso-eutrophic fen. The initial vegetation community was dominated by grasses (*Calamagrostis* sp.) and sedges (*Carex* sp.) whilst the presence of *Menyanthes trifoliata* suggests that the site was wet and may have contained some open water. The presence of the testate amoeba *Archerella flavum* in the lowermost 50 cm of the core clearly implies the presence of wet surface conditions. The lowermost macrofossil sample contains *Sphagnum obtusum* showing that the site had groundwater influence at this point. LOI of the lowermost sediments is high, showing considerable allogenic nutrient input but this rapidly declines up the core. Within only around 15 cm, representing little more than a hundred years, the peat had LOI of around 98%, which is typical for ombrotrophic bogs and implies mineral inputs primarily from atmospheric deposition. Plant communities appear to have taken some time to adjust to reduced nutrient input change, presumably because buried nutrients in the basal sediments remained accessible to plant roots. The moderately eutrophic *Sphagnum palustre* remained a significant component in the assemblage for about 800 years after peatland initiation.

This pattern appears similar to other peatlands in the East European Plain (Inisheva et al., 2013; Novenko et al., 2016; Payne et al., 2016).

The peats of the Klukvennoe site contain several distinct charcoal layers at the base of the core. This abundance of apparent burning events is apparently unusual within the Holocene and cannot be explained by low rates of peat accumulation. The prevalence of fires in the early Holocene is attested by other records from the Meshchera Lowlands (Novenko et al., 2016). It is interesting to speculate whether this burning may be related to the apparent timing of peat initiation. One possibility is that peat fires led to extensive loss of peat such that earlier deposits have been destroyed. Recent observations have shown that severe fires during drought periods (such as summer of 2010) can completely burn shallow peatlands in this region, leaving waterlogged depressions without peat (Grishutkin, 2012). Another possibility is that burning may have removed vegetation, reducing evapotranspiration and triggering paludification. This would parallel the situation in northwest Europe where charcoal layers have been widely found at the base of peats and suggested to relate to the proposed anthropogenic origins of blanket bogs (Caseldine and Hatton, 1993; Moore 1993).

The results of the pollen analysis indicate a series of consecutive phases of birch and birch-pine forests with an admixture of broad-leaved trees. *Picea* pollen occurred sporadically and in low proportions, suggesting that spruce may not have been locally present in forest stands (Birks 1989; Giesecke and Bennett 2004). Regional correlations of pollen data show that pine and birch-pine forests persisted in the study area much longer than in other regions of central Russia (Khotinsky and Klimanov, 1997; Krementski et al., 2000; Novenko et al., 2015). Pollen records from several lakes and peatlands in European Russia and adjacent countries show that birch and pine-birch woodlands expanded to the western and central part of the East European Plain during the early Holocene and were replaced by mixed coniferous-broadleaved forests (oak, lime, elm, ash and hazel) at about 8.0 ka BP or earlier (Seppä and Poska, 2004; Feurdean et al., 2014; Novenko and Olchev 2015). In the central part of the East European Plain broadleaved forests reached their maximum abundance during the Holocene Thermal Maximum, 8.0-5.8 ka BP (Kremenetski et al., 2000; Novenko et al., 2015). The increase in the proportion of broadleaved trees in the south-eastern part of Meshchera Lowlands (about 150 km south-west from the study area) occurred at 7.0 ka BP (Novenko et al., 2016). In the Volga Uplands, to the east of the reserve a simultaneous rise of *Quercus, Tilia* and *Ulmus* was identified from 6.0 ka BP (Blagoveshchenskaya, 2006). Based on the pollen percentage and accumulation rate data it appears that the abundance of broadleaved trees in the area surrounding the site remained low until 5.0 ka BP.

Frequent fires during the Holocene Thermal Maximum may have led to the persistence of birch and pine forests in the study area. Our reconstructions show that woodland coverage varied from 40 to 60% with a number of short-term phases of reduced cover of around 150-200 years (Fig. 7), equivalent in duration to those known to follow fires or other disturbances. The large number of charcoal bands detected in the Klukvennoye peat core during 7.0-5.0 ka BP suggests a series of intense fires with the fire return period fluctuating around 100 years but during several periods reaching as hight as a local fire every 10-20 years (Fig. 7). The reconstructed fire return period agrees well with charcoal data from other peatlands in Northern and Central Europe (Kasin et al., 2013; Robin et al., 2013). Between 7.0 and 5.0 ka BP, fire free intervals were 60-170 years in Finland and 40-100 years in Northern Karelia (Pitkänen et al., 2001). In the south-eastern part of the Meshchera Lowlands, fire frequencies were high in the period of 7.0-4.5 ka BP, with fires occurring every 40-200 years (Novenko et al., 2016).

The high fire frequencies in the study area between 7.0 and 5.0 ka BP could be explained by both climatic conditions and human impact. During this period annual and summer temperatures in Eastern Europe were higher than present (Seppä and Birks, 2001; Deavis et al., 2004; Seppa and Poska, 2004), while precipitation was lower or similar to modern values (Khotinsky and Klimanov, 1997; Novenko et al., 2009). Further evidence for warmer and drier climate during 7.0 – 5.0 ka BP comes from palaeohydrological studies by Sidorchuk et al., (2012) who showed that the river discharge from the Volga River basin was less than a half of modern values. Peatland surface moisture reconstructions based on testate amoeba assemblages for the Klukva peatland in the Upper Oka River basin also point to drier climatic conditions during the Mid-Holocene (Novenko et al., 2015), probably due to reduced summer precipitation.

There is no record of archaeological findings from the MSNR but several archaeological sites of Mesolithic, Neolithic and Bronze Age are reported within 30 km of the reserve (Kashkin, 2004). Four archaeological sites of Early and Middle Bronze Age were situated in the Moksha River valley close to the study area (10-20 km) and two settlements of Early Iron Age were discovered in the Satis River Valley, a tributary of the Moksha River (Shitov at al., 2008). Pollen assemblages from our core included taxa indicating arable land (Behre, 1981) such as Cerealia and *Centaurea cyanus* and ruderal communities (Chenopodiaceae, *Artemisia, Plantago major/media, Polygonum aviculare*-type and *Rumex acetosella*-type). Anthropogenic indicators were permanent components of pollen assemblages during the whole period of peat accumulation but were not particularly abundant until historical time. The Cerealia pollen did not exceed 0.5% until the last century. According to Koff and Punning (2002) quantities of Cereal pollen less than 2% can be considered as a regional background pollen influx. Pollen records from adjacent regions indicate the appearance of Cerealia pollen at 8.0 ka BP in the north-west of the Volga Uplands (Blagoveshchenskaya, 2006) and at 7.0 ka BP in the central part of Meshchera Lowlands (Dyakonov and Abramova, 1996). Clearly, the vegetation of the study area was influenced by human activity therefore the fires we identified could be either natural or human-induced.

The mid/late Holocene (5.0-2.3 ka BP)

Significant environmental changes in the Klukvennoye mire and the surrounding area occurred at 5.0 ka BP. The proportions of brown mosses in the local vegetation became higher while herbs such as *Menyanthes trifoliata, Scirpus, Carex* and *Calamagrostis* remained relatively abundant. The reasons for this local vegetation change are unclear but could be related to two broadly-coincident burning events identified in the charcoal stratigraphy.

Woodland cover in the pollen catchment of the Klukvennoye peatland expanded from 5.0 ka BP, reaching 70% at about 4.5, 4.0 and 3.7 ka BP. The proportion of broadleaved trees increased to 30-40%, spruce gradually penetrated the forests and alder became abundant on wetter ground. The high amount of *Pinus* and *Betula* pollen could be due to production by local mire vegetation and/or by pine-birch forests on the sandy hills and gentle ridges which are common in the study area. Seemingly deciduous broadleaved trees were not able to settle in these localities even under favourable climatic conditions due to their high nutrient-demand.

The increase in *Picea* pollen accumulation rate since 5.0 ka BP and subsequent permanent establishment could be considered a sign of the appearance of spruce in plant cover within the boreal forest (Birks 1989; Giesecke and Bennett, 2004). In this period spruce was already present in vegetation in the Valdai Hills (700 km north-west, Novenko et al., 2009), Smolensk-Moscow Upland (500 km north-west, Krementsky et al., 2000) and Volga Upland (150 km east, Blagoveshchenskaya, 2009) but was not abundant. Probably the southern boundary of the geographical range of *Picea* was situated in the vicinity of the study area.

The expansion of woodland coverage (to 60-70%), the increase in the proportion of broadleaved trees and the appearance of spruce all coincided with low fire frequencies with fire return periods of 300-500 years. Climatic reconstructions for the period from 5.7-5.5 ka BP indicate progressive cooling (Seppä and Birks, 2001; Davis et al., 2003; Mauri et al., 2015) and increases in humidity (Khotinsky and Klimanov, 1999; Novenko and Olchev, 2015). Based on the reconstructions of Seppä and Poska (2004), the mean annual temperature in Northern Europe decreased by 3-3.5°C since 5.7 ka BP. The general trend to cooling during the second half of the Holocene included several warmer phases (at 3.5 and 2.0 ka BP) and colder phases (at 5.0 and 2.5 ka BP).

The time period of 2.3-1.5 ka BP

The most dramatic local changes in vegetation at the study site occurred in the period 2.8-1.4 ka BP when *Sphagnum* species, herbs and sedges were replaced by *Menyanthes trifoliata, Typha latifolia* and *Equesetum* sp. This vegetation shift strongly implies change towards a wetter peatland surface with more nutrients available. The presence of bulrush (*T. latifolia*) in particular, strongly implies an increase in nutrient availability. This phase is noted by the beginning of a trend towards lower LOI values, implying that at least some of these nutrients were likely to be due to in-washed mineral material. No testate amoebae were identified in this zone, which may suggest rapid decomposition as has been frequently noted in fens (Payne, 2011). The apparent shift to wetter surface conditions contradicts findings from other regional sites (discussed below) and, in combination with the apparent increase in nutrient availability, may imply localized hydrological change (probably related to human activity), rather than broad-scale climatic change.

Broadleaf forests with oak, elm, lime and ash reached their Holocene maximum in this period while woodland cover overall was reduced to 40-50%. *Betula* pollen was abundant but its concentration remained low. Comparison of percentages to PAR of *Betula* indicates that birch, characterised by high pollen productivity, did not increase its share in the vegetation but occurred on sandy hills and peatlands. The abundance of *Pinus* in the vegetation declined and *Picea* disappeared completely. This shift in *Picea* geographical range was most likely caused by climatic factors and competition with broadleaved trees. The composition of pollen assemblages provided no evidence of increased human impact at this time.

Climatic reconstructions based on pollen and testate amoeba data from the Klukva mire in the Upper Oka River basin indicated warming and decreased surface wetness at 2.0-1.5 ka BP (Novenko et al., 2015). This phase of vegetation development could be coincided with the Roman Warm Period (~200 BC-600 AD/ 2.2 – 1.4 ka BP) which was characterised by increased temperature and decreased humidity (Davis et al., 2003). Despite the climatic conditions apparently being favourable for burning, fire frequencies were low with only one fire detected during this phase. In general broadleaf forests are characterised by lower fire activity then coniferous forests. Consequently, a long fire free interval may have been caused by a shift in forest species composition in combination with increased peatland wetness.

The late Holocene (1.5 ka BP – present)

The beginning of this period was marked by a further abrupt change in vegetation with a loss of the wet/minerotrophic taxa which characterised the previous phase (*Typha latifolia, Equisetum* sp., *Menyanthes trifoliata*). Decline in these species is matched by an increase in brown mosses, herbs and particularly *Sphagnum* species (*S. obtusum* and S. sect cuspidata). Simultaneously, *Pinus* appeared on the peatland surface with the highest abundance throughout the core. This transition suggests a return to a somewhat drier peat surface. While the assemblage of this zone indicates less nutrient availability, the presence of taxa such as *S. obtusum* clearly indicates the continuing presence of some nutrient enrichment. This may be related to continuing in-wash of mineral material, with LOI reaching a trough at around 90%. This zone marks the start of more consistent preservation of testate amoeba taxa. The testate amoeba assemblage supports the plant macrofossils in implying both moderately wet conditions (characteristic taxa *Arcella arenaria*) and moderately nutrient rich conditions (characteristic taxa *Tracheleuglypha dentata*). It appears that the increased nutrient supply and waterlogging in the previous zone was comparatively short-lived.

At 1.5 ka BP spruce reappeared in the study area, the proportion of pine increased and broadleaf trees declined. *Picea* pollen reached its greatest proportions in the assemblages with a maximum for the entire Holocene, indicating an active expansion of spruce at the boundary of the range. Based on pollen data from multiple sites in Northern and Eastern Europe it appears that deciduous species, in particular *Quercus, Tilia* and *Ulmus,* declined and were subsequently replaced by spruce at approximately 2.2-2.0 ka BP (Giesecke and Bennett, 2004; Seppä and Birks, 2001; Kremenetski et al., 2000; Clear et al., 2014). The same patterns were detected in the Meshchera Lowlands; deciduous trees declined from 2.2-2.0 ka BP as a result of climate cooling and increased humidity (Novenko et al., 2016). In the study area these processes began about 500-700 years later, probably, due to climate continentality and lesser human impact.

At about 1.2 ka BP woodland coverage increased to 60-70% and sharp fluctuations were detected probably caused by fire disturbance. Charcoal accumulation rate increased by an order of magnitude. Most likely, a series of low intensity fires occurred in the vicinity of the Klukvennoye peatland, but these did not affect the mire or the coring site directly due to relatively high surface wetness.

Environmental changes during the Medieval Climate Anomaly (MCA, ca. 900-1350 AD; e.g., Mann et al., 2009) led to shifts in vegetation and fire regime. The sample resolution and chronology of the peat core in the Klukvennoye peatland allowed us to roughly determine the MCA (Fig. 7). Climatic reconstruction by various proxy data and model simulations show that the MCA in Europe was characterised by warm and relatively dry climate (Goosse et al., 2005). Temperature-driven increases in potential evapo-transpiration probably exceeded the increased precipitation and led to summer droughts in several regions of Europe (Büntgen et al., 2010) which could be the reason for frequent fires (Overpeck et al., 1990). Charcoal evidence from across the forest zone of Europe indicates an increase in fire activity during the MCA associated with climate warming and anthropogenic influences (Robin et al., 2013, Clear et al., 2014). The charcoal accumulation rate in the Klukvennoye peatland achieved its maximum in the layers formed during the MCA reaching about 1.5 × 10^5 particles cm^{-2} yr^{-1}. Reconstructions of fire frequencies by charcoal bands in the peat core also indicate a series of fires at approximately 1.0 ka BP with an interval of about 30 years.

The subsequent cooling included the Little Ice Age (LIA, 1700-1400 AD.; Mann et al., 2009), the coldest phase of the Late Holocene. Based on temperature reconstructions using pollen data the mean annual temperature was 2 °C lower than at present (Seppä and Poska, 2004). Combined with high annual precipitation ranging between 600 and 800 mm $year^{-1}$ in the central part of East European Plain, this cooling led to a general decrease in fire activity (Lehndorff et al., 2015). During the last 1.2 ka BP the *Picea* pollen curve changed in antiphase to the micro-charcoal accumulation rate (Fig. 7). *Picea* is generally known as a fire-sensitive species (Sannikov and Goldammer, 1996) and most likely declined during phases of high fire activity, such as the MCA, and recovered during the LIA when fire free intervals increased.

The uppermost peat horizon at the Klukvennoye mire is defined by a distinct basal charcoal layer. Radiocarbon data from this horizon suggest that it was formed during the last 100 years. A peat survey in the Meshchera Lowlands showed a similar stratigraphy in a number of sites where a poorly humified *Sphagnum* peat layer at the top of peat cores was separated from the rest of the profile by a distinct charcoal layer dated between 80 and 40 years BP (Novenko et al., 2016). In terms of local vegetation, the macrofossil data show the expansion of comparatively oligotrophic species (*Sphagnum fallax, S. angustifolium* and *Eriophorum vaginatum*) at the expense of more mesotrophic species. LOI shows a decline in mineral input and peat accumulation is very rapid (3.5 mm yr^{-1}). These changes may reflect an ombrotrophication process with rapid peat growth increasingly decoupling the peat surface from more nutrient rich waters.

The pollen assemblages demonstrate dramatic changes in vegetation in this period due to human impacts. *Tilia, Ulmus, Quercus* and *Corylus* become quite rare, whereas *Betula* and *Pinus* are more abundant. Broadleaf forests were likely cut over an extensive area and replaced by arable lands and secondary *Pinus-Betula* forests, causing woodland coverage to decline to 40%. The proportion of spruce pollen in the upper 20 cm remained relatively high (3-7%). Seemingly the abundance of spruce increased after degradation of deciduous forests when competition with broadleaf trees, particularly oak, decreased.

The proportion of cultivated cereals in pollen assemblages of the last hundred years reached 7%, demonstrating the presence of arable lands adjacent to the peatland (Koff and Punning, 2002). Indicators of increasing human impact on vegetation include the presence of typical weed plants such as *Centaurea cyanus,* species indicating trampling and/or grazing (*Polygonum aviculare, Plantago major/media*), species typical of pasture lands (*Plantago lanceolata, Rumex acetosella*, Cichoriaceae (*Taraxacum*-type), Rosaceae (*Achillea*-type) and ruderal species (Artemisia, Asteraceae (*Cyrsium*-type) and Chenopodiaceae) (Behre 1981; Khotinsky, 1993). A relatively high proportion of herbaceous plants such as Poaceae, Polygonaceae, Ranunculaceae, Fabaceae, Brassicaceae suggests the existence of meadows and hayfields. It is likely that the large glades inside forest areas of the reserve (readily apparent on remote sensing images) are remnants of these former agricultural lands. Today any land use is prohibited in the area of the reserve.

Pollen records from various regions in Europe demonstrate that humans have had a considerable impact on vegetation since the Bronze Age (5.5-3.2 ka BP). During the Early Iron Age (3.2-2.0 ka BP) anthropogenic disturbances of plant cover increased (Behre 1981; Kalis et al., 2003; Saarse et al., 2010; Bradley et al., 2013; Kunes et al., 2015). In the central part of European Russia the beginning of these processes varies from 2.5 ka BP in the forest-steppe zone (Novenko et al., 2014) to 1.7-1.4 ka BP in broadleaf forest zone and southern taiga (Khotinsky, 1993; Krementski et al., 2000; Novenko et al., 2015). It is likely that significant human-induced changes in vegetation in the study area began prior to the last 100 years. For example, the town of Temnikov, the district centre close to the reserve, was founded in 1536 and several villages around it are similarly old.

Conclusions

The record from the Klukvennoye peatland located at the southern boundary of mixed coniferous-broadleaved forest zone shows that Holocene vegetation dynamics were primarily determined by climate and fire frequencies. This ecotone region was characterised by a reduced precipitation-evapotranspiration ratio and a high fire activity during the Holocene thermal maximum (6.9–5.3 ka BP) that led to the persistence of birch-pine forest with the forest coverage of about 40%. After 5.3 ka BP the increase of climate humidity and low fire frequency resulted in the expansion of broadleaf forests (oak, lime and elm), which reached their maximal expansion between 2.3 and 1.5 ka BP. The later appearance of broadleaf forests in this region in comparison to the central and western parts of the East European Plain may be explained by greater climate continentality. Human activities could affect the vegetation starting from the Neolithic, but those impacts were relatively limited until the recent past. Over the last century human impacts considerably increased due to harvesting of broadleaf trees and in combination with forest fires led to the predominance of *Picea*, *Pinus* and *Betula* and formation the current mixed coniferous-broadleaf forests.

Projected changes of climate conditions in the 21st century (IPCC 2013) will clearly have a significant impact on forests within the study area. Based on our paleoecological evidences, expected rise of air temperature will cause higher fire frequencies and make unfavorable conditions for broadleaf forests. We conclude that by climatic trends of the current century broadleaf trees are more vulnerable in comparison to coniferous species and require special protection measures.

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Table 1. Details of radiocarbon dates of the peat core from the Klukvennoe peatland in the Mordovia State Nature Reserve

Laboratory code	**Depth (cm)**	**Material**	**Radiocarbon date (^{14}C yr BP)**	**Calibrated age range, 95% confidence interval (probability)**
IG RAS 4585	35-40	Bulk peat	104.78%±3,04%*	46-80 BP (95.0%)
IG RAS 4586	75-80	Bulk peat	2660±70	2519-2525 BP (0.3%) 2539-2587 BP (2.9%) 2617-2632 BP (1.1%) 2699-2950 BP (90.7%)
IG RAS 4587	125-130	Bulk peat	3680±80	3734-3741 BP (0.3%) 3776-3788 BP (0.5%) 3827-4248 BP (94.1%) 4278-4280 BP (0.1%)
IG RAS 4588	175-176	Bulk peat	4910±90	5472-5554 BP (11.4%) 5571-5894 BP (83.6%)
IG RAS 4593	220-225	Bulk peat	5850±90	6453-6863 BP (93.8 %) 6866-6881 BP (1.2%)
IG RAS 4589	245-250	Bulk peat	5980±100	6569-6584 BP (0.8%) 6629-7032 BP (87.9%) 7040-7088 BP (2.4%) 7093-7156 BP (3.9%)

*This date is reported here on the basis of percent modern carbon.

Captions for figures

Figure 1. Location of study site within Eastern Europe and position of the stadied peatland

1 – location of study area; 2 – location of peat core.

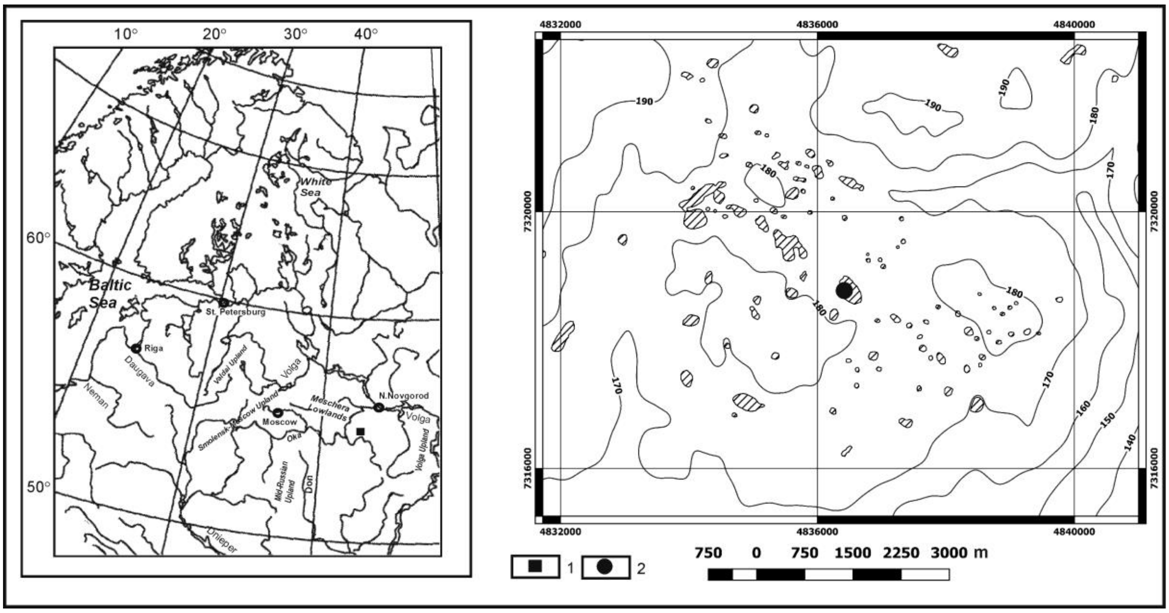

Figure 2. Age-depth model for the peat core from the Klukvennoe mire based on the radiocarbon dates in table 1

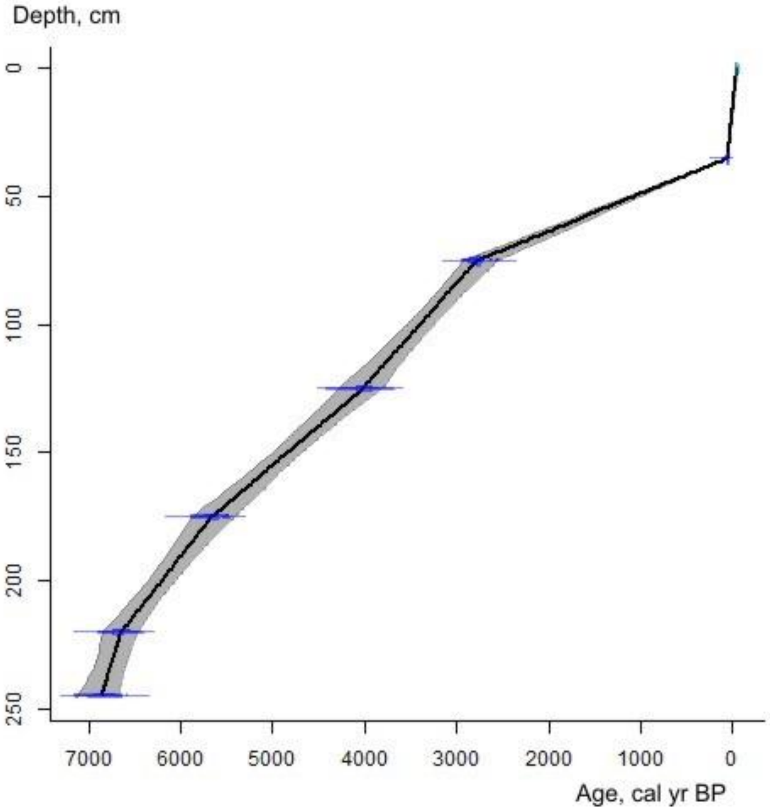

Figure 3. Plant macrofossil diagram, peat humification and LOI for the peat core from the Klukvennoe peatland in the Mordovia State Nature Reserve

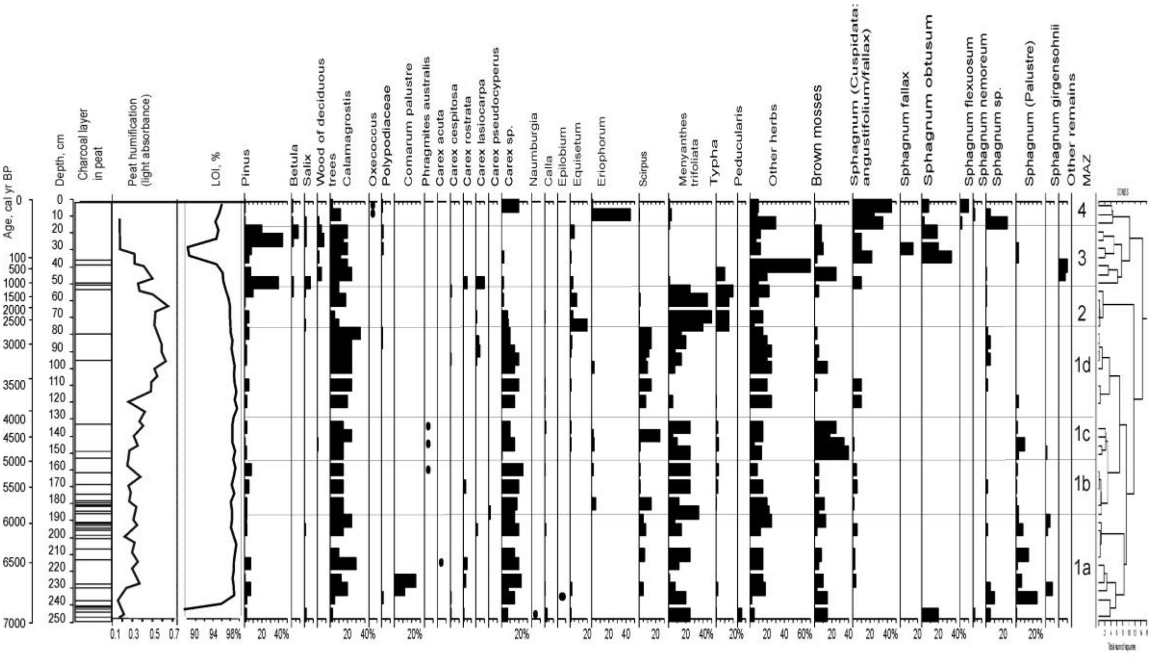

Figure 4. Testate amoeba diagram of the peat core from the Klukvennoe peatland in the Mordovia State Nature Reserve

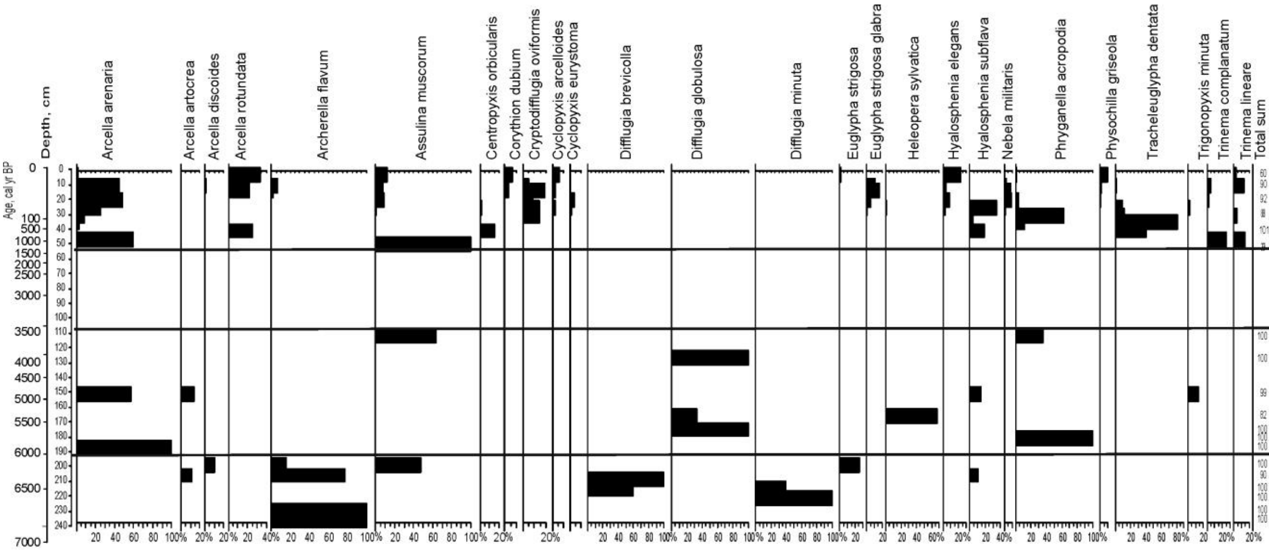

Figure 5. Pollen diagram of the peat core from the Klukvennoe peatland in the Mordovia State Nature Reserve

Pollen sum: AP+NAP; additional curves represent x10 exaggeration of base curves.

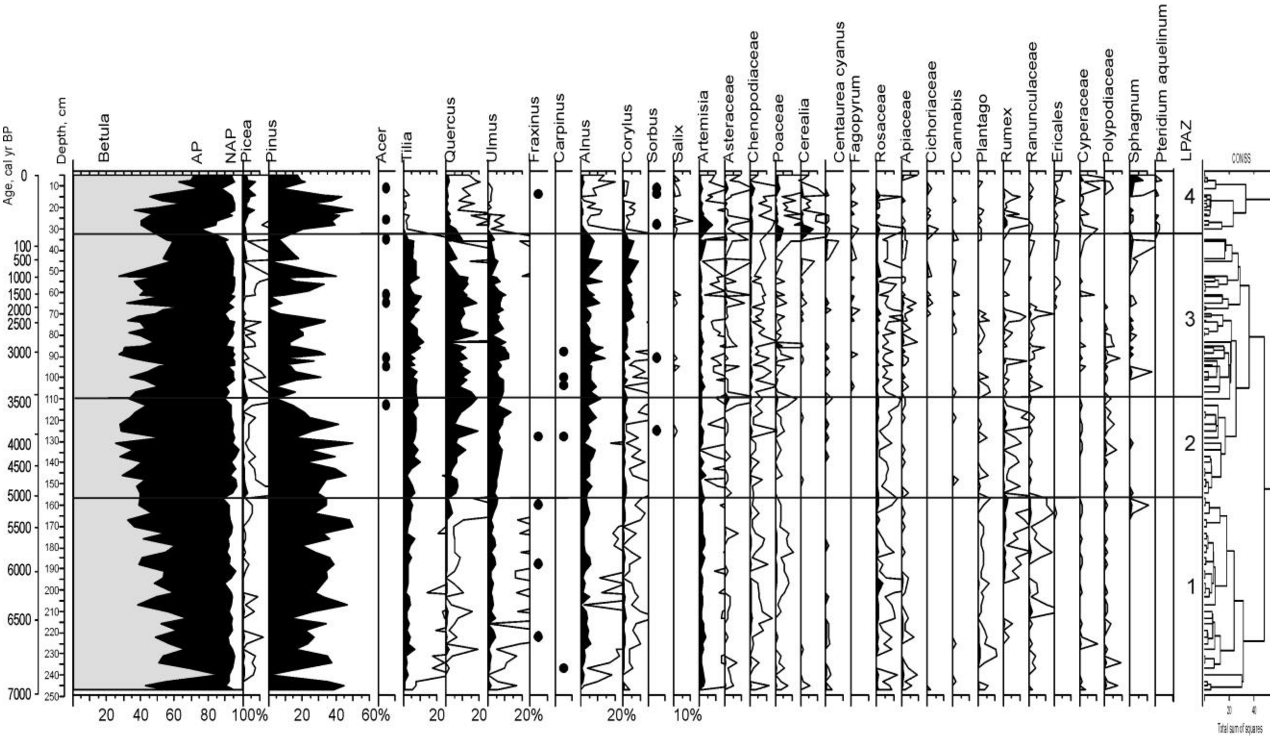

Figure 6. Pollen and micro-charcoal accumulation rate (PAR: number of pollen grains cm^{-2} yr^{-1}) of the peat core from the Klukvennoe peatland in the Mordovia State Nature Reserve (selected taxa)

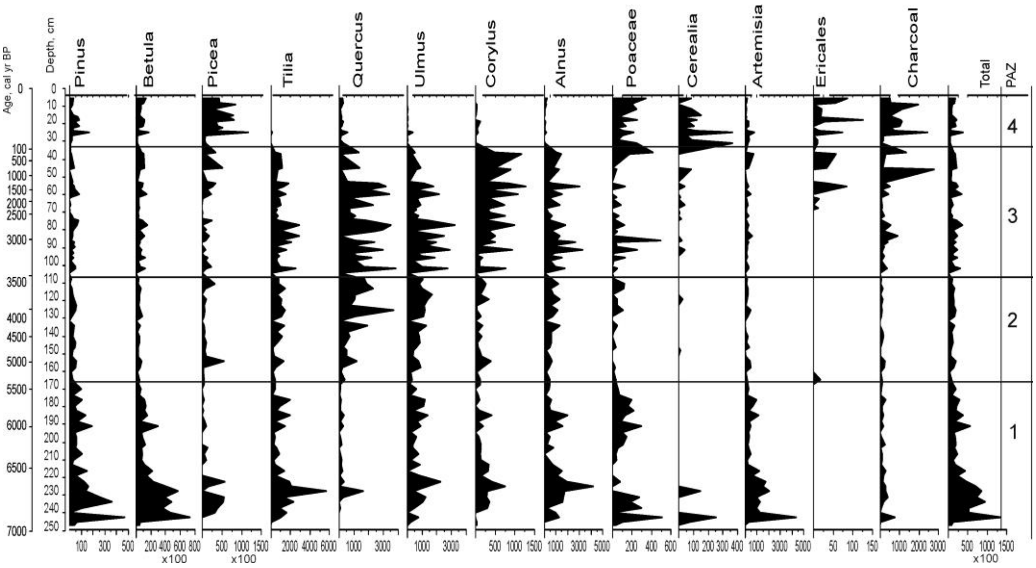

Figure 7. Summary of the results of the multi-proxy analysis of the Klukvennoe peatland, including peat properties (LOI, peat humification), characteristic pollen taxa, micro-charcoal accumulation rate, woodland coverage (%) and fire free interval. The Sum of broadleaf trees includes pollen of *Quercus, Ulmus, Tilia, Fraxinus, Acer* and *Carpinus*.

MCA – Medieval Climate Anomaly.