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From Modern Pollen–Plant Relationships to Holocene Vegetation Diversity Reconstructions

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Declaration:
I hereby declare that this doctoral thesis, my original investigation and achievement, submitted for the doctoral degree at the Tallinn University of Technology, has not been submitted for a doctoral or equivalent academic degree.

Ansis Blaus

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ANSIS BLAUS

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Contents

List of Publications

The list of author's publications, based on which the thesis has been prepared:

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II. **Blaus, A.**, Reitalu, T., Gerhold, P., Hiiesalu, I., Massante, J.C., and Veski, S. (2020). Modern pollen–plant diversity relationships inform reconstructions of functional and phylogenetic diversity in calcareous fens. Frontiers in Ecology and Evolution, 8:207. https://doi.org/10.3389/fevo.2020.00207;

III. **Blaus, A.**, Reitalu, T., Poska, A., and Veski, S. (2020). Mire development trajectories and related biodiversity changes over the last 10,000 years in Western Saaremaa, Estonia. *Manuscript;*

IV. Amon, L., **Blaus, A.**, Alliksaar, T., Heinsalu, A., Lapshina, E., Liiv, M., Reitalu, T., Vassiljev, J., and Veski, S. (2020). Postglacial flooding and vegetation history on the Ob River terrace, central Western Siberia based on the palaeoecological record from Lake Svetlenkoye. The Holocene, 30, 618–631. https://doi.org/10.1177/0959683619895582;

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Author’s Contribution to the Publications

Contributions to the papers in this thesis are:

I. The author is the principle conceiver of the publication. The author contributed to fieldworks on sediment core collection and carried out laboratory analyses of pollen, NPP and loss-on-ignition. The author is partly responsible for statistical analysis, result visualisation and interpretation.

II. The author is the lead author of the publication, contributed to fieldworks of vegetation surveying and modern pollen sample collection, and laboratory analyses of pollen. The author is partly responsible for data compilation, statistical analysis, result visualisation, and interpretation.

III. The author is the leading author of the manuscript, was responsible for conducting statistical analysis, compilation of figures, and result interpretation.

IV. The author was responsible for pollen analysis, related result visualisation and interpretation, and was involved in writing the paper.

V. The author was partly responsible for data preparation and interpretation and was involved in writing the paper.

1 Introduction

Biodiversity or biological diversity is a term that embodies all the variety of life found in a particular place on Earth. This variety and complexity of life is organised in different hierarchical levels that start with kingdoms and end with species and populations. Biodiversity can also be organised in ecological complexes such as communities, ecosystems, biomes, etc. Species richness (taxonomic richness) is by far the most used measure to quantify biodiversity. However, community ecology increasingly emphasises the importance of other metrics, such as phylogenetic and functional diversity to fully capture biodiversity (Mason et al., 2005; Flynn et al., 2011; Brocchieri, 2016).

Phylogenetic diversity and structure can be determined by using phylogenetic lineages in an evolutionary framework (Webb et al., 2002). Since the introduction of the field by Faith (1992), phylogenetics have been progressively applied as a complementary measure in community ecology to study processes shaping community and species coexistence, their evolution and extinction (Flynn et al., 2011; Cadotte et al., 2012; Mienna et al., 2020). Species assemblages can be phylogenetically overdispersed (loosely related) or clustered (closely related) depending on species' preferred environmental niches or competitive relationships, or the phylogenetic structure can be random, driven by stochastic processes (Hardy and Senterre, 2007). Functional diversity captures physical properties and community structure, as expressed through the range of various functional traits (Tilman, 2001; Mason, et al., 2005). Functional traits define species' life strategies and are used to predict ecosystem function and ecosystem services from the community to the biome level (Anacker and Harrison, 2012; Echeverría-Londoño et al., 2018) along climatic and environmental gradients (de Bello et al., 2006; Muscarella and Uriarte, 2016). Multidimensional indices such as functional richness, functional evenness and functional dispersion are commonly used to express functional diversity (Laliberté and Legendre, 2010).

Different dimensions of biodiversity have been shown to be critical for providing different ecosystem services and supporting human well-being (Levin, 2000; Hooper et al., 2005; Lavergne et al., 2010). The conservation and protection of biodiversity should, therefore, be self-evident. Nevertheless, severe biodiversity loss that exceeds background extinction rates, species range shifts, and biome transformations is happening at unprecedented rates hand-in-hand with global climate change and increasing anthropogenic pressure (Wilson, 1985; Pimm et al., 2014; Legagneux et al., 2018). Since the origin of life, the climate has constantly shaped biodiversity, determined its distribution and species assemblages, and will continue this reciprocal alteration in future (Canfield et al., 2007; Lavergne et al., 2010). In the face of ongoing climate change, the knowledge of historical environment, variability of species, communities and general biodiversity in response to the changing climate and human impact is critical for future predictions, policymaking, biodiversity conservation and protection (Wingard et al., 2017; Whitlock, 2017).

Advances in radiocarbon ^{14}C dating (Libby, 1955) and understanding the age of organic material (Pavlish and Banning, 1980; Povinec et al., 2009; Manning et al., 2020) have helped to interpret the fossil records in terms of biodiversity development, dynamics and community assemblages along the geological timescale. Palaeoecology and particularly Quaternary palaeoecology (concerning the last 2.58 million years of Earth history) have contributed extensively to understanding the ecological systems and past environments (Lawrence, 1971; Birks, 2012; Seddon, 2013). Palaeoecological analysis of pollen and spores from sediment sequences and presenting the results in terms of a pollen diagram were first introduced by Swedish naturalist and geologist Lennart von Post (von Post, 1918) and have been used up until today. Pollen analysis has an important role in studying vegetation history and historical environments, and provides useful proxies of past climatic conditions and various other factors (Davis, 2014; Birks et al., 2016; Parnell et al., 2016). Shortly after the introduction of pollen analysis, in the 1920s, it was adopted in Estonia by Paul William Thomson, who laid the foundations for interpreting post-glacial vegetation history in the Baltic region (Thomson, 1925). After that, many prominent studies have used pollen analysis to elucidate vegetation history, biostratigraphy, archaeology, sea level fluctuations, and human impact in Estonia (e.g. Ilves and Sarv, 1975; Veski, 1996; Königsson et al., 1998; Poska and Saarse, 1996, 2002; Saarse et al., 2009). Recent advances in palaeoecology methods have provided novel insights to the land-cover history (Poska et al., 2018) and development of biodiversity patterns (Reitalu et al., 2015). The latter study provides an attempt to link palaeoecology to community ecology by applying functional traits and phylogenetic diversity on sediment pollen data, thus providing a significant but unexplored avenue for studying historical communities in more depth.

Despite its widespread application, pollen analysis possesses certain biases and complexities that can result in misleading interpretation of historical data. The main concern is related to undefined spatial resolution that originates from the different, taxon-specific effectiveness of pollen production and dispersion (Shaw and Whyte, 2020). The first attempts to tackle this production bias originate from Davis (1963), who introduced the representation factors (R-values) that quantify the ratio between the abundance of pollen type in the sample and the abundance of plants producing the pollen in surrounding vegetation. Andersen (1970) introduced correction factors, where the effect of dominant taxa is downweighed, thus increasing the relative weight of pollen taxa with low production. Later Parson and Prentice (1981) developed extended R-values that correct for production and dispersion bias simultaneously. Development of the field and advances in statistics and computing have resulted in sophisticated models like the Landscape Reconstruction Algorithm (LRA) (Sugita 2007a, 2007b) and Multiple Scenario Approach (Bunting and Middleton, 2009). The framework of the LRA is based on the Regional Estimates of Vegetation Abundance model from Large Sites (REVEALS) and Local Vegetation Estimate model (LOVE) from smaller sites. The LRA has been widely used in Europe and other parts of the world for quantitative estimates of historical land-cover and its response to changes in climate and human impact (e.g. Mazier et al., 2012b; Matthias et al., 2015; Li et al., 2020).

Like species richness in ecology, palynological richness is the most applied biodiversity index in palaeoecology (Birks and Line, 1992; Odgaard, 2001; Giesecke et al., 2012; Birks et al., 2016). In addition to the abovementioned biases, taxonomic precision (limitation in pollen identification) and counting effort (pollen count per sample) add to this complication, and the relationship between pollen richness and plant richness in surrounding vegetation is not straightforward (Birks and Line, 1992; Odgaard, 2008; Birks et al., 2016). This has led to several attempts to test pollen–plant richness relationships with the help of modern analogues, by using sediment surface samples, traps or moss samples, and detailed information of surrounded vegetation. Different studies show that pollen–plant richness relationships are significantly positive in different spatial scales (Odgaard, 2008; Meltsov et al., 2011; Felde et al., 2016, Reitalu et al., 2019) and that pollen richness reflects landscape diversity (Meltsov et al., 2013; Matthias et al., 2015);

however, negative relationships have also been found (Goring et al., 2013). The current knowledge derived from these studies emphasises that pollen data collected from different sediment basins (lakes, bogs, forest hollows), different groups of taxa (insect vs wind pollinated; herbs vs trees) do not reflect surrounding vegetation uniformly, and further studies that would help to understand these relationships from different perspectives are required.

So far, pollen studies have been predominantly carried out from lake sediments and large mires that reflect regional and landscape-scale vegetation and processes (e.g. Carrión, 2002; Hjelle et al., 2015; Feurdean et al., 2017), but smaller basins that reflect local and *in situ* processes (Sugita, 2007b) have had less attention (but see Overballe-Petersen et al., 2013; Kuosmanen et al., 2017; Waller et al., 2017). Reconstructions from small sites are particularly important for the environments where vegetation and site development are interrelated such as in peat-accumulating environments (Clymo, 1984). Peatlands or mires are valuable sediment archives (Chambers et al., 2011) that are usually subdivided into ombrotrophic bogs and minerotrophic fens, according to their hydrological regimes – rainwater fed and groundwater fed, respectively (Lindsay, 2010). Both bogs and fens are important on the local and global scales in different contexts (Minayeva et al., 2017; Leifeld and Menichetti, 2018; Jurasinski et al., 2020). These habitats play a crucial role in the global carbon cycle, are rich in habitat specialists making vital contribution to biodiversity and provide many other ecosystem services (Fontaine et al., 2007; Hooijer et al., 2012; Beadle et al., 2015; Hanis et al., 2015; Glenk and Martin-Ortega, 2018). Nevertheless, due to their unique hydrology, these habitats are extremely vulnerable and are sensitive to several factors such as climate change, drainage, land use transformation, as well as autogenic succession that possess threats to their persistence and related biodiversity (Mauquoy and Yeloff, 2007; Hooijer et al., 2012; Swindles et al., 2019).

In the global context, Estonia holds an exclusive amount of mires – approximately 22% of the state territory (Orru and Orru, 2008); however, the knowledge about their origin, succession and biodiversity trends is scarce, especially in case of spring fens (but see Saarse and Königsson, 1992; Veski, 1996; Sillasoo et al., 2007). Differences in fen and bog hydrology and thus water chemistry result in a distinct vegetation continuum that can be scored along a poor–rich gradient (Tahvanainen, 2004). This gradient strongly depends on soil reaction and calcium concentration and serves as a natural bipartition of bogs and fens. Overall, bogs are associated with low pH and poor vegetation, whereas fens are grouped into poor, moderate and rich fens, and usually have a high pH and calcium concentration (Wheeler and Proctor, 2000; Lamers et al., 2015).

The unique characteristics of these habitats have attracted significant attention in applied ecology, particularly to studying species' habitat requirements and biodiversity responses along environmental gradients (e.g. Wassen et al., 1990; Godwin et al., 2002; Hájek et al., 2006; Ilomets et al., 2010). For this purpose, the application of Ellenberg indicator values (EIVs), which is a plant ordinal classification based on their realised ecological niche and environmental gradient (Ellenberg et al., 1991), has a long tradition (Diekmann, 1995; Hill et al., 2000). Despite existing concerns of the implicit methodology and deviance on species ecological requirements (niches) across different geographical areas (Schaffers and Sýkora, 2000; Smart and Scott, 2004), calibrations of EIVs that were originally developed for Central Europe have opened potential for their application in different parts of the world (Lawesson et al., 2003; Diekmann, 2003; Hill et al., 2000; Bartelheimer and Poschlod, 2015).

The inference on species' realised niches is one of the main principles in fossil assemblage interpretation and historical environment reconstruction in palaeoecology (Hill et al., 2000). In the context of environmental gradients, however, sediment pollen assemblages have mostly been used for temperature reconstructions (Seppä et al., 2004; Mazier et al., 2012a; Salonen et al., 2012; Veski et al., 2014), mostly neglecting other environmental gradients. However, phosphorus availability, soil reaction, productivity and moisture have been reconstructed with the help of pollen data (Kuneš et al., 2011; Reitalu et al., 2015), highlighting the potential of pollen data to reconstruct different environmental gradients in palaeoecological investigations.

Regional and global extinctions serve as major metrics for the predictions of future biodiversity trajectories and inform conservation policies (Gaston, 2000; Santamaría and Méndez, 2012; Rosa et al., 2020). Local extinctions that in many cases have occurred long before global extinction (Wiens, 2016) have received less attention. Similarly, in palaeoecology large-scale biodiversity reconstructions have prevailed over local scales (Birks et al., 2016; Reitalu et al., 2015; Giesecke et al., 2019). Although large-scale studies provide valuable insights into biodiversity changes, the actual sources of biodiversity loss might be undetected. In the global context, assigning the conservation priority to the recognised hotspots of diversity, those with a high number of endemic species and those experiencing habitat loss, is believed to be one of the most effective and low-cost ways to support the biodiversity (Myers et al., 2000). On the local scale, mires and especially minerotrophic fens have been recognised as such hotspots by many researchers (Moen, 1995, Jiménez-Alfaro et al., 2012; Saarimaa et al., 2019) and organisations such as European Environmental Agency (EEA, 2017) and NATURA 2000 (Šefferová et al., 2008). Mires are significant for landscape heterogeneity, regional species pools, yet a great number of them are not under protection. Studies of different historical biodiversity dimensions from mire habitats would better represent their biodiversity development and could guide conservation efforts more precisely.

Abbreviations

AD	calendar age after Christ, Anno Domini
AMS	accelerator mass spectrometry
AR	accumulation rate
BC	calendar age before Christ
cal yr BP	calibrated years before present (AD 1950)
CWM	community weighted mean
EIV	Ellenberger indicator value
FD	functional diversity
FDa	functional alpha diversity
GAM	generalised additive model
HTM	Holocene Thermal Maximum
IVM	indicator value method/analysis
ka	kiloannum, thousands of years before the present (AD 1950)
LOI	loss-on-ignition
LM	linear model
m.a.s.l.	meters above sea level
MM	mineral matter
NPP	non-pollen palynomorph
OM	organic matter
PCA	Principal Components Analysis
PD	phylogenetic diversity
RDA	Redundancy Analysis
RF	Random Forest
RSAP	relevant source area of pollen
SFAP	spheroidal fly-ash particles
Ellenberg indicators	
F	moisture
K	continentality
L	light
N	productivity
R	soil reaction
T	temperature
Plant functional traits	
AH	average height (m)
AM	arbuscular mycorrhiza
EM	ectomycorrhiza
ERM	ericoid mycorrhiza
LDMC	leaf dry matter content
SLA	specific leaf area

Aims of the study

The present thesis is a synthesis of detailed research from the field of palaeoecology comprised in five scientific papers with the main emphasis being on new approaches in pollen analysis. An important part of the thesis is devoted to pollen–plant relationships on local and regional scales, which is one of the most discussed ambiguities in this field. For this purpose, modern pollen–vegetation relationships are used. Species diversity and vegetation composition relationships are tested based on surface pollen data and detailed information on surrounding vegetation from lake surface samples and spring fen moss polsters. In addition to pollen richness, other important yet palaeoecologically unexplored biodiversity metrics – namely functional diversity and phylogenetic diversity – are tested. Another aspect that is investigated in the current thesis is the potential of pollen to reflect different environmental gradients and how these gradients correlate with biodiversity metrics. The inferences from modern pollen–plant relationships on both biodiversity metrics and environmental gradients are used to better interpret sediment pollen-based reconstructions and to understand community processes within the Holocene (the last 11,700 years). More specifically the aims of the current thesis are the following:

1. To use pollen analysis as the main proxy to study vegetation development, palaeohistory and biodiversity from various environments (Papers I–V);
2. To infer the pollen signal from mire ecosystems and give the overview of mire origin and development on Saaremaa Island (Papers I–III);
3. To investigate modern pollen–plant relationships on regional and local scales in order to better interpret historical reconstructions (Papers II, III and V);
4. To understand modern pollen–plant functional and phylogenetic diversity relationships and to test their applicability to reconstruct sediment pollen-based historical trends of plant community assembly (Papers II, III);
5. To test modern pollen–plant relationships of environmental gradients expressed as Ellenberg indicator values and their applicability to reconstruct sediment pollen-based historical environmental gradients (Papers II, III);
6. To compare modern pollen–plant relationships and biodiversity trends among the subset groups of woody and herbaceous taxa (Papers II–IV);
7. To discuss the impact of different autogenic and allogenic processes on vegetation and biodiversity through time (Papers I–IV).

2 Material and methods

The extra value from integrating various proxies in palaeoecology to understand different historical processes and systems is clear and the multi-proxy approach is often used in palaeoecological studies (Vandenberghe, 2012). In the current thesis, various methods and multi-proxy analyses were used in Papers (I–V), and only general information on their application is presented in this paragraph. For more detailed information on study areas, material, methods and statistical analyses see the individual papers.

2.1 Study area and sites

The current thesis is based on samples and studied sites covering Northern Europe and reaching to the West Siberian Plain. Estonia and particularly Saaremaa Island in Western Estonia and the Karula region in Southern Estonia are the focus in Papers I–III, where the local spring fens and bogs are studied. Palaeoecological reconstructions from Lake Svetlenkoye in Paper IV focus on the West Siberian Plain and the floodplain of the Ob River. Paper V comprises the samples from the entirety of Northern Europe and partly covers NW Russia until the Ural Mountains. The map of the study area is shown in Fig. 1.

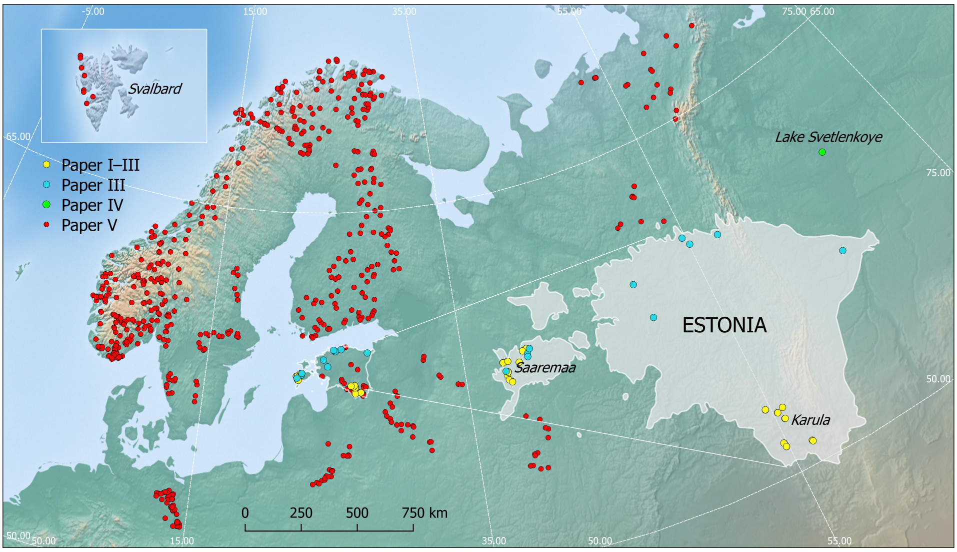

Figure 1. *Study areas in research Papers I–V. Yellow dots represent the spring fens where the modern moss samples are derived (Papers I–III). Blue dots are the surface samples from the Bogs (Paper III). The green dot marks the location of Lake Svetlenkoye (Paper IV). Red dots represent surface pollen samples from the lakes from N and NE Europe, including Svalbard (Paper V).*

In general, the study area of the current thesis lies on the West and East European Plains, surrounded by the North Atlantic in the west and Arctic Ocean in the north. The climate, relief and vegetation strongly vary across the region. The western part of the region is characterised by maritime and maritime-subarctic climate strongly affected by the Gulf Stream. In the northern and central parts, subarctic and temperate climate prevails. The region belongs to some of the world’s largest biomes, such as temperate forests, boreal forests and tundra (Bradshaw, 2002). Temperate coniferous and temperate broadleaf forests are the most common biotopes in European territory, whereas tundra, boreal forest and small-leaved deciduous forest characterise the East European and West Siberian Plains. The northernmost part of Europe and Russia despite its rich landscape diversity has relatively low levels of biological diversity compared to areas further south. In this part of the world, some of the environments have remained more-or-less untouched by humans, yet other parts have experienced human impact for several millennia (Shahgedanova, 2002).

The study sites that concern local and landscape scales are located in Estonia (Papers I–III). Situated on the east coast of the Baltic Sea, Estonia is subjected to a maritime-continental climate gradient with overall cool summers and mild winters. The Estonian landscape has been modified by the Weichselian glaciation over 100,000 years (Raukas and Kajak, 1997) and the final deglaciation took place ca 14,000–11,000 years ago (Kalm and Lasberg, 2013). The postglacial rebound is still perceptible in the region and according to the rebound model, land uplift rates vary between -0.5 and +2 mm/yr (Kall et al., 2013). The Quaternary sediment cover left by deglaciation seldom exceeds 5–10 m on the islands and northern Estonia but attains up to 200 m in southern Estonia (Systra, 2010). In the regional context, the country is relatively flat, with average elevation ca 50 m.a.s.l. For example, the highest points of Estonia, situated in southeast part of the country, lies at 318 m.a.s.l. In addition to deglaciation, the regressions and transgressions of historical stages of the Baltic Sea have reworked the landscape particularly on the islands (Saarse, 2009). Estonia, with its two biggest islands Saaremaa and Hiiumaa, is characterised by extensive and shallow coastline that spans almost 3800 km. Nearly 50% of the country is covered with forests, ca 22% with mires, and the rest includes a large number of lakes and agricultural land. Estonia belongs to the boreo-nemoral ecotone, with most of the forest composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*), two birch species (*Betula pendula* and *B. pubescens*), two alder species (*Alnus glutinosa* and *A. incana*), and other small-leaved deciduous trees in different proportions (Paal, 1998).

Estonia has been characterised by high biodiversity, and in comparison, with similar geographies, both flora and fauna have been recognised as among the richest in Europe. Factors such as geographical location, peculiarities of climatic conditions, soil diversity and large areas of natural landscapes have favoured biodiversity in Estonia. Yet similarly to other European countries, Estonia is currently facing the challenges of biodiversity preservation due to land use intensification (O'Riordan and Stoll-Kleemann, 2002).

2.2 Modern pollen data

Modern pollen data in Papers I, III and V come from various sources. Moss polster samples (n=34) were collected from spring fens on Saaremaa Island and the Karula region (Fig. 1.) during fieldwork in July–August 2017. Open and forested spring fens alike were sampled for studying pollen signal related to openness and overgrowing (Papers II and III). Samples were collected and preserved according to the protocol of the Crackles Bequest Project (Bunting et al., 2013). Pollen sample preparation followed the same method as for sediment pollen (see paragraph 3.6), except that the HF treatment was not used. Approximately 1000 pollen grains were counted from each sample.

Bog surface samples (topmost part of sediment core) from different parts in Estonia were gathered from previous studies and have varying numbers of pollen grains counted per sample (n=308–1673). For references of the data sources, see Paper III.

Surface samples used for analysis in Paper V are compiled from various data sources but mainly from Salonen et al. (2012). These samples have been collected from small and medium-size lakes. For the extent of lake distribution, see Fig. 1. Since data come from different specialists, taxonomic harmonisation was applied to reduce the effect of taxonomic incompatibilities among the sites. Pollen sums varied from 200 to 1000 grains among the samples. Certain samples were pooled together to reduce the effect of extremely low pollen sums. For data particularities and references, see Paper V.

2.3 Vegetation data

Detailed vegetation surveying was performed around the moss samples from the open and forested spring fens to study modern pollen–plant relationships. The fieldwork was carried out in July–August 2017 and 2018. The procedure of vegetation surveying and estimating species abundances in nine radii (0.5, 1.5, 3, 6, 10, 20, 50, 70, 100 m) was conducted according to the protocol in the Crackles Bequest Project (Bunting et al., 2013). The schematic illustration of vegetation recording is shown in Fig. 2. Within a 10 m radius, a vegetation survey was conducted from systematically placed 1×1 m squares (n=21). Additionally, species outside of the squares were recorded for corresponding radii. Vegetation within 10–100 m was mapped as vegetation types with their species composition characterised in the field. Cover estimates in percentages and Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964) were used for woody and herbaceous taxa, respectively. For more detailed information on vegetation inventory, see Paper II.

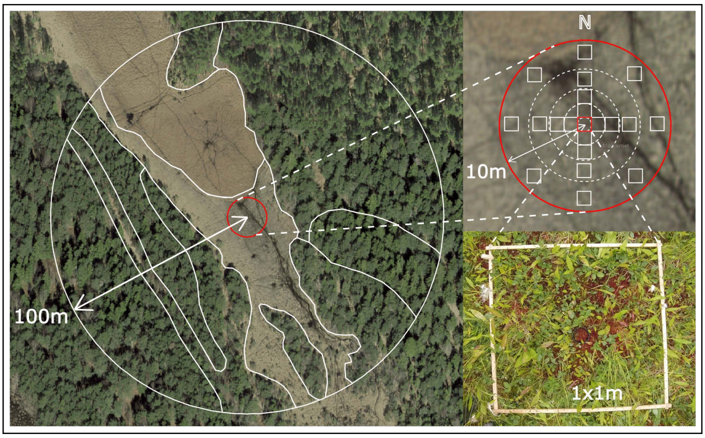

Figure 2. *The schematic overview of the vegetation inventory strategy modified from the Crackles Bequest Project protocol (Bunting et al., 2013).*

Information on the species richness of surrounding vegetation of lake surface samples in Paper V is merged from plant atlases available in Europe (see Paper V for references and additional information). The compiled dataset contains comprehensive information on the distribution of the majority of European plant species in the spatial resolution of 50×50 km.

Original modern pollen and vegetation data produced for this thesis and detailed information on site location is publicly available at the Dryad Digital Repository under the following Digital Object Identifier: https://doi.org/10.5061/dryad.wstqjq2hh (Blaus et al., 2020b).

2.4 Sediment coring and sampling

Fieldwork for sediment coring was conducted for three research papers: Lake Svetlenkoye (Paper IV) was cored in March 2014, Kanna calcareous spring fen (Paper I) in October 2016, and the Viidumäe 1–2 sites (Paper III) in January 2020. All sites were sampled with a Russian-type corer, but a Willner-type sampler was used for the upper Svetlenkoye sediment part (54 cm) because of the loose sediment properties characteristic to lakes. Lake Svetlenkoye was cored from the ice surface. Several cores were collected from the sediment basins, but only the deepest cores were examined in more detail. The sediment depth was 325 cm in Svetlenkoye, 225 cm in Kanna, 90 and 105 cm in Viidumäe 1 and 2, respectively. The stratigraphy of sediment cores was immediately described in the field, cut to 1-cm subsamples or wrapped in plastic and transported to the laboratory for palaeoecological analyses. Svetlenkoye sediment consisted of gyttja with different proportions of organic material and silt at the basal part, whereas sediment sequences from Kanna spring fen and Viidumäe 1 and 2 consisted overall of well-decomposed peat with coarse sand at the basal part.

Other sediment cores whose pollen assemblages are used to study mires on Saaremaa Island (Paper III) have been cored in similar way to Kanna spring fen in earlier studies. More detailed information on their properties and lithology can be found in Paper III and in original publications by Hansson et al. (1996), Veski (1996), Saarse and Königsson (1992), Poska and Saarse (2002).

2.5 Chronology

All the age-depth models used in the present study are compiled based on accelerator mass spectrometry (AMS) radiocarbon (14C) dates. The age-depth model for Lake Svetlenkoye is based on seven 14C dates derived from gyttja and wood twigs (Table 1). Eleven 14C dates derived from plant macrofossils, charcoal and bulk peat were used for the Kanna age-depth model. The dates for both sediment sequences were obtained from the Poznań Radiocarbon Laboratory. OxCal 4.2.4 deposition model (Bronk Ramsey, 2008, 2009) and IntCal13 calibration curve (Reimer et al., 2013) were used to draw the models. Additionally, spherical fly ash particle (SFAP) analysis, which marks industrialisation intensification (Rose, 1990), was used to improve the age-depth models from both sediment sequences.

The ages for chronologies of other mires presented in Paper III were gathered from previous studies (Hansson et al., 1996; Veski, 1996; Saarse and Königsson, 1992; Poska and Saarse, 2002) and were calculated by calibrating 14C dates with standardised methodology by using the same OxCal 4.2.4 deposition model and IntCal13 calibration curve. For Viidumäe 1 and 2, new material from the sediment basal part was dated to get to know the age of the previously undated sediment core. The same AMS and 14C dating method from the Poznań Radiocarbon Laboratory and above-described calibration were used to derive the ages. Weighted average ages with 95.4% probability errors are expressed as “cal yr BP” – calibrated years before the present (with the present as 1950). In the text of this thesis, age may also be referred to as “ka” (kiloannum) – thousands of years before the present.

2.6 Pollen data and laboratory analysis

The standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986) and hydrofluoric acid (HF) treatment (Bennett and Willis, 2001) were used for Svetlenkoye and Kanna pollen sample preparation, n=88 and n=53, respectively. A known amount of *Lycopodium* spores was added during the sample preparation to permit the calculation of pollen concentration and pollen accumulation rates (AR) (Stockmarr, 1971) in Paper IV.

The pollen reference collection from the Department of Geology, Tallinn University of Technology and various pollen identification keys (Fægri and Iversen, 1989; Reille, 1992; Beug, 2004) assisted with the identification. Pollen sums of 500 and 1000 grains per sample were aimed for the Svetlenkoye and Kanna samples, respectively. Magnifications of ×250, ×400 and ×1000 were used for identifying microfossils under the microscope (ZEISS Axio Imager).

Alongside pollen, spores of seedless plants were also counted. "Pollen data" in the thesis text refers both to pollen and spores if not explicitly stated otherwise. For more detailed information on sediment pollen preparation and analysis see Papers I and IV.

2.7 Other proxies

Plant macrofossil analysis was another important palaeobotanical method to study *in situ* (Amon et al., 2014) vegetation succession in Kanna and Svetlenkoye. Additionally, different non-pollen palynomorphs (spores, fungi, green algae and testate amoebae in the Kanna samples), microscopic and macroscopic charcoal were identified and counted alongside the pollen analysis in Papers I and IV. Information on sediment composition was obtained with the help of geochemical analysis by the loss-on-ignition (LOI) method (Heiri et al., 2001) in Papers I and IV. LOI provides the sediment composition in terms of organic matter (OM), mineral matter (MM), water content and carbonate content. Total organic carbon and nitrogen content expressed as a C/N ratio were analysed from the sediments of Svetlenkoye (Paper IV). Diatom analysis was used to study changes in water quality and pH in Lake Svetlenkoye. The peat humification index was used to study changes in peat decomposition levels in Kanna spring fen (Paper I).

In addition to biostratigraphical and geochemical analyses, the average modelled summer and winter temperatures from the ECBilt-CLIO-VECODE climate model (Renssen et al., 2009) were used to study the climate-forcing effect on vegetation succession in Kanna spring fen (Paper I).

In Paper V, several contemporary climate and landscape variables (for example, mean annual temperature, annual precipitation, human population density, and landscape openness) were used to describe variation in plant and pollen richness.

2.8 Diversity measures

Pollen richness (taxonomic richness) is the most common method to reconstruct temporal changes and to assess historical perspective in plant diversity from pollen assemblages (Birks and Line, 1992, Birks et al., 2016). This measure, whether with sediment or modern pollen data, is used in all papers in this thesis and was calculated with the help of rarefaction analysis, which corrects for the bias on the pollen counting effort (Birks and Line, 1992). Additionally, richness calculated with Andersen correction factors (Andersen, 1970) was used in Papers I, II, and V. Application of Andersen correction factors reduces the effect of dominant taxa, and increases the effect of underrepresented taxa, resulting in better pollen–plant correlations (Felde et al., 2016). Shannon diversity and Simpson's evenness were used to express modern pollen diversity in Paper II.

Richness, Shannon diversity and Simpson's evenness were used in Paper II, to express plant diversity. Both total plant richness and transformed richness to pollen equivalents were used in Paper V. In Papers II, III and V, diversity measures were calculated for different subset groups based on plant growth forms – herbaceous vs woody plants. Herbaceous taxa included dwarf shrubs from Ericaceae. In Paper V, additional subset groups of insect pollinated vs wind pollinated taxa were used. In Papers I and IV, only the pollen richness of all taxa was used to study diversity changes.

Functional diversity (FD) refers to a variety of functional characteristics and thus reflects the biological complexity of a particular ecosystem or community and is expressed based on selected plant traits that represent a broad range of plant functions and adaptations (Tilman, 2001; Laureto et al., 2015). In Paper II, plant functional traits such as clonality, plant height, specific leaf area (SLA), leaf dry matter content (LDMC), seed size, seed number and three mycorrhizal types – arbuscular mycorrhiza (AM), ectomycorrhiza (EM) and ericoid mycorrhiza (ERM) – were selected to represent functional characteristics. Two indices – community weighted mean (CWM), which reflects functional composition and functional alpha diversity (FDa) – were used separately for each trait to capture FD. FDa is characterised by the standardised effect size of mean pairwise distance (SESmpd) (de Bello et al., 2016) and reflects functional dispersion. FD indices were used for testing modern pollen–plant relationships and were applied on Kanna spring fen sedimentary data to study their variation and response to different autogenic and allogenic factors through time. Like pollen taxonomic diversity measures, FD indices were calculated for the same subset groups in Paper II. R package "FD" (Laliberté et al., 2014) was used for FD calculations.

Phylogenetic diversity (PD) was another biodiversity facet used in Papers II and III. PD reflects species' phylogenetic relationships in the community, which is represented by a phylogenetic tree (Brocchieri, 2016). For both papers, a phylogenetic tree was assessed using the mega phylogeny of vascular plants in R package – "V.PhyloMaker" (Jin and Qian, 2019). Similar to FDa, phylogenetic dispersion was calculated as SESmpd and was the only metric used to reflect PD. Modern pollen–plant-based PD relationships were studied in Paper II, and in Papers II and III, PD was applied on sediment pollen to study the phylogenetic dispersion of communities and its variation in time.

2.9 Environmental gradients based on EIVs

The feasibility of pollen to reflect different environmental factors was tested with the help of Ellenberg indicator values (Ellenberg, 1992). Ellenberg indicators reflect species' realised ecological niches and tolerance to different conditions. In Papers II and III, Ellenberger indicators of temperature (T), moisture (F), light (L), soil reaction (R), productivity (N) and continentality (K) were used. The modern pollen–plant relationships of these factors were tested for the subset groups of herbaceous and woody taxa, to infer their potential applicability on sediment pollen assemblages (Paper II). EIVs were applied on sediment pollen of Kanna spring fen and other mires from Saaremaa Island (Papers II and III). The associations between EIVs and biodiversity through time were investigated both in the local and landscape contexts (Papers II and III).

2.10 Data analysis

Various statistical analyses were applied on the investigated data in Papers I–V with the help of R programming software version 3.6.1 (R Core Team 2018; 2019).

Constrained hierarchical clustering (CONISS) (Grimm, 1987) with the Bray-Curtis vegetation dissimilarity (Faith et al., 1987) was used on pollen and NPP data in Papers I, III, and IV. The broken stick method (Jackson, 1993) was used to assess the number of statistically significant ($p<0.05$) zones. CONISS and broken stick analyses were performed with the help of “rioja” R package (Juggins, 2017).

The principal component analysis (PCA) performed on Hellinger-transformed data was used to study the underlying patterns of pollen and NPPs in Papers I, II, III. The broken stick method was used to estimate the number of significant ordination axes and the “envfit()” function was used to superimpose different environmental factors onto an ordination. Permutation tests from the “envfit()” function provided the significances for associations between environmental factors and ordination axes. The “vegan” R package was used for ordination analyses (Oksanen et al., 2017).

Procrustes analysis (Jackson, 2001) based on PCA ordinations of modern pollen and plant data was used to test pollen–plant community compositional relationships in different radii in Paper II. This method compares multivariate datasets and uses rotation and scaling of their matrices to minimise the sum of the squared distance between the corresponding ordinations coordinates. The PROTEST test was used to determine the significance of associations between two ordinations (Jackson, 1995). The “vegan” R package (Oksanen et al., 2017) was used for the analyses.

Linear regression models (LM) and linear mixed effect (LME) models from the “nlme” package (Pinheiro, 2000) were used (Papers I, II, III, V) to test how different predictor variables (e.g. environmental factors, climate, human impact, region, openness) predict pollen richness, pollen–plant relationships and other biodiversity measures. The significance of predictors and model outcome at the confidence levels ($p<0.05$–0.001) was clarified with the backward selection of variables in the multiple regression models. The assumptions for linear modelling were tested prior to the analyses.

In addition to the LMs, variation partitioning (Borcard et al., 1992) was used in Paper V to clarify the explanatory power of different sets of variables determining pollen and plant richness. Variation partitioning provides the outcome in the form of proportions explained by different explanatory datasets and unexplained variation in the response data. The “varpart()” function from the “vegan” R package (Oksanen et al., 2017) was used for the analysis.

Correlation tests based on Pearson’s product moment correlation (Pearson, 1895) or Kendall’s Tau coefficient (Kendall, 1938) were used to test pollen–plant diversity relationships and other factors in Papers II, III, and V. Log-transformation was applied on some variables prior to correlation tests to ensure normal distribution of the variables. Benjamini and Hochberg (1995) correction was applied to correct for the effect of multiple tests. Bootstrap method (Davison and Hinkley, 1997) from the “boot” package (Canty and Ripley, 2019) was used to provide the confidence intervals for pollen–plant diversity and composition correlations in Paper II.

In Paper III, the indicator value method (IVM) (Dufrêne and Legendre, 1997) and random forest (RF) classification method (Breiman, 2001) were used to study the strength of pollen to reflect and separate different habitat types (open fen, forested fen, bog). The IVM uses species (or pollen taxon) specificity and fidelity to determine species’ significance to certain habitats (Dai et al., 2006). The RF method is based on a large number of individual decision trees used to predict a class confusion matrix. The “labdsv” R packages (Roberts, 2006) and “indval()” function were used for the IVM, and the “randomForest” package (Liaw and Wiener, 2002) was used for the RF analysis.

Locally weighted regression fitting (LOESS) (Cleveland and Devlin, 1988) in Paper I and Generalised Additive Models (GAM) in Papers II and III) were used as smoothing functions to fit different variables in time. A span of 0.1 was used for LOESS and 95% confidence intervals for GAM, with the help of the “mgcv” R package (Wood, 2011).

3 Results

3.1 Modern pollen signal and pollen–plant relationships

3.1.1 Pollen signal from different types of mires

Results of pollen assemblage composition from open and forested fens and from bogs (Paper III) are summarised in Fig. 3. In addition to visual interpretation, the indicator value method (IVM) was used to infer the taxa indicative to different habitats and the resulting indicator taxa are shown in sample ordinations in Fig. 4.

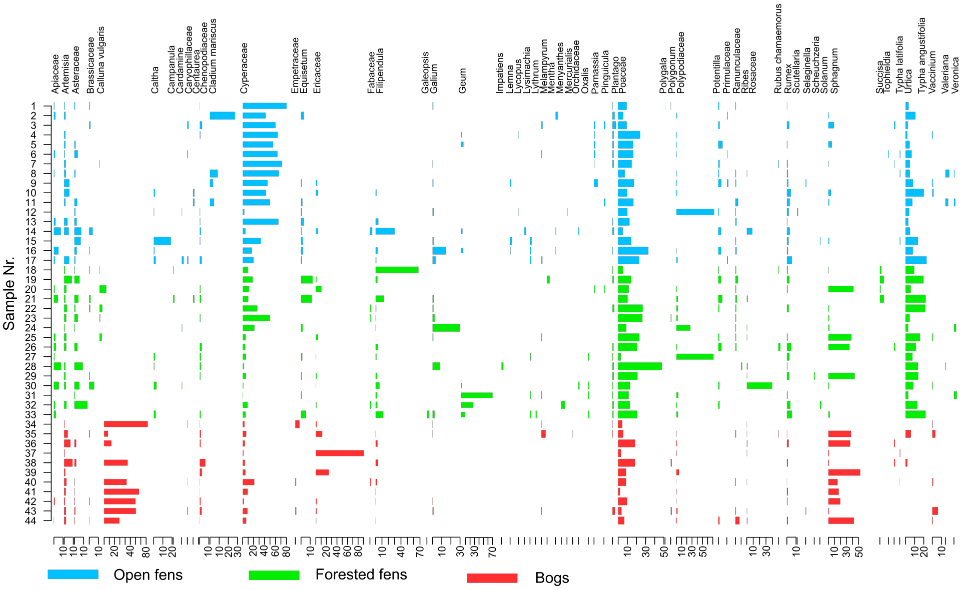

Figure 3. Pollen/spore assemblages with selected herbaceous taxa from modern surface samples – open fens (blue), forested fens (green) and bogs (red), expressed as percentages.

Based on pollen/spore percentages, bog and fen samples were rather clearly distinguishable with taxa such as *Calluna vulgaris*, Cyperaceae, Ericaceae, *Sphagnum*, separating between bog and fen. The difference between open and forested fens was less visible, except for Cyperaceae dominance in herbaceous pollen (60–80%) and the presence of *Cladium mariscus* in open fens. According to the IVM Cyperaceae was a statistically significant indicator of open fens ($p=0.002$) despite its presence in other habitats as well. Primulaceae and *Parnassia* were other statistically significant indicators of open fens. Pollen taxa such as *Geum* and *Filipendula*, along with Polypodiaceae spores, appeared more in forested fens than in open fens but were not recognised by the IVM. Instead, *Oxalis*, *Succisa*, *Frangula*, *Prunu*s and *Sorbus* were significantly associated with forested fen habitats according to the IVM. Pollen assemblages from the bogs were clearly dominated by *Calluna vulgaris* (up to 80% of herbaceous pollen). In addition, other Ericaceae and *Sphagnum* spores prevailed in bogs and with *Vaccinium* and Empetraceae were significant indicators of bogs according to the IVM.

The results of both PCA and random forest classification showed that based solely on woody taxa it is not possible to separate between bogs, forested and open fens.

According to the RF based on herbaceous taxa, bogs had the smallest classification error (17%), suggesting a clearer distinction in taxa associated with the bogs compared to open and forested fens.

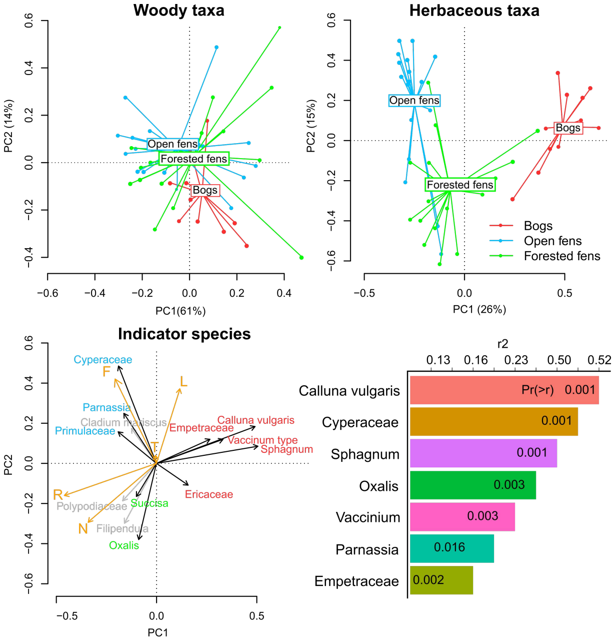

Figure 4. *Separating modern open and forested fens and bogs with the help of modern pollen data. Upper panel: PCA based on modern surface samples for woody (on the left) and herbaceous taxa (on the right). On the lower left: IVM-based indicator species and environmental gradients (pollen-based EIV estimates) fitted on herbaceous PCA where taxa are coloured according to associated habitat – open fens (blue) forested fens (green), bogs (red). Species that showed association with habitats in PCA but were not recognised by the IVM are coloured in grey. On the lower right: indicator taxa ordered by the strength of their relation to herbaceous PCA with squared correlation coefficients (only significant correlations are shown).*

3.1.2 Richness and composition relationships

Modern pollen–plant richness and composition relationships from spring fens (Paper II) are summarised in Fig. 5. The results of richness relationships showed that significant positive correlations (r=0.42–0.47) exist for herbaceous taxa in the plant survey radii up to 6 m, whereas for woody taxa, there were no significant richness correlations at any scale of the vegetation estimate.

Procrustes' analysis showed that for herbaceous taxa, positive composition relationships exist at all estimated vegetation scales (r=0.50–0.62), but for woody taxa they were significant at the scales from 6 to 100 m (r=0.50–0.67). According to linear regression models, plant richness and region were significant pollen richness determinants of herbaceous taxa at the 6 m scale, t=4.26, $p < 0.001$ and t=-5.02, $p < 0.001$, respectively, with a determination coefficient of R2=0.5.

The pollen–plant relationships from lake surface samples and surrounding regional vegetation (Paper V) were studied among wind pollinated and insect pollinated (not wind pollinated) taxa, as well as between the subset groups of woody and herbaceous taxa. Results showed that pollen and plant richness of wind pollinated taxa and woody taxa are well correlated (r=0.75 and r=0.83, respectively). Total pollen–plant richness correlations were comparatively lower (r=0.53) and were clearly influenced by insect-pollinated taxa, which showed the lack of the correlation (r=−0.05).

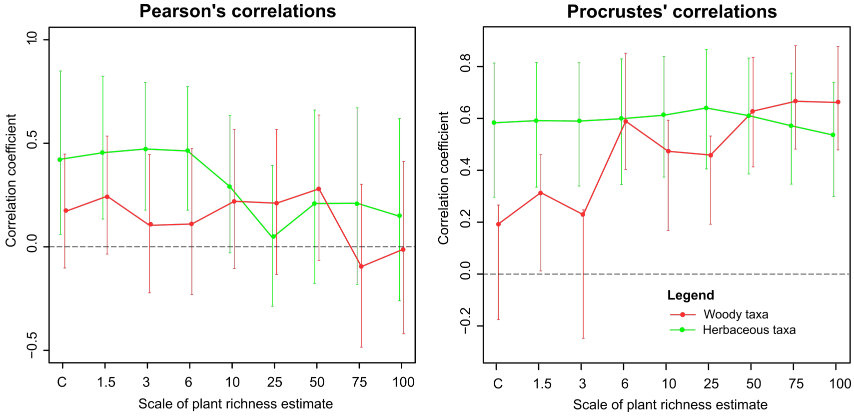

Figure 5. *Modern pollen–plant richness (Pearson's correlations) and composition (Procrustes' correlations) relationships of woody (red) and herbaceous (green) taxa in different scales (radii) of plant estimates. Bootstrapped 95% confidence intervals for the correlations (vertical lines) are given.*

3.1.3 Functional diversity relationships

Significantly positive pollen–plant CWM trait correlations were shown for SLA, seed number, AM, LDMC, clonality and plant height, when tested among the woody taxa in plant survey radius of 100 m (Paper II). Linear models (LM) where the significance of plant-based CWM of corresponding trait and region (Western vs Southern Estonia) were tested for explaining pollen-based CWM values showed that for woody taxa, both plant-based CWMs and region were significant, but not their interaction. For SLA, the interaction term of region and plant SLA was significant, indicating that the relationship between plant and pollen-based CWM SLA differed between the regions.

For herbaceous taxa, significant positive pollen–plant CWM trait correlations were shown for ERM, SLA, LDMC and seed number in a plant survey radius of 6 m. Plant-based CWM was the only significant predictor of pollen-based LDMC and seed number in LM. CWM relationships of SLA differed significantly between the regions for herbaceous taxa.

Seed number, SLA, clonality and AM showed significant and positive pollen–plant-based FDa relationships for woody taxa in vegetation survey radius of 100 m. FDa LMs of woody taxa showed that plant-based FDa was significant predictor of pollen-based FDa of SLA and clonality. Region was a significant predictor of pollen-based FDa of SLA and clonality. ERM, clonality and SLA showed positive significant correlations for herbaceous taxa in a vegetation survey radius of 6 m. According to the LMs among the herbaceous taxa, vegetation based FDa was significant predictor of pollen-based FDa for ERM and clonality. Pollen-plant FDa relationships for SLA differed significantly among the regions. For detailed results of the analyses, see Paper II.

3.1.4 Phylogenetic diversity relationships

From the studied fens, a positive significant pollen–plant phylogenetic diversity (PD) correlation was shown only for herbaceous taxa (r=0.63, p=0.003). However, the significance disappeared when pterophytes (ferns and clubmosses) were excluded from the analysis (r=0.20, p=0.349). Among the woody taxa, a positive but not significant pollen–plant PD relationship existed when all taxa were considered (r=0.23 p=0.089). When only angiosperms were considered, there was no relationship. LM showed that pollen–plant relationships of herbaceous taxa differed significantly between the regions (Paper II).

3.1.5 Environmental gradient relationships

Results showed that pollen–plant-based EIVs of woody taxa had positive significant relationships for the indicators of light (L) (r=0.72, p<0.000), temperature (T) (r=0.59, p=0.001), soil reaction (R) (r=0.50, p=0.007) and moisture (F) (r=0.41 p=0.002). LM for woody taxa showed that pollen-based indicators of temperature, light and moisture were significantly associated with corresponding plant-based indicators. Both light and moisture were also significantly associated with the region, whilst for R, region was the only significant predictor.

For herbaceous taxa, L (r=0.66, p<0.000), T (r=0.34, p=0.010), and N (r=0.39, p=0.003) had positive significant pollen–plant correlations. For all three pollen-based indicators, corresponding plant-based indicators were a significant predictor according to LM models. For indicators of L and T, region was also a significant predictor (Paper II).

3.2 Sediment pollen-based reconstructions

3.2.1 Chronology

To assign pollen assemblages and other analysed proxies to a certain time period, AMS 14C dating and age-depth models were reconstructed for the Kanna, Viidumäe 1 and 2, and Svetlenkoye sediment profiles. Calibrated 14C ages for the sediment profiles are shown in Table 1. For the details of age-depth models, see Papers I, III and IV. The age-depth models revealed that sediment accumulation began ca 9200 cal yr BP in Kanna spring fen, ca 3390 cal yr BP in Viidumäe 1, ca 2990 cal yr BP in Viidumäe 2, and ca 11,400 cal yr BP in Lake Svetlenkoye. Three dates were recognised as outliers in case of the Kanna fen sediment profile and one in Lake Svetlenkoye and were excluded from the age-depth model. According to the models and lithology, continuous peat/lake sediment accumulation was recorded in all profiles and no hiatuses were observed. In the Kanna fen and Lake Svetlenkoye profiles, SFAP-derived ages allowed the intensification of industrialisation to be determined, which in the Kanna fen was captured in ca 1960 AD, and in Lake Svetlenkoye in ca 1978 AD.

***Table 1**. Results of radiocarbon dating and SFAP-derived ages. Poz: laboratory code of the Poznań Radiocarbon Laboratory (Poland). Dates marked with asterisks were not used for Oxcal modelling. 95.4% probability range and weighted average for modelled ages are given as cal yr BP, where 0=AD 1950.*

Sample depth (cm)	Laboratory Code, SFAP/14C	SFAP age (yr AD) 14C age (yr BP)	Calibrated/modelled ages at 95.4% probability cal yr BP	Dated material
		Kanna spring fen (Paper I)		
4.5	SFAP 1980	1980±5 AD	-32±5	
11.5	SFAP 1950	1950±5 AD	1±5	
17	SFAP 1910	1910±10 AD	40±10	
10	Poz-99538*	110.68±0.33 pMC	-42±13	Bulk peat

***Table 1** continued*

25	Poz-99572*	1355±30 BP	1280±25	Carex seed scales
40	Poz-89179*	5030±35 BP	5790±70	Wood twigs
40	Poz-99569	1245±30 BP	1210±45	Bulk peat
51	Poz-99363	2100±30 BP	2040±40	Wood pieces
80	Poz-89178	2820±30 BP	2930±40	Charcoal and twigs
115	Poz-99364	3785±35 BP	4180±60	Moss stems
140	Poz-99571	4510±35 BP	5210±70	Bulk peat
160	Poz-89177	5600±40 BP	6380±40	Charcoal and twigs
191	Poz-99366	7715±50 BP	8450±40	Wood and bark pieces
224	Poz-89172	8190±50 BP	9270±100	Charcoal
Lake Svetlenkoye (Paper IV)				
50	Poz-66540	1845±30 BP	1780±41	Gyttja
100	Poz-66541	3840±30 BP	4239±64	Gyttja
150	Poz-66542	5590±35 BP	6359±35	Gyttja
190	Poz-62573*	5970±40 BP	6718±85	Wood twigs
190	Poz-66543	6160±40 BP	7089±54	Gyttja
250	Poz-66544	7040±40 BP	7875±45	Gyttja
306	Poz-62572	9250±50 BP	10415±81	Wood twigs
Viidumäe 1 (Paper III)				
100	Poz-123515	3160±30 BP	3390±40	Charcoal
Viidumäe 2 (Paper III)				
80	Poz-124455	2865±30 BP	2990±50	Wood twigs

3.2.2 Lake Svetlenkoye

Svetlenkoye pollen assemblages were grouped into five significant zones (Fig. 6) according to Hierarchical clustering and broken stick results – LSP1 (ca 11,400–10,900 cal yr BP), LSP2 (ca 10,900–8000 cal yr BP), LSP3 (ca 8000–6800 cal yr BP), LSP4 (ca 6800–4400 cal yr BP) and LSP5 (4400 cal yr BP to ~ AD 2003). At the initial stage of the site development, surroundings were covered with the vegetation dominated by *Pinus* forests and admixture of *Picea* and *Betula* in similar proportions. Cyperaceae and Poaceae had high proportions and no other terrestrial herbs were encountered. *Sphagnum* and *Thelypteris palustris* type spores along with green algae were found. In LSP2 from 10,900 to 8000 cal yr BP, an abrupt increase of *Betula* pollen, appearance of *Salix*, *Ulmus*, *Juniperus* and a significant decrease in conifers characterised the adjacent landscape. Different terrestrial herbs became present in the pollen record during this phase. A significant abundance of aquatic plants such as *Nymphaea, Nuphar, Myriophyllum spicatum, Ceratophyllum, Typha/Sparganium* indicative to lakes, ponds or slow-moving rivers makes this phase distinctive among the others. The LSP2 phase exhibits the highest palynological richness in comparison to other phases. The period from ca 8000 to 6800 cal yr BP (LSP3) is differentiated by the maximum values of *Picea* and the drop of *Betula* pollen. Many terrestrial herbs became absent or had a definitive decline.

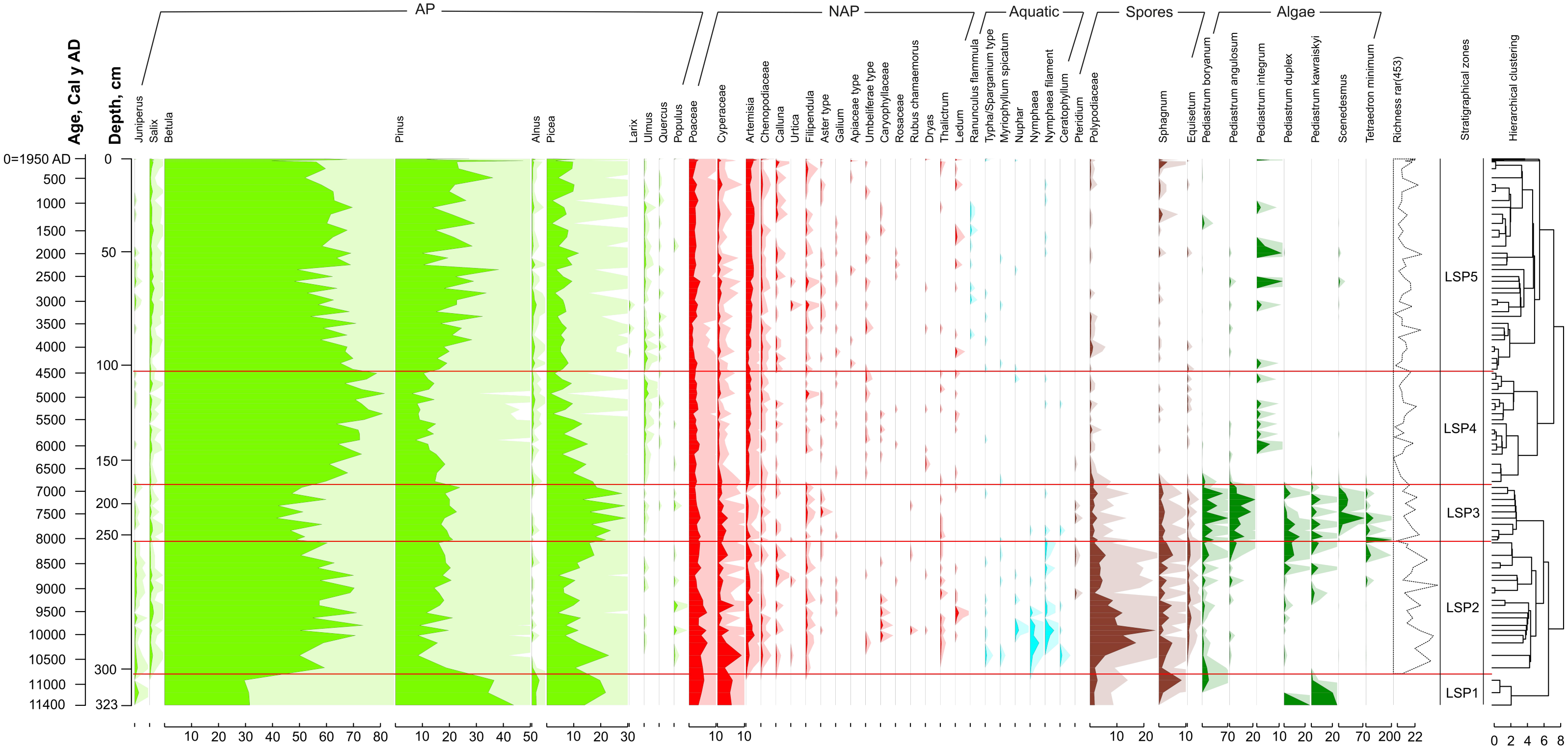

Figure 6. *Pollen diagram of selected taxa from the Lake Svetlenkoye sediment profile. To see the full diagram with all taxa and pollen accumulation rates see the supplementary material in Paper IV.* AP – arboreal pollen taxa (trees and shrubs); NAP – nonarboreal pollen taxa (herbs and grasses).

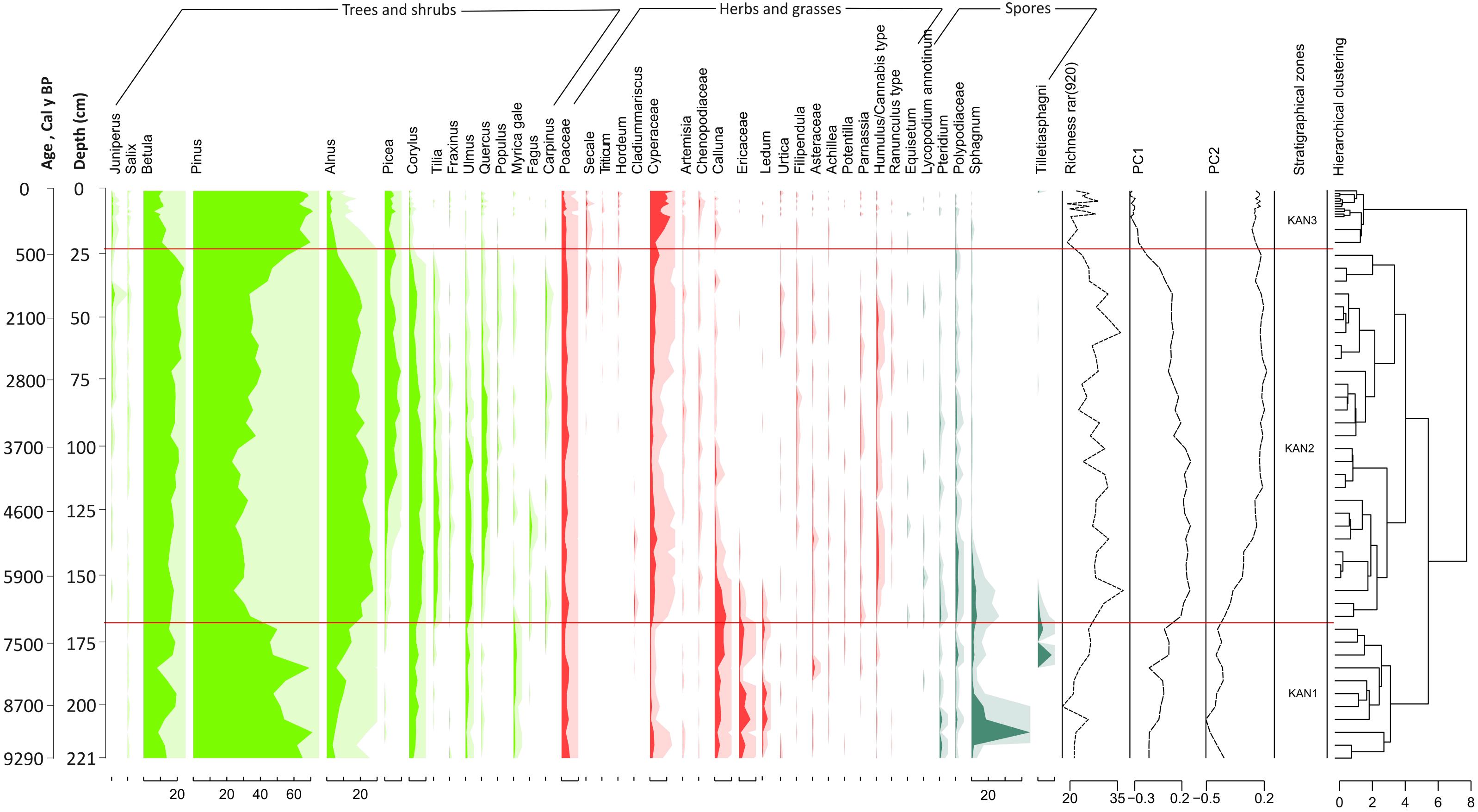

Figure 7. *Pollen diagram of selected taxa from Kanna spring fen sediment profile. For the full diagram with all taxa, see supplementary material in Paper I. Herbs and grasses include perennial shrubs of Ericales. PC1 and PC2 are first two axes of Principal component analysis in Paper I.*

In LSP3 sporophytes have also declined, whereas green algae have increased considerably. In comparison to other phases, this period coincides with the highest pollen AR (see Paper IV).

Comparatively low palynological richness and relatively uniform herbaceous pollen abundance and composition is shown in further stages 6800 cal yr BP to present (LSP4–LSP5). Sporophytes and green algae are nearly absent. In the surrounding landscape forest composition, varying proportions of *Betula* and *Pinus* are present. Stratigraphic zones based on pollen and spore assemblages rather precisely correspond to changes in other proxies such as macrofossils, diatoms and AR (Paper IV).

3.2.3 Kanna spring fen

Hierarchical clustering and the broken stick model revealed three significant pollen zones in Kanna sediment pollen data (Fig. 7). The first zone KAN1 covers the period from 9200 to 7200 cal yr BP, when *Pinus* was most likely the dominant tree in the surrounding landscape (50–70% of pollen). Low-growing perennial shrubs of Ericaceae, *Calluna vulgaris* and *Ledum*, along with *Myrica gale* had the highest proportions compared to other periods. The highest amount of *Sphagnum* spores and the presence of *Tilletia sphagni* fungal spores were recorded at the initial development stage, which overall had the lowest palynological richness.

The second zone KAN2 from 7200 to 400 cal yr BP indicates important restructuring of surrounding forest cover with a two-fold decrease in *Pinus* and an increase in deciduous taxa such as *Alnus*, *Corylus, Ulmus* and *Quercus*. The diminishing of *Sphagnum* and Ericales was followed by an increase in Cyperacea, among which *Cladium mariscus* was encountered. An increase in the abundance in other forbs (e.g. Potentilla, *Parnassia*, Ranunculaceae) coincides with the highest palynological richness up to 2000 cal yr BP. The shortest zone KAN3 from 400 cal yr BP to the present shows restructuring in forest cover again, which in fact seems to have started ca 1500 cal yr BP. A decrease in deciduous trees and a significant increase in *Pinus* – with a sharp increase in Cyperaceae – is shown in the last phase. The three distinguished phases correspond well to the results of peat physical properties, macrofossil analysis and NPPs (Paper I).

3.2.4 Mire origin and succession on Saaremaa Island

Information on pollen signal from different modern mire states (Paper III) was applied on sediment pollen assemblages from six mires in western Saaremaa Island for studying their development, succession and related biodiversity changes. The results of habitat indicators reconstructed from pollen assemblages throughout site development accompanied with significant clusters from the constrained hierarchical clustering are shown in Fig. 8.

According to the results of different studied sites, sedimentation started first in Surusoo and Pitkasoo at 10,800 cal yr BP and 10,500 cal yr BP, respectively. Jõhvika originated at 9800 cal yr BP and was further followed by the origin of Kanna at 9270 cal yr BP, Vedruka at 8300 cal yr BP, Viidumäe 3 at 7500 cal yr BP, Viidumäe 1 at 3390 cal yr BP and Viidumäe 2 at 2900 cal yr BP. Note that because of poor pollen data quality the Viidumäe sites are not included in Fig. 8 and are further discussed only in the context of site origin. The proportions of indicator taxa at the initial stage of the sites suggest that the majority of them have developed as fens, except for Kanna, which shows pollen composition dominated by bog indicator species. For most of the cases, the results of the cluster analysis coincide with successional shifts indicated by the proportions of indicator taxa, except for Pitkasoo, where clusters seem to be independent of composition changes of indicator taxa. Overall, cluster analysis and turnovers in indicator taxa composition suggest that shifts from one mire type to another have taken place at different times in different sites.

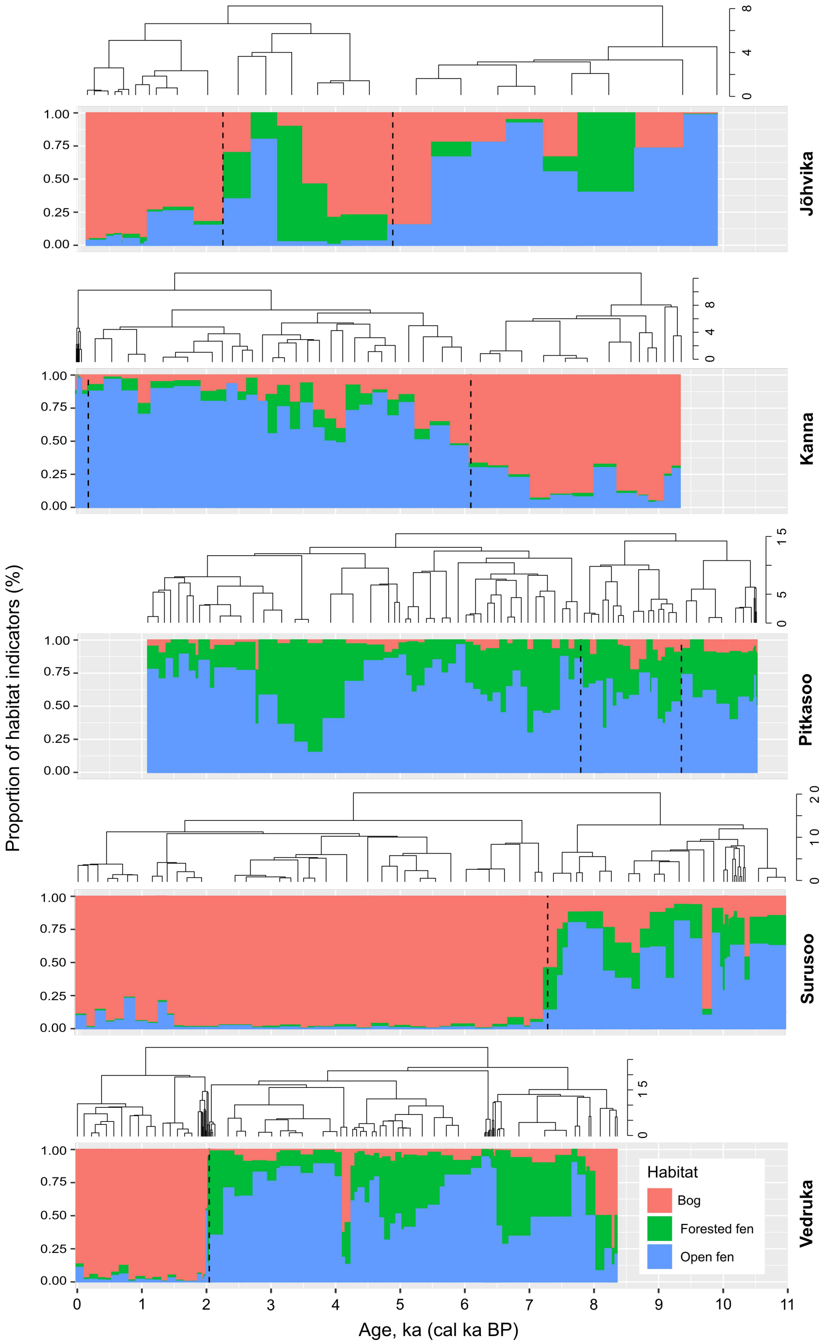

Figure 8. The proportion of indicator taxa assessed with the IVM and PCA grouped into corresponding habitats throughout the last 11,000 years. Figures are accompanied by constrained hierarchical clustering and the borders of significant clusters based on herbaceous taxa are shown as dashed lines.

3.2.5 Biodiversity and environmental gradients in time

Diversity reconstructions showed that relatively high total (woody + herbaceous taxa) palynological richness was recorded during the early Holocene from Lake Svetlenkoye (Paper IV), but it decreased during the early to mid-Holocene transition and remained relatively low and stable until the present day (Fig. 6). The low palynological richness of all taxa was shown in Kanna spring fen during the early to mid-Holocene transition followed by a rapid increase and high values in the mid-Holocene, but richness decreased close to the present day (Paper I, Fig. 7).

In Papers II and III, palynological richness and other diversity measures were reconstructed for the subset groups of herbaceous and woody taxa. Various trends were shown for the palynological richness of herbaceous taxa among the investigated sites. The PD of all herbaceous taxa had relatively similar trends among the studied sites with the highest PD at the early stage of site development (Fig. 9). The PD of herbaceous angiosperms exhibited a random community phylogenetic structure. The environmental gradients of L, T and F reconstructed on herbaceous taxa showed relatively small changes in time except for N and R, which were considerably higher at early site development stages and reflected the fen–bog gradient.

Diversity trends and environmental gradients based on woody taxa were relatively similar among the studied sites (Papers II and III, Fig. 11). In general, the early Holocene was the poorest in woody taxon palynological richness in all sites, the mid-Holocene showed the highest richness and the late Holocene showed a distinct decrease in diversity. The PD of all woody taxa was the highest in the early and late Holocene with the lowest values in the mid-Holocene, but the PD of woody angiosperms had opposite trends. The environmental gradients of R and N had patterns similar to the palynological richness and PD of angiosperms, but L and F followed the same trends as the PD of all taxa.

The FD of herbaceous taxa (CWM and FDa) reconstructed in Paper II reflected the different site development stages well (Fig. 10). When the CWM of woody taxa had three distinct phases related to the early, mid and late Holocene, FDa showed no consistent patterns (Fig. 10).

Explanatory parameters, such as water content, OM, MM, calcium carbonate, humification, charcoal, proportion of cultivated plants, sedimentation rate and modelled summer and winter temperatures were tested for their effects on influencing pollen richness in Kanna spring fen (Paper I). Among these parameters, the results of LM showed that modelled winter and summer temperatures, and charcoal alike had a statistically significant effect on total pollen richness (Table 2).

***Table 2**. Linear regression results showing statistically significant ($p<0.05$) predictors of pollen richness in Kanna spring fen. Backwards selection was used to assess the effect of explanatory variables on Andersen transformed pollen richness from 53 rarefied samples.*

Variable	**Estimate**	**t-value**	***p*-value**	**Model summary**
Winter temperature	1.89±0.42	4.49	<0.001	Residual SE 2.96 F-statistic: 13.2 R^2=0.41
Summer temperature	1.81±0.42	4.27	<0.001	
Charcoal (0–100 µm)	1.21±0.42	2.90	0.006	

In Paper III, the correlations of taxonomic richness and PD with different environmental gradients and habitat age were tested (Table 3). The results showed that herbaceous pollen richness had a significantly negative association with habitat age, but was positively correlated with T and R. The PD of all herbaceous taxa showed a positive correlation with habitat age, T, and R, but was negatively associated with L. The PD of herbaceous angiosperms was positively associated with T and N. Among the woody taxa, pollen richness had positive associations with R and N, but was negatively associated with habitat age, L and F. The PD of all woody taxa showed positive associations with L and F, but the PD of woody angiosperms was positively correlated with T, R and N.

Table 3. *Correlation matrix of herbaceous and woody taxa diversity measures and EIVs from five mires. Partial Pearson's correlation coefficients (with site accounted for) and Benjamini-Hochberg (Benjamini and Hochenberg, 1993) adjusted p-values. Statistically significant correlations (p<0.05) are in bold. PD—comprises phylogenetic diversity among all taxa, whereas PD ang. stands for phylogenetic diversity among angiosperms. The abbreviations of EIVs are the following F – moisture; L – light; N – productivity; R – soil reaction, T – temperature.*

	Age		**L**		**T**		**R**		**N**		**F**	
	r	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p-value*
Herbaceous taxa												
Richness	0.01	0.8435	**-0.16**	0.0082	0.08	0.2156	**0.14**	0.0200	**0.19**	0.0016	0.02	0.8238
PD	**0.39**	0.0000	**-0.77**	0.0000	**-0.62**	0.0000	**0.36**	0.0000	**0.49**	0.0000	-0.01	0.8435
PD ang.	0.01	0.8435	-0.07	0.2467	**0.19**	0.0020	0.11	0.0829	**0.17**	0.0048	-0.02	0.8423
Woody taxa												
Richness	**-0.32**	0.0000	**-0.57**	0.0000	-0.02	0.8238	**0.53**	0.0000	**0.45**	0.0000	**-0.50**	0.0000
PD	0.05	0.5262	**0.55**	0.0000	**-0.30**	0.0000	**-0.42**	0.0000	**-0.50**	0.0000	**0.55**	0.0000
PD ang.	-0.10	0.1145	**-0.69**	0.0000	**0.44**	0.0000	**0.65**	0.0000	**0.72**	0.0000	**-0.77**	0.0000

4 Discussion

Palaeoecology is believed to provide the most objective and comprehensive information on past environmental conditions, vegetation, and biodiversity. Pollen analysis has a long tradition and wide application in palaeoecology, yet there is no clear consensus on different aspects of methodology and it possesses unexplored avenues that might deepen the understanding of long-term changes in biodiversity and community assemblages in relation to the environment (Reitalu et al., 2015; Felde and Birks, 2019; Birks et al., 2020). Therefore, studying modern pollen–plant relationships and applying ecological traits and attributes, and investigating the phylogenetic context both in modern and sediment pollen in combination with other proxies helps to understand the scales and the processes pollen data reflect and to clarify how plant communities behave under changing climatic, environmental and anthropogenic pressure.

4.1 Modern pollen–plant relationships

4.1.1 Pollen signal from different types of mires

Mires have become increasingly valued at the global level (Erwin, 2008; Landry and Rochefort, 2012); however, the current projections on mire progression in Northern Europe and other parts of the world are unsatisfactory. To predict future scenarios of mire development, such as fen–bog transition, site-overgrowing levels that could show how these habitats react to changing climates and could indicate possible future trajectories of related biodiversity, careful interpretation of sediment records is needed. Our understanding of sediment pollen signal can be improved with the help of modern pollen studies (Gaillard et al., 1992; Hicks and Birks, 1996; Räsänen, et al., 2004). In the current thesis, modern moss polster pollen signal from bogs, open and forested fens is studied to clarify how accurately they can be distinguished based on sedimentary pollen data and what the taxa indicative to these habitats are. Several studies have pointed out that differences in the pollen deposition period might cause a difference in pollen composition between the moss samples (Räsänen et al., 2004; Lisitsyna and Hicks, 2014). The results of the current thesis indicate that the uniform sampling effort in terms of the moss polster size and sampled part of it provides overall relatively uniform pollen assemblages among the similar habitat types. Modern pollen rain is often studied in the context of major vegetation zones (Schüler et al., 2014; Felde et al., 2014; Julier et al., 2018) where the woody taxa have been shown to be an important component for vegetation differentiation. In the current study, the random forest classification and PCA ordination showed that based on woody taxa, the differentiation between bogs, and open and forested fen habitats was impossible. However, the IVM method recognised *Frangula, Prunus,* and *Sorbus* as indicators of forested fens. Indeed, all these taxa have been present and associated with wet meadows and wooded vegetation in various studies in Europe (Dietre et al., 2012; Shumilovskikh et al., 2015; Waller et al., 2017; Filbrandt-Czaja, 2017) and could be kept in mind for recognising forested fen phases in sedimentary data. The generally vague association between woody taxa and investigated habitats could be due to relatively uniform forest cover in the region or can be attributed to the general characteristics of these habitats dominated by herbaceous taxa that particularly favour open conditions. With the help of the IVM, modern pollen assemblages allowed herbaceous taxa associated with bogs, open and forested fens to be determined. *Sphagnum* and *Calluna vulgaris* had highly significant indicator values for bog habitats and additionally, Ericaceae, *Vaccinium,* and Empetraceae contributed to this classification. A high Cyperaceae abundance with *Parnassia* and Primulaceae were shown to be indicative to open fens, but *Oxalis* and *Succisa* with the abovementioned woody taxa were significant indicators of forested fens. Our results corroborate several previous studies concerning mire habitats and their related vegetation from different parts in the northern hemisphere (e.g. Chambers et al., 2011; Blaauw and Mauquoy, 2012; O'Reilly et al., 2014, Waller et al., 2017). It has to be kept in mind that neither of these taxa is exclusive for mire habitats and their application as indicators must be critically considered; however, a combination of multiple taxa indicative to the same habitat, and their dominance in the samples can increase confidence.

4.1.2 Taxonomic richness

Pollen richness or palynological richness is a common measure in palaeoecological studies that have been used as an important indicator to reflect regional biodiversity and vegetation changes, climate, landscape openness and human impact (Poska and Saarse, 2002; Stivrins et al., 2015; Birks et al., 2016; Giesecke et al., 2019). In the current thesis, modern pollen–plant richness associations were investigated in local and regional spatial scales, in pollen samples from spring fens and lakes, respectively (Papers II and V). Spring fens as very specific types of mires are among the most endangered habitat types in Europe and are particularly sensitive to climate changes and anthropogenic pressure because of their strict dependence on groundwater discharge (Bragg and Lindsay, 2003). So far, these unique habitats have not been studied in terms of modern-pollen plant relationships and are, therefore, in the centre of attention within the framework of this thesis (Papers II and III). Additionally, modern-pollen plant diversity relationships of different subset groups were investigated from the lake surface pollen samples and surrounding vegetation in Paper V. This could potentially improve the interpretation of sediment pollen-based reconstructions for the studies that consider regional scales such as Paper IV. Results in both local and regional scales showed that there are statistically significant correlations between pollen and plant richness, and thus these results add to the studies that have demonstrated positive pollen–plant associations (Odgaard, 2008; Meltsov et al., 2011; Matthias et al., 2015; Birks et al., 2016). Analysis indicated that pollen–plant relationships clearly differed between different subset groups and spatial scales (Papers II and V) and that needs to be considered for more meaningful palaeoecological richness reconstructions. For instance, on the local scale reflected by the spring fen pollen, the pollen–plant richness relationship based on woody taxa was missing, whereas in the regional scale investigation, the pollen richness of woody taxa had the strongest correlation. In a study of small lakes in southern Estonia, Meltsov et al. (2011) showed a similar lack of pollen–plant association in the wind-pollinated and woody taxa within 250 meters, suggesting that the relevant source area of pollen (RSAP) for these pollen types is generally much larger. Larger RSAP for woody taxa has been already shown by several studies (Sugita, 1994; Broström et al., 2005; Mazier et al., 2008; Poska and Pidek, 2010). Conversely, insect-pollinated (mostly herbaceous) taxa lacked the pollen–plant richness relationships on the regional scale (Paper V), but herbaceous taxa had a significant richness correlation within a 6 m radius in spring fen environments (Paper II). This resonates well with the studies that have investigated the RSAP from moss polsters and have shown that the pollen–plant correlation of non-arboreal taxa does not improve beyond 10 m (Bunting, 2003; Bunting and Hjelle, 2010).

Differences in pollen production and dispersal are well-known factors that affect pollen–plant relationships (Odgaard, 2001; van der Knaap, 2009). With this in mind, Andersen correction factors (Andersen, 1970) were applied for the major taxa. Andersen transformed pollen sums improved pollen–plant richness correlations in both studies that considered pollen–plant relationships (Papers II, V). This is in agreement with other theoretical and empirical studies showing that pollen richness per sample is potentially influenced by the abundance in dominant pollen taxa (Andersen, 1970; Odgaard, 1999) and that Andersen's or other similar correction factors help to reduce this bias (Felde et al., 2016).

4.1.3 Functional diversity

Functional diversity (FD) has become an increasingly popular approach in modern ecology and palaeoecology, adding another dimension to the understanding of plant communities and their response to environmental constraints (e.g. Mason et al., 2005; Lacourse, 2009; Reitalu et al., 2015; Miller et al., 2019; van der Sande et al., 2019; Birks, 2020). In the current thesis, plant traits with a wide range of functional significance were used to test modern pollen–plant relationships for community weighted mean traits (CWM) and functional alpha diversity (FDa) reflecting community functional structure and functional dispersion, respectively (Paper II). The most relevant vegetation scales assessed by pollen–plant diversity relationships for woody and herbaceous taxa were applied to test FD associations. The FD relationships expressed as CWM between modern pollen and vegetation have been tested in one earlier study (Carvalho et al., 2019), surprisingly also in the fen environment. Despite the lack of taxonomic richness relationships within a 100 m radius, woody taxa, in general, showed better pollen–plant CWM and FDa associations compared to herbaceous taxa. Similarly, Carvalho et al. (2019) showed better pollen–plant fits for woody taxa CWMs, emphasising the influence of trait averaging where low taxonomic resolution in certain herbaceous taxa influences the pollen-based CWM estimates. The taxonomic resolution has a strong influence both in the studies that have used sediment pollen for assigning functional traits without testing modern relationships (Brussel et al., 2018; van der Sande et al., 2019) and in pollen analysis in general. However, woody taxa-based traits with positive pollen–plant correlations, such as SLA, seed number, AM, LDMC, clonality, height have a potential for being applied on sediment pollen assemblages to study the general long-term community responses to climatic changes and human disturbances over larger spatial scales (Reitalu et al., 2015; Brundrett and Tedersoo, 2018). Traits with positive present-day pollen–plant correlations among the herbaceous taxa in fen environments, such as ERM, SLA, LDMC, and seed number can be used to study, for example, nutrient stress, competition, changes in soil reaction and other disturbances (Jabłońska et al., 2019). Their application to other habitat systems would require replication of modern pollen–plant studies from different environments. The results of Paper II indicate that mycorrhizal-type AM and EM, plant height and seed weight might not be good traits to assign for the pollen data from fen systems, likely because of large trait variation within certain pollen taxa such as Cyperaceae or Poaceae. Therefore, other proxies such as macrofossils or sedaDNA could be used to study long-term patterns in these traits (Birks and Birks, 2000; Parducci et al., 2014; Felde and Birks, 2019; Jabłońska et al., 2019). To conclude, functional traits can provide important additional information on community dynamics where diverse communities are associated with greater stability, and a functional diversity decline could lead to instability (Connor et al., 2017).

Traits that showed positive pollen–plant FD relationships both for woody and herbaceous taxa were applied on Kanna spring fen sedimentary data and their response to vegetation community changes. Possible autogenic and allogenic factors are discussed in paragraph 5.2.

4.1.4 Phylogenetic diversity

By providing the information on species genetic relatedness within the community, phylogenetic diversity (PD), similarly to FD, has gained great attention in community ecology, particularly in the context of biodiversity (Graham and Fine, 2008; Flynn et al., 2011; Anacker and Harrison, 2012; Brocchieri, 2016). Nevertheless, the studies on PD in palaeoecology are limited (but see Reitalu et al., 2015), and modern pollen–plant studies have not investigated PD relationships. Likewise, to other diversity metrics, PD showed differences in pollen–plant relationships between the subset groups of woody and herbaceous taxa. Significant positive correlations were shown only for herbaceous taxa; however, the significance was lost when only angiosperms were considered. Similarly, for woody taxa, correlation reduced when gymnosperms were excluded. Exclusion of these taxa was done following the theoretical and empirical studies that suggest that distant phylogenetic groups like pteridophytes and gymnosperms have a strong impact on phylogenetic structure (Reitalu et al., 2015; Massante et al., 2019; Bowe et al., 2000). Despite only a few pteridophytes and gymnosperms in our data, their significant impact on pollen–plant PD correlations suggests the strong pollen–plant associations of these taxa. It is likely that PD relationships in case of woody taxa would show stronger associations with the larger scale of vegetation estimates or over a wider range of woody communities, similarly to other diversity metrics. The current thesis presents the first attempt to test pollen–plant-based PD relationships; therefore, the interpretation of these results is limited and further studies from different systems and spatial scales and ranges are needed for better understanding of pollen–plant PD reflections.

4.1.5 Ellenberg indicators

The concept of Ellenberg indicator values (EIVs) has great potential for studying palaeoenvironments (Kuneš et al., 2011; Reitalu et al., 2015; Enevold et al., 2018; Felde and Birks, 2019). However, their application on pollen assemblages might possess certain challenges (Birks et al., 2020). Studying EIVs in modern pollen–plant data would clarify which EIV gradients are adequately reflected by pollen data and could be used for studying long-term changes in environmental conditions. In the study from spring fens (Paper II), woody taxa showed significant positive pollen–plant EIV correlations for L, T, F and R; for herbaceous taxa, significant positive correlations were shown for L, T, and N. Since most of the fens are waterlogged and have a relatively high pH, our results failed to show significant herbaceous pollen–plant associations for F and R indicators, likely due to uniform study sites having short environmental gradients (cf. Diekmann, 2003). Water availability and pH have been recognised as the main drivers of species richness in fens (e.g. Hájková and Hájek, 2003; Sekulová et al., 2013), and the results of Paper II do not necessarily mean that pollen data does not reflect changes in these EIVs in other circumstances or habitats. In fact, Williams et al. (2011) showed that Ellenberg R can be weekly associated with pH in wetlands and might better reflect calcium content than pH (Schaffers and Sýkora, 2000). Modern ecology studies have widely used EIVs from wetlands and mire systems (e.g. Hettenbergerová and Hájek, 2011; Andersen et al., 2013; Koch and Jurasinski, 2014; Klimkowska et al., 2019) and the positive pollen–plant EIV relationships in Paper II indicate that pollen data allow for studying a wide range of EIV-related hypotheses from a historical perspective. Significantly positive pollen–plant correlations for L and N might have potential in palaeoecology, particularly from fens since both indicators have been shown to reflect major gradients in species composition in these environments (Kotowski and van Diggelen, 2004; Andersen et al., 2013).

4.2 Pollen-based vegetation, diversity and environmental gradient reconstructions in time

Based on the results of modern pollen–plant relationships of woody and herbaceous taxa where these subset groups reflected different spatial scales, diversity indices, and environmental gradients are discussed separately for these subset-groups.

4.2.1 Herbaceous taxa

It was clear from the sediment reconstructions (Papers I, III) that our investigated systems did not reflect palynological richness uniformly and that richness did not strictly follow changes in climatic or environmental conditions. In general, large diversity variations within and between the sites suggest that the herbaceous diversity signal can be attributed to site-specific conditions and autogenic succession, which in some site development stages has been influenced by a regional or landscape pollen signal.

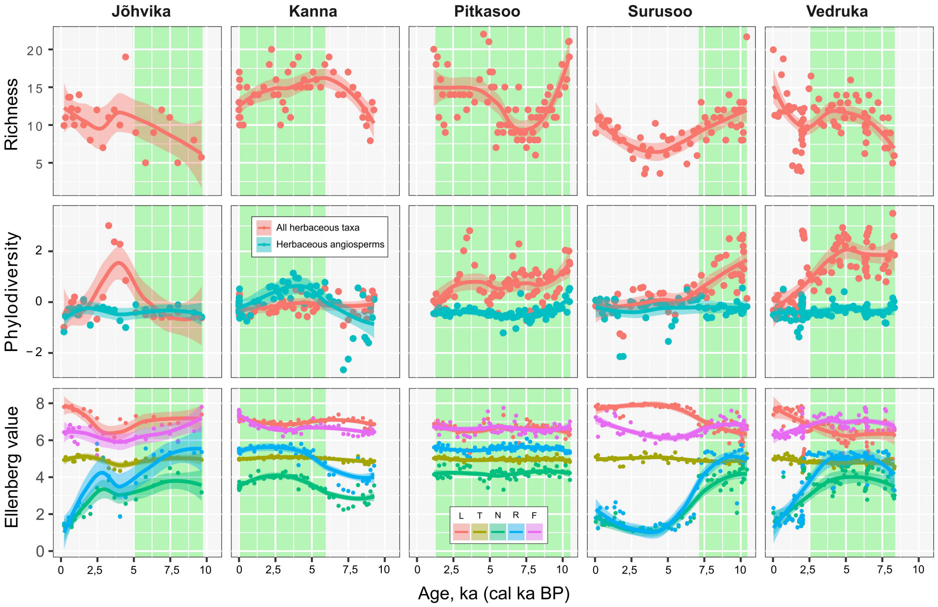

Figure 9. *Biodiversity and ecological attribute reconstructions over the last 10,000 years based on herbaceous taxa in five mires on Saaremaa Island. A green background indicates the fen habitat and grey background bog habitat according to the IVM and cluster analysis. GAM with 95% confidence intervals (shaded fill) is used to reflect the dynamics of indicators in time. The abbreviations of EIVs are the following: F – moisture; L – light; N – productivity; R – soil reaction; T – temperature.*

Nevertheless, several other factors might complicate comparisons between the sites such as differences in timing of site origin and succession, basin size, openness, and other geographical and topographical characteristics.

According to the statistical analyses (LME), fen phases were characterised by higher values of soil reaction (R), productivity (N), moisture (F), higher pollen richness, and PD in comparison to bogs (Paper III). R, N, and F indicators showed the highest variation within and between the sites in the reconstructions from pollen assemblages. Several studies have shown that pH (or calcium content), nutrient availability and moisture are the major determinants of species richness and composition in fen environments (Hájková and Hájek, 2003; Navrátilová et al., 2006; Wolf and Cooper, 2015; Palpurina et al., 2016) and that R provides a natural bipartition between the bogs and fens (Tahvanainen, 2004). Light (L) and temperature (T) had significantly higher values in bogs compared to fen phases. A gradual increase in trends of light gradient coincides with the development of the bogs. Light is also an important environmental filter in spring fens (Kotowski and van Diggelen, 2004); however, bogs, especially large raised bogs as in present-day Vedruka and Surusoo, are to a large extent dominated by shade and drought-sensitive species (Lachance et al., 2005). The higher temperature values in bogs could be related to the fact that fens are fed by cold groundwater that buffers surface temperatures (Fernández-Pascual et al., 2015) and fens often provide microrefugia for cold-water specialists (Horsáková et al., 2018).

The regional pattern of palynological diversity throughout the Holocene suggests that the early Holocene had relatively high diversity. Transition to the mid-Holocene had low pollen richness values and further on richness substantially increased towards the present-day (Reitalu et al., 2015; Birks et al., 2016). The high palynological richness in the early Holocene is associated with landscape openness, and this is relevant to our studied sites in Surusoo and Pitkasoo, which originated around 10,800 and 10,500 cal yr BP, respectively, and also showed high pollen richness at the beginning of the site development (Fig. 9). Open sites are likely to record a higher number of herbaceous taxa, due to lower overall pollen productivity or because of higher wind speeds and convection, thus herbaceous pollen might be better represented (Broström et al., 2008; Meltsov et al., 2011). However, richness signal at this time might not precisely reflect the local situation, because high landscape openness following deglaciation (or land emergence from the sea in case of Saaremaa Island) has allowed high extra-regional scale pollen input (Giesecke et al., 2012; Paper V). In addition to high pollen richness, Surusoo and Pitkasoo show a high PD signal of all herbaceous taxa at the beginning of the site development. Usually, young habitats are associated with low PD (Lososová et al., (2015) and high PD in the early stages of Surusoo and Pitkasoo might be related to the regional pollen input in the sites. On the other hand, Reitalu et al. (2015) have shown high PD in early Holocene and hypothesised that it is linked to harsh conditions and environmental stress after deglaciation. According to González-Caro et al. (2014), environmental stress causes the filtering of phylogenetic lineages adapted to environmental conditions and would mean that species adapted to these conditions originate from distant plant lineages (Reitalu et al., 2015).

The transition period between the early to mid-Holocene is associated with cold boreal forests in the region (Poska and Saarse, 2002; Papers I–II) that likely led to generally low vegetation evenness and diversity and is reflected in relatively low richness at the initial stages of the Kanna, Vedruka and Jõhvika sites (Fig. 9, Paper III). Surrounded by well-established forests at this phase the sites are likely to reflect mostly local pollen signals, although large basins could still reflect some regional signal. For the same three sites, herbaceous palynological richness increased up to the mid-Holocene where it attained maximum values and thereafter followed different pathways for each site. On the Kanna site, the highest palynological richness coincides with the transition from bog to fen. Laine et al. (2018) have recorded a similar pattern in mire studies from Finland and interpret the transition stage as the most diverse, rich in hammocks and pools with a habitat specialist from both mire types. In theory, site openness is positively correlated to pollen richness (cf. Meltsov et al., 2011); however, this was not the case of the Jõhvika site around 4000 years ago, when habitat indicators show overgrowing but palynological richness was the highest throughout the site’s history. On the other hand, Jõhvika was already a bog at that time and bogs are characterised by overall low species richness (Moore, 2002), and overgrowing might have been caused by terrestrialisation that in turn induced richness increase, which has been shown in other studies from peatlands (e.g. Locky and Baily, 2005; Lachance et al., 2005). The high richness period in Jõhvika coincides with divergence in PD among all herbaceous taxa, but no response of PD among angiosperms, reflecting the occurrence of pteridophytes, which likely occurred during terrestrialisation. Moreover, responses in environmental gradients of R, N, and L in Jõhvika around 4000 years ago suggest an increase in shade-tolerant species or canopy closure that resulted in organic matter and soil reaction increase (Fig. 9). Low species richness and poor conditions with the lowest R and N of bogs (Lachance et al., 2005) are well exhibited on the Surusoo site around 4000 to 5000 years ago when the lowest richness was recorded, in contrast to sites that had fen characteristics during the same period (Kanna, Vedruka, Pitkasoo) (Fig. 9).

A marked increase of palynological richness during the last 4000 to 2000 years has been shown by several studies (Giesecke et al., 2012; Reitalu et al., 2015; Birks et al., 2016), and has been associated with the introduction of agriculture and anthropogenic impact. This pattern is well reflected in Surusoo and Vedruka with a rapid increase in richness close to the present (Fig. 9); however, both sites are relatively large bogs that might have high proportions of regional pollen input. In contrast, Kanna, which is a much smaller site, shows a slight decrease in richness, and this pattern is likely determined by the increase in the proportion of Cyperaceae (Paper I). In the Saaremaa Island mires, PD has declined throughout the Holocene and the PD both of angiosperms and all herbaceous taxa had some of the lowest values on most of the sites (Fig. 9), despite the richness increase on certain sites. This on a regional scale has been explained by negative human impact on PD (Reitalu et al., 2015) by introducing phylogenetically related taxa, contrary to the ones that disappear and are usually phylogenetically more unique (Winter et al., 2009).

According to reconstructions from the investigated mires, PD did not necessarily covary with species richness contrary to some findings (Mooers et al., 2008; Kluge and Kessler, 2011) and in many cases, it was not associated with environmental gradients, especially when only angiosperms were considered (Table 3). To conclude, patterns in PD are complex and while adding an additional angle to the biodiversity change, PD will not always explain local scale historical community assemblages based on pollen data.

Functional diversity was investigated in Paper II and reconstructed only from Kanna sediment pollen assemblages. The fact that Kanna fen has a complete sediment record and long history of 9200 years and that it has experienced a shift from ombrotrophic to minerotrophic conditions makes it a great target site to study FD changes in time in respect to different factors. Functional trait reconstructions in Kanna corresponded rather precisely to different mire development stages. LDMC, ERM, and clonality are all traits positively associated to nutrient-scarce conditions (Read et al., 2004; Baastrup-spohr et al., 2015; Moor et al., 2017), and all had a high CWM during the ombrotrophic stage at the beginning of the site development (Fig. 10). Ericoid mycorrhiza (ERM) is particularly associated with poor and acidic conditions (Cairney and Meharg, 2003) and in addition to high CWM, it exhibited significant functional divergence, presumably reflecting high within-site functional heterogeneity (de Bello et al., 2013; Bergholz et al., 2017). All these traits experienced rapid turnovers during the ombrotrophic to minerotrophic transition and attained low CWM values during the fen phase when the CWM of SLA, AM, and the average height was high. This phase had a high abundance of fen specialists associated with increasing calcium content (Paper I). Likewise, Bartelheimer's and Poschlod's (2015) results in this thesis indicated the positive relationship of soil reaction with SLA and a negative relationship with LDMC in Paper II.

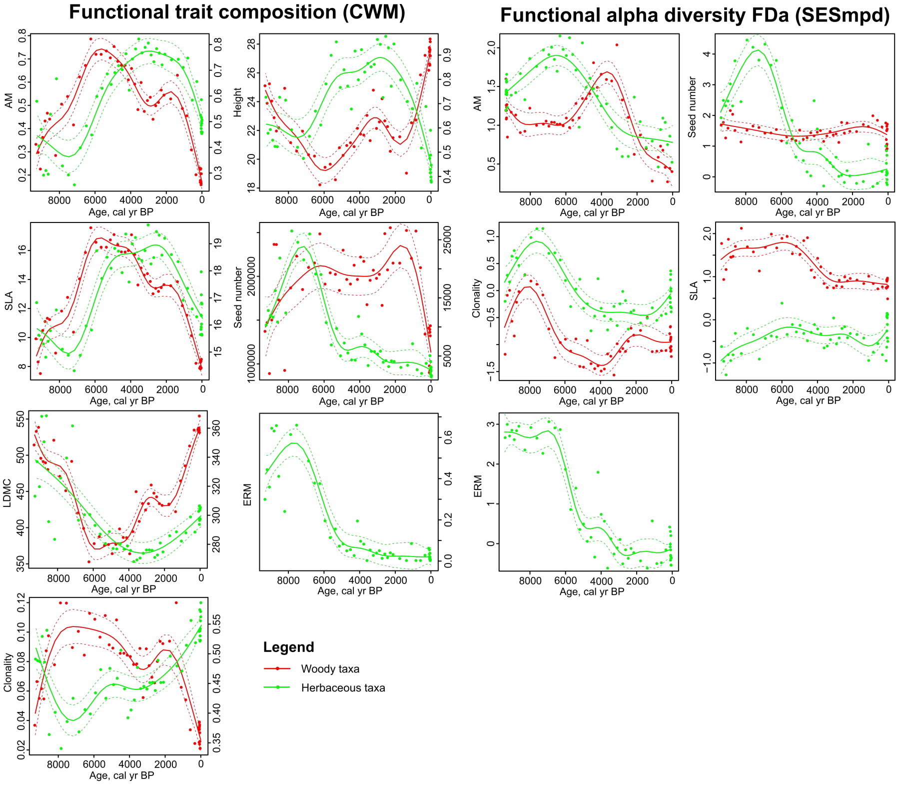

Figure 10. *Functional diversity expressed as CWM and FDa, reconstructed from traits with significant positive modern-pollen plant relationships based on Kanna sediment pollen assemblages for woody (red) and herbaceous (green) taxa. Note that the CWM for herbaceous taxa is plotted on the second Y-axes. GAM with 95% confidence intervals (dashed lines) is used to reflect the dynamics of indicators over time. AM – arbuscular mycorrhiza; ERM – ericoid mycorrhiza; LDMC – leaf dry matter content; SLA – specific leaf area.*

Increasing SLA within increasing nutrient availability is a well-known pattern (Díaz et al., 2004; Hedberg et al., 2013; Moor et al., 2015) and in the Kanna fen the increase in SLA coincided well with increases in environmental gradients of R and N (Figs. 9 and 10).

Another major change in trait composition coincides with richness decline from 2000 years ago to the present. The increasing CWM of LDMC, clonality, and decline in SLA and seed number are related to the increasing proportion of Cyperaceae in pollen assemblages. The Cyperaceae increase leading to higher LDMC and lower SLA in wetlands is indicative of dryer conditions (Baastrup-Spohr et al., 2015). Jabłónska et al. (2019) have shown that taxa with a short clonal spread (such as most of the fen Cyperaceae) tend to increase in abundance prior to fen termination (Jabłónska et al., 2019) and the change might thus indicate the initiation of ombrotrophication or terrestrialisation in the Kanna fen.

4.2.2 Woody taxa

Compared to the varying changes in herbaceous taxa, the trends in reconstructed woody diversity and environmental gradients were relatively similar among the studied sites (Fig. 11) indicating that woody taxa reflect similar large-scale vegetation and environmental conditions, despite the large variation in the basin size (5 to 112 ha).

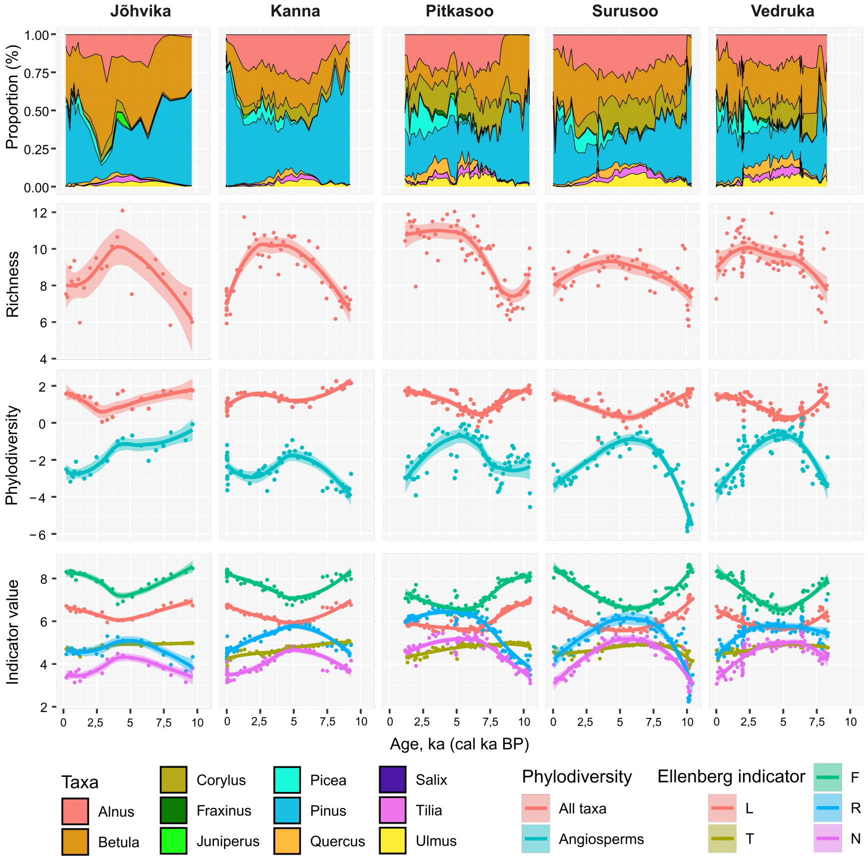

Figure 11. *The proportion of major woody taxa, richness, phylogenetic diversity and environmental gradients based on woody taxa over the last 10,000 years reconstructed from pollen assemblages from five mires on Saaremaa Island. GAM with 95% confidence intervals are used to reflect the dynamics of indicators in time. The abbreviations of EIVs are the following: F – moisture; L – light; N – productivity; R – soil reaction; T – temperature.*

Almost identical proportions and compositions of major tree taxa in different mires (Fig. 11) correspond to forest cover dynamics reported in other studies from the region (Poska and Saarse, 2002; Reitalu et al., 2013; Stivrins et al., 2015; Feurdean et al., 2017). Forest composition dominated by *Pinus*, *Betula,* and *Alnus* – commonly referred to as cold mixed forests (Davis et al., 2014) – characterises the early stages of sites' development. Low taxonomic richness, low PD of angiosperms, and relatively poor soils indicated by low R and N, but high PD of all woody taxa, high moisture, and light availability prevailed during this phase. Relatively homogeneous forest cover likely determined low taxonomic richness. The strong negative correlation of palynological richness and *Pinus* pollen influx has been shown from the study in Finland with similarly low palynological richness in the early Holocene (Seppä, 1998). Trends in PD among all taxa suggest that in the early Holocene when gymnosperms and angiosperms coexisted in more-or-less similar abundances were phylogenetically more diverse in terms of woody taxa, compared to the mid-Holocene when broad-leaved angiosperms prevailed. Adverse trends in the PD of all taxa and angiosperms could be explained by the fact that distantly related species respond differently to environmental changes (cf. Cadotte et al., 2012).

The community PD of angiosperms is particularly determined by the climate on a regional and global scale (Qian et al., 2017; Kubota et al., 2018), and some studies have shown that generally high PD can be explained by temperature and precipitation (Anacker and Harrisson et al., 2012; Li et al., 2019). Multiple studies on different proxies have recorded generally colder and wetter conditions over Northern Europe in the early Holocene (Birks et al., 2014; Luoto et al., 2014; Stansell et al., 2017), indicating that these are potential factors that have reduced the PD of angiosperms but favoured the PD of all taxa in the region. This is also supported by statistical analysis (Paper III), where woody angiosperm correlation with temperature (T) is positive ($r=0.44$, $p<0.0000$) but the correlation with moisture was significantly negative ($r=-0.77$, $p< 0.0000$).

The colonisation of deciduous forests in the region during the warmer and dryer climatic conditions in the mid-Holocene (Davis et al., 2003; Renssen et al., 2009; Birks and Seppä, 2010) coincides with increasing palynological richness, PD peaks of angiosperms, and PD decline among all the taxa. These patterns goes in hand with the environmental gradients of L, F, N, and R. Climatic changes during the mid-Holocene (Hammarlund et al., 2003; Stansell et al., 2017) have altered vegetation composition and evenness by the establishment of deciduous forests (Poska and Saarse, 2002; Papers I and II) that have suppressed the previously dominant taxa (Pinus) and increased the representation of other different taxa and thus palynological richness (cf. Giesecke et al., 2012). Richness and evenness relationships are complex, and several studies show that in pollen data they might be not independent (Odgaard, 2001; Peros and Gajewski, 2007).

Warmer climatic conditions and an increase in favourable soil properties have been linked to higher PD (Cavender-Bares et al., 2004; Spasojevic and Suding, 2012), which is presumably the result of reduced environmental filtering, allowing species from different lineages to coexist as indicated by the peak in the PD of angiosperms. Late Holocene trends can be analogously interpreted to those of the early Holocene; however, factors related to human impact could be of great importance here (Poska et al., 2004; Reitalu et al., 2013; Roberts et al., 2018). Overall cooler climatic conditions (Seppä and Poska, 2004; Renssen et al., 2004) have driven towards a decrease in deciduous forest abundance, and thus an increase in cool mixed forests again dominated by *Pinus* and portions of *Betula*, *Alnus* and of recently arrived *Picea* (Saarse et al., 1999). On the other hand, pollen-based synthesis in the work of Roberts et al. (2018) showed that forest loss in Central Europe accelerated around 4000 years ago, as a result of forest conversion for agriculture use, but in Northern Europe, the human-induced change occurred around 2000 years ago and with a much less superior alteration. An increase in human activities is usually associated with changes in forest cover and induced landscape openness, thus one could be expected to facilitate pollen richness during the late Holocene (Birks and Line, 1992; Seppä, 1998, Meltsov et al., 2013), but this is more applicable to herbaceous taxa as shown in the previous paragraph.

Disturbance by fire is another essential factor recognised to govern forest structure in time (Behling and Pillar, 2007; Whitlock et al., 2017), and has been well studied in the region (Kuosmanen et al., 2017; Feurdean et al., 2017). For instance, Feurdean et al. (2017)

suggest that the late Holocene's fire frequency could be attributed to the replacement of *Picea* and deciduous forest by *Pinus* since the latter one is more fire-tolerant. They also tested fire impact on floristic diversity but did not find a clear, evident link, however, few episodic diversity responses to fire frequency were observed. In Paper I, micro and macro charcoal were used as a proxy of fire to test the impact on palynological richness from the Kanna spring fen. The results of linear regression models suggested that in addition to both climatic parameters – modelled summer and winter temperatures – fire was a significant factor to explain total palynological richness. However, it might be intermixed with a general increase in human impact in the late Holocene, since the highest charcoal presence coincided with the onset of agriculture, likely indicating slash-and-burn practices in the landscape (Poska and Saarse, 2002).

Although FD was reconstructed only based on Kanna sediment pollen assemblages, rather uniform trends of other investigated diversity metrics and environmental gradients would suggest similar functional changes in the forest communities throughout the entire western part of Saaremaa Island. Reconstructions showed that the early Holocene was characterised by a low CWM of clonality, AM and SLA, but high CWM of LDMC and plant height (Fig. 10). SLA and LDMC are the traits that best explain the functional trade-off between the resource acquisition and conservation strategy known as "leaf economical spectrum" (Reich, 2014). Larger SLA is associated with resource acquisition related to fertile and favourable conditions, like in the mid-Holocene, which allows for rapid plant growth and photosynthesis, whereas LDMC is related to the resource conservation strategy to cope with the low resource environment (Polley et al., 2013; Qin and Shangguan, 2019), like in the early Holocene. Both traits have been shown to reflect the soil and climatic gradients well (Cornelissen et al., 2003; Laughlin et al., 2010) showing good correspondence to investigated environmental gradients in this thesis. Abiotic stress has been linked to increasing in clonality (Ye et al., 2014), high CWM of clonality at 8000 cal yr BP, and during the relatively favourable conditions in the mid-Holocene, it seems to contradict that and is rather a reflection of higher clonality among broadleaved trees and shrubs compared to gymnosperms. The correlation of AM fungal activity and increasing temperatures (Compant et al., 2010; Hempel et al., 2013) reflects the broad pattern of thermophilous taxa proportions in the region and corresponds to the immigration of taxa with AM associations, like *Ulmus glabra* and *Fraxinus excelsior* (Thomas et al., 2018; Seven and Polle, 2014). The decline in the CWM of SLA and AM but increase in height and LDMC in the late Holocene is also related to the above-discussed broad-leaved taxa decline and coniferous taxa expansion. Significant trait divergence or convergence was not observed in the reconstructions; however, niche differentiation, likely due to pivotal differences between gymnosperms and angiosperms (Brodribb et al., 2012), was shown during some episodes.

4.3 Role of pollen and palynological richness to reflect local and regional-scale vegetation and processes from mire and lake sediments

4.3.1 Kanna spring fen

Compared to Central Europe and Northern America, palaeoecological history and origin of spring fens in Northern Europe and particularly in Estonia have been relatively little studied, but see Hansson et al., 1996; Gałka et al., 2016; Väliranta et al., 2017. Therefore, the investigation of the Kanna spring fen provides one of the most detailed reconstructions of this habitat in the region. According to lithology, peat accumulation started right on the mineral soil at 9290 cal yr BP, and thus pollen and other proxies could be related to the initial stage of the site origin. The present-day topographical situation and the depth of the sediment basin suggest that the Kanna fen started to develop in the depression of the slope related to the regression of the Litorina Sea – historical stage of the Baltic Sea (Saarse, 2009). Three distinctive stages were recognised based on pollen analysis, which coincides well with macrofossils and NPPs, but were not so distinctly reflected among all indicators of peat physical properties. The unusual bog phase was recorded from ca 9200–7200 cal yr BP, dominated by various Ericaceae pollen, *Calluna vulgaris*, *Ledum,* and had a great abundance of *Sphagnum* spores. The presence of *Sphagnum* was supported by macrofossil analysis, which showed peat being composed of up to 80% Sphagnum. Additionally, NPPs and particularly testate amoebae like *Assulina muscorum*, *Arcella*-type, *Trigonopyxis*, which have been associated with ombrotrophic conditions, were encountered (Mazei and Bubnova, 2007). This finding does not follow the classical scenario, where bog succession is preceded by the fen phase and is usually referred to as a fen–bog transition (Hughes and Barber, 2003; Väliranta et al., 2017). Such an opposite development scenario is rare and has been reported only in a couple of other cases (Barber and Hughes, 1995; Hájková et al., 2012). Changes in the pollen composition in both herbaceous and woody taxa at ca 7000 cal yr BP indicate turnovers in vegetation composition that correspond to climatic changes from the early to mid-Holocene. The causal factors, global patterns, and temperature changes of this period are generally associated with a shift towards warmer and dryer climatic conditions in Northern Europe (Davis et al., 2003; Renssen et al., 2009; Birks and Seppä, 2010). These climatic changes might have initiated bog desiccation and thus the peat humification, which lead to the increasing role of mineral-rich groundwater and gradual transition to a fen. Bog taxa gradually disappeared and different fen-related taxa prevailed, e.g. Cyperaceae, *Potentilla,* and *Parnassi*a. In fact, *Cladium mariscus*, a species mostly limited in present-day base-rich fens (Theocharopoulos et al., 2006), was encountered both in pollen and plant macrofossils at the initial fen stage. Increasing different taxa on the site and diversification of surrounding landscape vegetation by different small-leaved deciduous trees at this point was clearly reflected by the highest values in palynological richness for the entire study period. This supports the general view of undamaged fens as important hosts of diversity emphasised by many ecological and palaeoecological studies (e.g. Lamers et al., 2002; Tahvanainen, 2004; Grootjans, 2005; Horsáková et al., 2018). The Kanna fen is still present today; however, noticeable changes in vegetation composition and an increasing abundance of Cyperaceae during the last ca 400 years suggest its transformation *in situ* and changes have also happened in the surrounded landscape revealed by rather homogeneous woody vegetation and a decrease in palynological richness.

Since the interpretation of the cause on palynological richness decline was complicated, due to lack of a clear association with any environmental factors, in Paper II the richness of the subset groups of herbaceous and woody taxa was investigated separately in order to understand the spatial scale of the changes. Consequently, the results showed a marked drop in woody richness and relatively stable herbaceous richness in the Kanna fen indicating changes in the surrounding landscape rather than in the fen itself. This contradicts the Northern European studies that have shown increasing palynological richness in the late Holocene because of human-induced landscape changes (Berglund et al., 2008; Reitalu et al., 2015; Birks et al., 2016). However, these studies provide general richness trends concerning larger spatial scales and in the current case, changes might well reflect the homogeneous landscape relatively far away from human settlements with the forest cover nowadays dominated by *Pinus*.

These different interpretations of pollen richness changes in Papers I and II provide a cautionary tale calling for critical usage and interpretation of total palynological richness.

4.3.2 Lake Svetlenkoye

The second detailed investigation comes from Lake Svetlenkoye in the West Siberian Plain, a region that spans thousands of square kilometres and is recognised as the largest wetland in the northern hemisphere (Kremenetski et al., 2003). Compared to Northern Europe, the knowledge of deglaciation and climatic changes in the region is much more ambiguous (Arkhipov et al., 1999); therefore, any palaeoecological investigations from the region might shed the light on different aspects of climate and environmental change and related vegetation development. According to the multi-proxy results, the origin of the lake and the sedimentation in the basin happened ca 11,400 cal yr BP, following the last deglaciation. Although based on pollen analysis, five significant periods in vegetation development were recognised, which likely reflect mostly regional changes, the combination with other proxies highlights three distinctive phases of the lake's environment. During the initial stage, no macrofossils were encountered from the sediment, and only pollen and spores could be used to interpret the environment. A negligible amount of pollen from herbaceous taxa (Poaceae and Cyperaceae) along with *Betula*, *Pinus,* and *Picea* likely reflect periglacial vegetation and arctic tundra, very similarly what was shown by Zolnikov et al. (1997). From 10,000 to 8000 cal yr BP, macrofossil analysis suggested the local presence of *Betula* and *Picea*, and their high proportions in pollen records with those of *Pinus* likely reflect the expansion of forest-tundra. Turnovers in most of the investigated proxies at this time indicate the changes both in the catchment and in its surroundings. The high number of telematic and aquatic plants recorded in pollen analysis and macrofossils indicates the flooding of the area and later paludification of the lake shore, which well corresponds to large-scale flooding in the same region and during the same period (Turunen et al., 2001). In addition, two different studies have reported elevated levels of precipitation and available humidity in the region for this period (Blyakharchuk, 2009; Groisman et al., 2013), likely due to the decay of marine ice in the North Atlantic and the western Arctic, which in turn caused the wet airmass transfer over the arctic belts of Eurasia. This period exhibits the highest palynological richness throughout the site's history, likely as the result of high habitat variety that contributed with taxa typical to bodies of water, wet meadows and bogs, surrounded by mixed forests. Another drastic change that occurred at ca 8000 cal yr BP was, in fact, more visible through the elevated AR of pollen and diatoms than in pollen or macrofossil composition. Evidence on increased AR, presence of green microscopic algae and diatom species composition characteristic to Siberian rivers convincingly shows a lake connection to or overflooding by the Ob river, which can be tied to warmer and wetter climatic conditions during the Atlantic period (Groisman et al., 2013). Pollen analysis shows a distinct decrease in *Betula* pollen, a similar amount of *Pinus* compared to the previous stage, and the highest values of *Picea*. During this time according to Zolnikov et al. (1997), forest vegetation expanded towards the north by approximately 300–400 km compared to the early Holocene, consisting mostly of *Pinus* and *Betula* and with noticeable amounts of broad-leaved trees. Although this study shows slightly different proportions in pollen composition, the extra material brought by the flooding might hinder the interpretation of the actual situation. From ca 6800 cal yr BP to the present, relatively uniform vegetation composition is revealed by pollen analysis both in woody and herbaceous taxa. Compared to the previous phase, pollen AR rapidly decreased and remained stable, and almost no macrofossils were encountered during this phase. The set of evidence from all the proxies indicates an isolated lake with a stable catchment basin, terrestrial soils, and vegetation – a situation that is likely attributed to dryer climatic conditions in the West Siberian forest zone (Blyakharchuk, 2009). Palynological richness is relatively low during this phase and no major signs in pollen spectra that would indicate changes in climatic conditions or significant human impact are shown.

This study is a great example of how different proxies complement each other and how some of them reflect the environmental changes that other proxies are not sensitive to, and thus this kind of multi-proxy view provides a more complete picture of site development.

4.4 Mire succession on Saaremaa Island

The outcome of modern pollen signals from different mire types confirmed that the Kanna fen has originated as a bog, contrary to other investigated sites on Saaremaa Island that began their development as fens (Paper III). Long mire histories are shown among the studied sites, where the oldest – Surusoo and Pitkasoo – originated as a lake ca 10,800 cal yr BP and a lagoon ca 10,500 cal yr BP, respectively, influenced by the historical stages of the Baltic Sea (Saarse, 2009). Changes in Baltic Sea water levels due to postglacial land uplift and eustatic sea-level changes have clearly determined the origin of the majority of mires, except for two sites – Viidumäe 1 and 2, which began to develop much later, ca 3300 and 2900 thousand years ago. At the initial stages, presumably high groundwater levels existed and the geological bedrock consisting of limestone provided calcium carbonate discharge, a significant factor that favours fen development (Almendinger et al., 1998; Grootjans et al., 2005). Early to mid-Holocene transition with its distinct climatic changes and the cooling in the late Holocene are both well documented in peat inception stages in the Northern Hemisphere (Walker et al., 2012; Väliranta et al., 2017; Dendievel et al., 2020). Although initiation of peat accumulation or fen–bog transitions from some Saaremaa Island mires could be linked to these climatic changes, different and presumably independent development pathways are also shown, thus supporting the theory that peatlands can become ombrotrophic under different water table conditions and under different climatic regimes (Hughes et al., 2003; Hájková et al., 2012). The long persistence of Pitkasoo as a fen for ca 9000 years and of Surusoo as an ombrotrophic bog for ca 7000 years, on the other hand, shows how resilient mires can be against the climatic changes and how stable ecosystems they are (Klinger et al., 1990; Hájková et al., 2013). Various degrees of forested and open fen indicators can be seen in most of the sites, but similarly to fen–bog transitions, forested fen periods occur at different times in different mires. Only the rather distinct overgrowing in the Jõhvika and Pitkasoo sites ca 4000 to 3000 cal yr BP occurring more-or-less at the same time could be initiated after the Holocene Thermal Maximum (HTM), when an overall warmer and dryer climate prevailed (Davis et al., 2003, Seppä et al., 2005). In contrast, Surusoo as an ombrotrophic bog during HTM shows no response to climatic conditions, suggesting that without additional human disturbances these sites might withstand different future climatic scenarios. The fact that our investigated sites have maintained their ecological functioning after species turnovers related to overgrowing resonates well with recent findings of Lamentowicz et al. (2019), who showed that this is possible because *Sphagnum* community functional diversity has remarkable stability regardless of hydrological changes.

4.5 Future Perspectives

Surely, pollen-based diversity reconstructions will continue their role in understanding past vegetation, and modern pollen–plant relationships will elucidate reflecting scales and processes. Moreover, relatively unexplored metrics and indicators will comprehend important angles on community characteristics and processes, which will help to anticipate future community changes related to different factors. However, their application, whether on pollen assemblages or other proxies, will strongly depend on advances in pollen taxonomic resolution, the research aim and required resolution.

In terms of mire future biodiversity trajectories in the region, the effect of postglacial land uplift must be stressed, which is an ongoing process, and its vertical velocity according to the Estonian land uplift model reaches 2 mm per year in northwestern Estonia (Kall et al., 2013). Land uplift leads to decreased groundwater levels and, for example, in Finland land uplift has been estimated to account for an up to 11 cm decrease in water level in certain parts of the country (Gong et al., 2012). The main study area on Saaremaa Island is experiencing the same scenario but likely to a smaller extent. Additionally to land uplift, factors such as increasing air temperature and decreasing precipitation have caused oscillations of 3–22 cm in groundwater levels of local bogs (Lode et al., 2017). Changes in climatic factors to a larger extent along with growth in peat thickness are believed to account for fen–bog transitions and current trends of bog terrestrialisation (Väliranta et al., 2017), causing a loss of biodiversity (Jensen and Schrautzer, 1999; Swindles et al., 2019). Species of northern biogeographic affinity, like those in fens and bogs, are particularly important for regional species pools, which in turn determine the high phylogenetic diversity of local communities (Anacker and Harrison, 2012). Even if increasing temperatures might increase plant productivity and local species richness due to terrestrialisation, it will likely result in loss of habitat specialists because of increasing competition (Harrison et al., 2010; Li et al., 2019). In a long-term perspective, this will lead to these habitats vanishing, and a loss of species and phylogenetic diversity across the region or continent (Thuiller et al., 2011) – a process that so far has been buffered by physical and biotic heterogeneity (Li et al., 2019).

Several avenues have been proposed to reduce the threats related to the above-discussed changes – emphasising special monitoring programs focused on habitat specialist conservation, counteracting successions and terrestrialisation, and increasing mire connectivity (Myers et al., 2000; Grootjans et al., 2005; Flinn et al., 2008; Jiménez-Alfaro et al., 2012). For the landscape scale, prioritising ecosystem services, replanting tree species and allowing habitat natural regeneration, reduction of landscape fragmentation, and conservation of native habitats have been proposed as a possible tool to fight biodiversity loss (Duan et al., 2016; Barnosky et al., 2017; Whitlock et al., 2017).

5 Conclusions

The current thesis focused on multifaceted modern pollen–plant diversity relationships, among which ecological attributes and plant functional traits provide new aspects in palaeoecology. The inference on relationships guided the reconstructions and allowed us to better study how plant communities have changed in terms of their composition, richness, and functional and phylogenetic diversity along environmental gradients. However, the complexity of pollen analysis and the interrelated nature of different climatic and environmental processes often complicate modern pollen–plant relationships, and the interpretation of the reconstructions might be challenging. Pollen assemblages complemented by other proxies and investigations from multiple sites for different plant subset-groups provide a better understanding of community responses in different spatial scales. The main conclusions from this work are summarised below.

1. Modern pollen–plant studies allow for a better understanding of spatial scales reflected by pollen data for different plant subset groups. Pollen diversity reconstructions should separate herbaceous and woody taxa; the first allows local community changes in small mires to be studied, whereas the second reflects regional-scale community changes.
2. In large spatial scales and over the wide spatial range (the whole of Europe), both pollen and vegetation richness are significantly associated with climate parameters, whereas landscape openness facilitates pollen richness, but not vegetation richness.
3. Pollen data can be used to infer long-term changes in the functional diversity of certain traits (SLA, LDMC, clonality, height, and seed number). Their reconstructions on both regional and local scales well reflects plant adaptation strategies to climate and environmental gradients related to resource acquisition, conservation, and interspecific competition.
4. Pollen–plant-based phylogenetic diversity relationships are strongly influenced by gymnosperms and pteridophytes. Distantly related taxa (gymnosperms vs angiosperms) shows different responses to climate and environmental gradients. Despite the increase in palynological richness, PD suggests a diversity decline both on the local and regional scales, presumably due to the human impact.
5. Pollen data can be used to reconstruct different environmental gradients with the help of Ellenberg indicator values or a similar ecological indicator concept. In the studied system, the Ellenberg indicator values of light, temperature, moisture, and soil reaction are significantly reflected by pollen data for woody taxa, and light, temperature, and productivity for herbaceous taxa.
6. Different types of mires have distinct pollen signals and indicative taxa that can be used to infer mire succession and other long-term processes. In general, fen phases exhibit higher species richness and PD, compared to bog phases of the same mires, and fen community diversity is positively associated with R and N, while bog phases with T and L.
7. Mire origins on Saaremaa Island, which began ca 10,000 years ago, are closely linked to major changes in historical Baltic Sea water levels, which had a decisive role on groundwater table fluctuations, but the fen–bog transitions and forested periods occurred at different times, suggesting that site-specific changes play an important role in mire changes additionally to climate.

8. The multi-proxy study from the Kanna spring fen played a significant role in interpreting exceptional bog-fen succession and revealing naturally rich fen phases with different important habitat specialists. The study from the West Siberian Plain comprehended the palaeohistory of the vegetation development in the region and revealed flooding, likely caused by large-scale changes in the hydrological regime.
9. This research stresses the importance of testing modern systems and different diversity indicators on multiple spatial scales prior to pollen-based reconstructions. The trends of different diversity indices often do not covary, especially for herbaceous taxa, emphasising the uniqueness of each metric.

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Abstract

From modern pollen–plant relationships to Holocene vegetation diversity reconstructions

Evidence inferred from a diverse array of palaeoecological methods has revealed important information to understand past climatic and environmental conditions and processes that have shaped the Earth's current ecosystems. This information has become an important baseline in modern ecosystem management and conservation biology. Because of their unique set of attributes, plant pollen and spores are preserved in the waterlogged sediments and can be identified to the species or family level, thus, allowing surrounding vegetation to be reconstructed through several millennia back in time. However, various factors complicate the vegetation representation in pollen data and despite the significant progress that has been made to study and improve the understanding of the sedimentary pollen signal, certain ambiguities remain.

This thesis studies modern pollen–plant relationships on local and regional scales, from spring fens in Estonia and from lakes in Northern Europe, to investigate how the pollen–plant relationship differs for different spatial scales and different plant subset-groups. Surface moss polsters, lake surface samples, and detailed information on surrounding vegetation assessed in field surveys and gathered from vegetation atlases were used. The current thesis tested modern pollen–plant relationships in terms of taxonomic richness, functional diversity (FD) calculated from plant functional traits, phylogenetic diversity (PD) reflecting community evolutionary relatedness, environmental gradients expressed as Ellenberg indicator values. All investigated diversity metrics and indicators were applied on sedimentary pollen data from mires on Saaremaa Island to study biodiversity and vegetation community structure changes over the last 10,000 years. Additionally, the indicator value method, cluster analysis, and random forest classification were used to study modern pollen signals and indicator taxa from different mire types to better interpret historical mire succession. Mires were in the focus of attention throughout the present study because of their high value for nature conservation and are regarded to be especially endangered by climate and land-use changes. Multi-proxy analysis – pollen, macrofossils, geochemical analysis, diatoms, and other non-pollen palynomorphs – were used to study two sites in detail: Kanna calcareous spring fen on Saaremaa Island, Estonia and Lake Svetlenkoye in the West Siberian Plain.

Statistical analysis revealed positive pollen–plant relationships on local and regional spatial scales; however, while woody pollen taxa were reflecting landscape or regional scale vegetation diversity, pollen of herbaceous taxa from mires was associated with local within-mire environmental changes. Temperature and landscape openness were shown to be the strongest predictors of pollen richness on a regional scale. Phylogenetic diversity, Ellenberg indicator values, and functional diversity based on multiple plant functional traits such as specific leaf area, leaf dry matter content, height, clonality, had positive pollen–plant correlations and thus have good potential for long-term reconstructions based on pollen data. The investigated herbaceous pollen signals differed between the mire types with specific indicator taxa for each type (bog, open fen, forested fen), allowing mire succession to be reconstructed from pollen data.

Woody pollen richness, phylogenetic and functional diversity, and Ellenberg indicator values showed uniform patterns among the studied mires throughout the time reflecting general regional-scale changes in vegetation communities likely mostly determined by

Holocene climate changes. The local scale reconstructions based on herbaceous taxa were more complex, exhibiting high variability among the studied sites as a reflection of site-specific conditions. Environmental gradients reflected fen and bog phases well. Diversity reconstructions from mires showed that fen phases had higher richness, phylogenetic diversity, soil reaction and nutrient content but lower light availability and temperature than the bog phases of the same mires. Detailed investigations from the Kanna spring fen and Lake Svetlenkoye suggested that pollen analysis in combination with other proxies can reflect local processes, where herbaceous, aquatic taxa and spores are of particularly great indicative importance.

To conclude, the results of the current thesis emphasise the importance of testing different palaeoecological indicators in modern systems prior to using them in reconstructions. Using functional and phylogenetic diversity and pollen-based environmental gradients in addition to conventional pollen analysis provides unique perspectives to study past long-term changes in community structure and mechanisms that underlie changes in biodiversity patterns. This information might be a crucial supplement for projections on future biodiversity trajectories and ecosystem services.

Lühikokkuvõte

Õietolmu ja taimestiku seostest tänapäeva maastikes taimede mitmekesisuse rekonstruktsioonideni läbi Holotseeni

Tänapäevased ökosüsteemid on mineviku kliima, keskkonna ja bioloogiliste protsesside tulem. Teadmised neist mineviku protsessidest on tulnud tänu mitmekesistele paleoökoloogilistele meetoditele ja annavad arusaama algtingimustest, millest tänapäeval lähtuvad ökosüsteemide majandamise ja kaitsmise otsused. Mineviku taimestiku kohta annavad informatsiooni soo ja järvesetetes säilinud taimede õietolmuterad ja eosed. Kuna õietolmu hulk ja levimine on liigiti erinev, on õietolmu põhjal mineviku taimede mitmekesisuse kohta järelduste tegemiseks vaja uuringuid tänapäeva õietolmu signaali ja taimestiku seostest.

Käesolev doktoritöö uurib õietolmu ja ümbritseva taimestiku vahelisi seoseid eri skaalades ja erinevates taimerühmades: kohalikus skaalas Eesti allikasoodes ja regionaalses skaalas Põhja-Euroopa järvedes. Õietolmu analüüsiti soode samblaproovidest ja järvede pinnasetetest ning võrreldi õietolmu andmeid detailse ümbritsevat taimestikku iseloomustava andmestikuga, mida koguti välitöödel (soodes) ja taimede levikuatlastest (järvede ümbruses). Õietolmu ja taimestiku vaheliste seoste testimiseks kasutati mitmeid indekseid: liigirikkus; funktsionaalne mitmekesisus, mida arvutati taimede erinevate tunnuste põhjal; fülogeneetiline mitmekesisus, mis peegeldab koosluste sisest evolutsioonilist sugulust; Ellenbergi indikaatorväärtused, mis on seotud keskkonnatingimustega. Lisaks selgitati välja eri soo arengufaaside indikaatorõietolmu tüübid, mis võimaldavad paremini välja selgitada soode suksessiooni läbi nende arenguajaloo. Kõiki tänapäeva andmetega testitud mõõdikuid kasutati Saaremaa soode 10000-aastase ajaloo uurimiseks vana õietolmu põhjal. Sood on käesolevas doktoritöös tähelepanu keskmes kuna on looduskaitseliselt olulised ja kliima ning maakasutuse muutuste poolt ohustatud. Käesolev doktoritöö sisaldab ka kahte põhjalikku setete uuringut Kanna allikasoost Saaremaal ja Svetlenkoye järvest Lääne-Siberis, kus lisaks õietolmule analüüsiti ka taimede makrojäänuseid, setete geokeemilisi omadusi, ränivetikate ja teiste setetes leiduvate organismide jäänuseid.

Doktoritöö tulemused näitavad, et õietolmu ja taimestiku andmeid on statistiliselt oluliselt seotud nii kohalikus kui regionaalses skaalas. Kui puude õietolm peegeldab pigem regionaalset taimestikku, siis rohttaimede õietolm on seotud muutustega kohalikus sookoosluses. Regionaalses skaalas (Põhja-Euroopa) on õietolmu mitmekesisus seotud eelkõige temperatuuriga ja maastiku avatusega. Ellenbergi indikaatorväärtused, fülogeneetiline mitmekesisus ja funktsionaalne mitmekesisus (arvutatud erinevate taimetunnuste põhjal nagu lehe eripindala, lehe kuivainesisaldus, taime kõrgus, klonaalsus) näitasid statistiliselt olulisi seoseid taimestiku ja õietolmu põhjal arvutatud indeksite vahel. Rohttaimede õietolmu signaal oli rabades, metsastunud ja avatud madalsoodes erinev. Tulemused näitavad, et õietolm võimaldab rekonstrueerida mineviku taimestiku mitmekesisuse eri aspekte ja soode arengu eri etappe.

Puittaimede liigirikkuse, fülogeneetilise ja funktsionaalse mitmekesisuse muutused läbi 10000 aasta olid erinevates Lääne-Saaremaa soodes sarnased ja olid põhiliselt mõjutatud Holotseeni kliimamuutustest. Rohttaimede põhised mitmekesisuse indeksite rekonstruktsioonid olid Saaremaa soodes erinevad, peegeldades kohalike asukohapõhiste faktorite olulisust sootaimestiku mitmekesisuse arengule. Rekonstrueeritud keskkonnatingimused (Ellenbergi indikaatorväärtused) ja mitmekesisuse indeksid olid selgelt erinevad soode madalsoo ja raba arenguetappides: madalsoo faasides oli kõrgem liigirikkus, fülogeneetiline mitmekesisus, happelisus, toitainerohkus, aga madalam valguse tase ja temperatuur kui samade soode raba faasides. Kanna soo ja Svetlenkoye järve detailsed uuringud näitasid, et rohttaimede õietolmu analüüs kombineeritult teiste näitajatega peegeldab kohalikke muutusi, eriti kõrge indikaatorväärtusega oli info sammalde ja sõnajalgtaimede ning veetaimede esinemise kohta.

Kokkuvõtvalt võib järeldada, et erinevate paleoökoloogiliste indikaatorite testimine erinevates tänapäevastes maastikes ja eri skaalades peaks alati eelnema nende indikaatorite kasutamisele rekonstruktsioonides. Õietolmu põhised funktsionaalse ja fülogeneetilise mitmekesisuse rekonstruktsioonid ning indikaatorväärtustel põhinevad keskkonnagradiendid täiendavad traditsioonilist õietolmuanalüüsi ja võimaldavad lähemalt uurida pikaajaliste mitmekesisuse muutuste põhjuseid. Teadmised mineviku taimestiku mitmekesisusest ja seda mõjutavatest faktoritest on väärtuslikuks sisendiks tuleviku mitmekesisuse ja ökosüsteemi teenuste muutuste ennustamisel.

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Appendix

Publication I

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ORIGINAL ARTICLE

From bog to fen: palaeoecological reconstruction of the development of a calcareous spring fen on Saaremaa, Estonia

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Abstract

This study of the Kanna calcareous spring fen on Saaremaa, the largest island of Estonia, elucidates its history of fen development and vegetation diversity over the last 9,200 years. Pollen, spores, non-pollen palynomorphs, macrofossils, loss-on-ignition and humification index analyses were carried out to reconstruct fen succession, vegetation development, environmental changes and human impact. Hierarchical clustering, ordination analysis and linear regression were applied to examine the vegetation composition and richness patterns through time and to identify the potential environmental drivers underlying these patterns. Our results suggest reverse mire development from bog to fen, a rare occurrence and contrary to typical mire autogenic succession from groundwater fed to rainwater fed. Kanna developed as a small bog for the first 2,000 years from 9,200 to 7,200 cal yrs BP. Changes to the hydrological regime around 7,200 cal yrs BP, due to a warmer and drier climate and land uplift, caused a change from an ombrotrophic to a minerotrophic environment. Typical spring fen characteristics developed ca. 5,000 cal yrs BP and continued until ca. 400 cal yrs BP, when the fen was fed by calcareous mineral-rich groundwater and reached very high floristic diversity with various calciphilous and relict plant taxa. We conclude that general changes in the Kanna fen succession, vegetation community and diversity are associated with climatic changes. The present high diversity of the fen is a result of a long-term stable fen environment, which may have been even higher in the past. However, the pollen richness has decreased during the last 400 years, possibly due to human or natural factors.

Keywords Calcareous fen · Mire succession · Holocene · Pollen richness · Climate · Human impact

Introduction

Springs and spring fens are characterized by a continuous flow of cold water, uniform in temperature and rich in oxygen and minerals. The water in spring fens seeps up through the ground or flows on the peat surface, thereby enabling the growth of specialized vegetation. The invertebrate fauna is often specific to this habitat and the flora rich in northern taxa (IMEUH 2007). The water of calcareous spring fens is strongly alkaline, which leads to a specifically calciphilous vegetation and often to precipitation of carbonates or tufa (Rodwell 2016). Calcareous spring fens in Europe are classified into three biotopes by the Council Directive 92/43/EEC (Council of the European Communities 1992), calcareous fens with *Cladium mariscus* and species of the Caricion davallianae (code 7210), alkaline fens (code 7230), and petrifying springs with tufa formation (Cratoneuron) (code 7200).

Calcareous fens are hotspots of biodiversity (Hájková et al. 2012a), yet their area in Europe has declined by 50% during the last 50 years (Rodwell 2016). In many places they have disappeared from the agricultural landscape, having been selectively damaged and destroyed by artificial drainage, which has caused mineralization of nutrients in the fen sediment and the spread of nutrient-demanding plants. Fens can also be negatively affected to some extent by overly intensive livestock grazing (Breitsameter et al. 2017), which is a critical scientific and resource management issue for nature conservation (Wolf and Cooper 2015).

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The decrease in the distribution and area of calcareous fens is continuing even in nature reserves due to overall eutrophication of the landscapes, water table decline and lack of management (Nilsson 2016). Calcareous fens hold high conservation priority in Europe owing to their increasing rarity and declining quality (Šefferová Stanová et al. 2008).

Many of the remaining calcareous fens are located in nature reserves. There are also numerous restoration projects on fens and their biodiversity (Bragg and Lindsay 2003; Minayeva et al. 2017). Restoration is done mainly by re-wetting and management by mowing, cutting shrubs or extensive cattle stocking (Breitsameter et al. 2017). The complex nature of fen reconstruction requires background knowledge from several different scientific fields. To date most fen research concentrates on contemporary processes or relatively short-term effects of management, water chemistry and recent climate change (Jordan et al. 2007; Rozbrojová and Hájek 2008; Laitinen et al. 2011; Völlm and Tanneberger 2014; Priede et al. 2016).

Spring fens are well suited to palaeoecological studies. The permanently wet conditions in fens help to preserve pollen, spores and plant macroremains, which results in sediment records that offer insights on the long-term development of fens and their surrounding landscapes throughout their entire history. Although the palaeoecology of calcareous rich fens in central Europe has been relatively well studied (Hájek et al. 2011; Hájková et al. 2012a, b, 2013, 2015; Pidek et al. 2012; Jamrichová et al. 2014; Galka et al. 2017, 2018), there are few such studies from northern Europe (but see Galka et al. 2016; Väliranta et al. 2017).

Estonia can be considered the leading country in Europe in terms of density of calcareous spring fens (Šefferová Stanová et al. 2008), which occupy approximately 900 ha (ca. 0.02% of the state area). About half of Estonian spring fens are located on Saaremaa, mostly along the slopes of the Saaremaa keskkõrgustik (west Saaremaa upland) (Paal and Leibak 2011). More than one-third of previously known spring fens have disappeared or become degraded (Paal and Leibak 2011). Numerous rare plant species are associated with spring fens in Estonia, such as *Rhinanthus osiliensis*, *Selaginella selaginoides*, *Saxifraga hirculus*, *Dactylorhiza incarnata*, *D. baltica*, *D. russowii* and *Epipactis palustris*. Many fen plants such as *Juncus subnodulosus*, *Selaginella selaginoides*, *Pinguicula alpina*, *Cladium mariscus* are considered to be relicts of former climatic conditions (Ilomets et al. 2010). Several palaeoecological studies on Saaremaa have focused on the history of vegetation development, shore displacement and human impact, for example from Surusoo (Veski 1996; Poska and Saarse 2002), Vedruka (Poska and Saarse 2002), Pitkasoo (Königsson and Poska 1998) and Jõhvikasoo (Hansson et al. 1996). However, all these studies examined present-day bogs rather than fens.

The primary aim of this study was to study the development of spring fens by using palaeo-reconstructions from the Kanna calcareous spring fen in Viidumäe looduskaitseala (Viidumäe nature reserve), Saaremaa, Estonia, to reconstruct its historical development, vegetation succession and vegetation diversity patterns. We used palaeoecological data from pollen and spores, macrofossils, non-pollen palynomorphs (NPPs) and physical characteristics of the sediment core. In addition, we aimed to better understand the main processes and environmental factors, for example grazing, drainage and climate change, that are likely to have affected the particular development of this fen.

Study area

Kanna spring fen (22.096721°E; 58.325031°N) is situated in Viidumäe looduskaitseala (nature reserve) in the western part of Saaremaa (Fig. 1) on the slope of the higher part of the Saaremaa keskkõrgustik (west Saaremaa upland), 29 to 32 m a.s.l. The highest point of the nature reserve is 59 m, and lies on the highest and oldest part of the island, which emerged from the sea in the Baltic basin at about 11,600 years BP (Saarse and Vassiljev 2010). Saaremaa lies on the western edge of the East European Shield with the bedrock composed entirely of Silurian carbonate rocks, primarily limestone. Large parts of the island surface are either covered by glacial sediments from the last Ice Age or reworked by waters of the Baltic Sea (Saarse et al. 2009).

The climate on Saaremaa is more oceanic than the Estonian mainland. The end of spring and beginning of summer are the driest periods with 34 to 67 mm of precipitation out of a 550–820 mm yearly average. The mean air temperature on the western coast of Saaremaa is − 3.5 to − 4 °C in February, 3°–4° warmer than in eastern Estonia. The mean July temperature is ca. 19 °C (Riigi Ilmateenistus 2018). The nature reserve that surrounds Kanna spring fen, which was founded in 1957, covers 2,598 ha. About 85% of the reserve is covered with woods in which *Pinus sylvestris*, *Picea abies*, *Betula pubescens*, *Alnus glutinosa* and *Quercus robur* are currently the most common trees. These woods are scattered among traditionally managed meadows, wooded meadows, fens and bogs. The reserve is situated along the coastal escarpment of the former Ancylus Lake (the stage of the Baltic Sea ca. 10,700–9,800 cal BP, with a maximum water level here about 31.5 m) and the spring fens are located at the foot of a relatively steep slope (25°–30°) from which the calcareous ground water flows. Due to the diverse natural conditions, the nature reserve is extremely rich in plant taxa. Approximately 700 species of vascular plants grow in the reserve (about half of the total Estonian flora), of which 58 are designated as protected in Estonia, including *Rhinanthus osiliensis* (Saaremaa yellow rattle), an endemic species growing only in spring fens on Saaremaa (Talve et al. 2014).

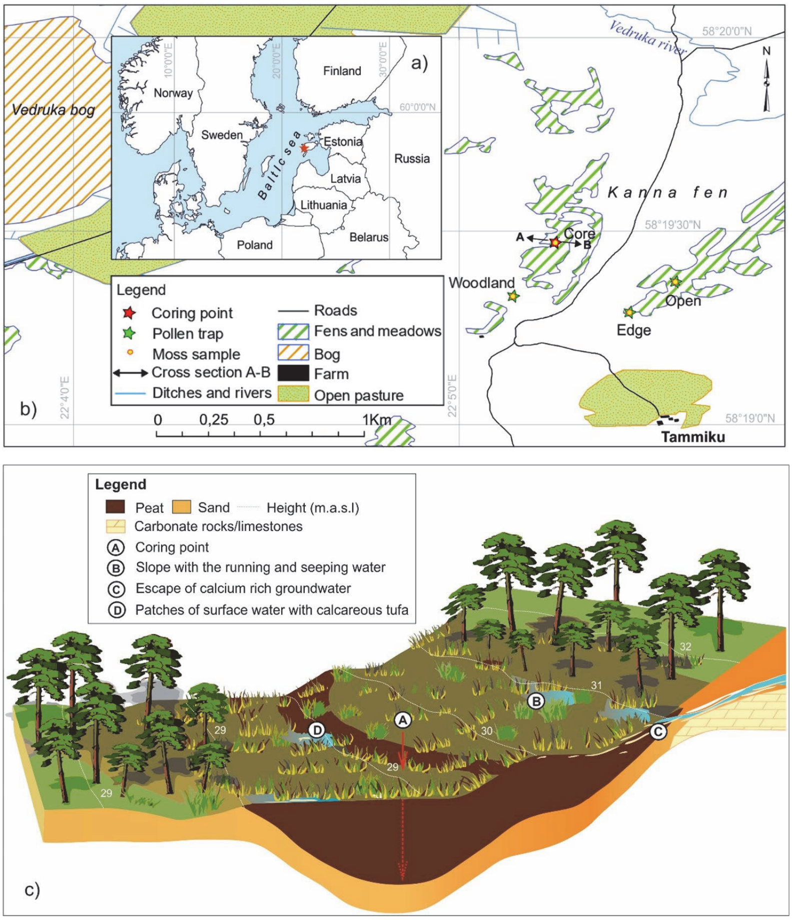


Fig. 1 **a** The study site and its location in northern Europe; **b** Location of coring point, pollen traps and collected moss pollsters from coring point (core); open fen landscape (open), edge of the fen (edge); and wooded fen (woodland); **c** Visualized cross section of Kanna fen

The highest and oldest part of Saaremaa also has the oldest human settlements on the island. Loona, an early Neolithic settlement, covered by a large Bronze Age stone cist grave field and burials from the 13th century AD, is situated ca. 4 km west of the Kanna site. There is also a pre-Viking and early Viking sacrificial site dating to AD 600–900, 2 km south of the fen (Mägi et al. 2014). These archaeological sites prove that Saaremaa was inhabited relatively soon after its emergence from the sea and was one of the most densely populated regions in Estonia in the 11th–13th centuries AD (Jänes-Kapp et al. 2007). The closest farms to the Kanna site are approximately 500 m from it and were inhabited until the mid 20th century; the hay meadows of Tammiku farm are still not overgrown by woods. The closest currently inhabited farms in the villages of Viidu, Viki and Vedruka are ca. 2 km away in different directions.

The Kanna site is a typical example of spring fens in western Saaremaa with vegetation belonging to the Scorpidio-Schoenetum association according to Paal (1997). The local vegetation is dominated by *Schoenus ferrugineus*. The subdominant taxa include other Cyperaceae (*Carex panicea, C. hostiana, Eriophorum latifolium*), Poaceae (*Phragmites australis*, *Molinia caerulea*), *Juncus subnodulosus* and *Menyanthes trifoliata.* There are numerous forbs growing in low frequencies, *Pinguicula vulgaris*, *Drosera anglica*, *D. rotundifolia*, *Parnassia palustris, Epipactis palustris, Dactylorhiza incarnata* etc.

Materials and methods

Sampling

The sediment was sampled in the part of Kanna fen with the thickest peat layer in October 2016 (Fig. 1c). Three replicate peat cores were obtained with lengths of 228, 230 and

231 cm, using a Russian-type peat sampler. The cores were described visually in the field, wrapped in plastic, transported to the laboratory and stored at 4 °C.

Three samples from Tauber pollen traps, installed and used according to the Pollen Monitoring Programme (PMP) guidelines (Hicks et al. 1996), were analysed to associate the sedimentary pollen data with the pollen rain from modern vegetation. In addition, four moss polster samples were collected following the sampling protocol by Bunting et al. (2013).

Chronology

The age-depth graph of the Kanna core was drawn using the OxCal 4.2.4 deposition model (Bronk Ramsey 2008, 2009) and the IntCal13 calibration curve (Reimer et al. 2013), combining lithological boundaries, dates from spherical fly ash particle (SFAP) analysis and radiocarbon dates from accelerator mass spectrometry (AMS). Altogether 11 AMS radiocarbon dates were obtained from terrestrial macrofossils, plant remains, wood twigs, bark pieces, charcoal, and bulk peat samples by the Poznań Radiocarbon Laboratory (Table 1).

In order to improve the age-depth model in the upper 17 cm of the core, we used an indirect dating method of spherical fly-ash particles (SFAP), the by-product of high-temperature combustion of fossil fuels, which are an important indicator of environmental pollution and atmospheric deposition from industrialization (Zhang et al. 2011). The sample preparation followed the method of Renberg and Wik (1985) to remove organic matter with H_2O_2. For the fen peat, we also used 3 M HCl treatment to remove carbonates (Rose 1990). A known amount of *Lycopodium* spores was added for the SFAP concentration calculations. SFAP particles together with *Lycopodium* spores were counted with a light microscope at × 125 magnification. The distribution of the SFAP concentration was compared with the known fossil fuel combustion history to obtain dates (Alliksaar 2000; Heinsalu et al. 2007).

Analysis of peat physical properties

Loss on ignition (LOI) was used to measure the organic matter content of the sediment (OM). This method provides one of the most widely used simple physical lines of proxy evidence in palaeolimnology (Dean 1974; Boyle 2004) and has been found to be a remarkably good summarising proxy for many changes in different ecosystems. In addition, water, mineral matter (MM) and carbonate (CC) contents were estimated. Altogether 225 samples, representing the complete core at 1 cm intervals, were used for analysis. All heating and weighing procedures followed the protocols by Matthiesen et al. (2005) and Hoogsteen et al. (2015). Peat humification, an indicator of the degree of peat breakdown or decomposition, was estimated for every 5 cm of the sediment core at Eesti Geoloogiakeskus (Geological Survey of Estonia). The analyses were carried out using the centrifuging method designed for determination of the disintegration degree of the peat according to the Russian peat standard GOST 10650-71 (Malterer et al. 1992).

Table 1 Radiocarbon dates and SFAP-derived ages from the Kanna peat profile

Depth (cm)	SFAP/^{14}C Lab.code	SFAP age (yrs AD) ^{14}C age (yrs BP)	Modelled age (cal yrs BP)	Material
4,5	SFAP 1980	AD 1980 ± 5	− 41…− 23 (− 32 ± 5)	
11,5	SFAP 1950	AD 1950 ± 5	11–8 (1 ± 5)	
17	SFAP 1910	AD 1910 ± 10	20–56 (40 ± 10)	
10	Poz-99538*	110.68 ± 0.33 pMC	− 54…(− 42 ± 13)	Bulk peat
25	Poz-99572*	1,355 ± 30 BP	1,190–1,330 (1,280 ± 25)	Carex seed scales
40	Poz-89179*	5,030 ± 35 BP	5,660–5,900 (5,790 ± 70)	Wood twigs
40	Poz-99569	1,245 ± 30 BP	1,090–1,280 (1,210 ± 45)	Bulk peat
51	Poz-99363	2,100 ± 30 BP	1,950–2,120 (2,040 ± 40)	Wood pieces
80	Poz-89178	2,820 ± 30 BP	2,850–3,010 (2,930 ± 40)	Charcoal and twigs
115	Poz-99364	3,785 ± 35 BP	4,080–4,290 (4,180 ± 60)	Moss stems
140	Poz-99571	4,510 ± 35 BP	5,080–5,310 (5,210 ± 70)	Bulk peat
160	Poz-89177	5,600 ± 40 BP	6,300–6,460 (6,380 ± 40)	Charcoal and twigs 0.8 mg C
191	Poz-99366	7,715 ± 50 BP	8,390–8,530 (8,450 ± 40)	Wood and bark pieces
224	Poz-89172	8,190 ± 50 BP	9,110–9,420 (9,270 ± 100)	Charcoal 0.7 mg C

Modelled ages at 95.4% probability range and weighted average ages in brackets are given as cal yrs BP, where 0 = AD 1950 (Hua et al. 2013). Radiocarbon dates marked with asterisks were not included in the age-depth model

Pollen and non-pollen palynomorph (NPP) analysis

For pollen analysis, 1 cm^3 subsamples of material were taken at 5 cm intervals from most of the core, but the uppermost 10 cm was studied at 1 cm intervals due to particular interest in modern disturbances related to fen drainage or grazing. The samples were treated with HCl and 10% KOH followed by the standard acetolysis method (Berglund and Ralska-Jasiewiczowa 1986; Fægri and Iversen 1989). Altogether 53 samples were examined under a light microscope with magnifications of × 250, × 400 and × 1,000. Approximately 1,000 pollen grains were counted from each sample (min = 920, max = 1,115). The pollen collection at the Department of Geology at Tallinn University of Technology and relevant literature (Reille 1992; Beug 2004) were used to assist identification. Various types of non-pollen palynomorphs (NPPs) such as *Trichocladium*, *Arcella* sp., *Assulina* sp., *Podospora*, *Neurospora* and *Habrotrocha angusticollis* etc., were recorded together with the pollen and identified using existing literature and published photographs (Ohenoja 1995; van Geel 2001; Cugny et al. 2010; Miola 2012; López-Vila et al. 2014; Shumilovskikh et al. 2015). Spores and NPPs were excluded from the pollen count, but their percentages were calculated in relation to the pollen sum (Chambers et al. 2011a). In addition to pollen and NPPs, microscopic charcoal particles were noted and categorized in two groups, 10–100 µm and > 100 µm.

A detailed pollen diagram that includes all the identified taxa and spores was created using TILIA v.1.7.16 (ESM; Grimm 2011). In addition to the sedimentary samples, four moss polster and three Tauber trap samples were analysed to characterize the present-day pollen rain.

Macrofossil analysis

For macrofossil analysis, the peat sequence was cut into 10 cm thick layers, from which samples of 5 cm^3 were taken. The material was soaked until it was wet, transferred to a Petri dish and scanned with a stereo microscope at × 20–120 magnification and/or light microscope at 160 ×. Fruits and better preserved vegetative tissues were examined with a light microscope and identified using atlases (Dombrovskaya et al. 1959; Katz et al. 1977) and a personal reference collection. Additionally, the whole of each sample was searched for the seeds. The percentages of plant vegetative remains were estimated as the average from five random views of three Petri dishes (in total 15 views) during the scans (Mauquoy et al. 2010). The plant and peat type systematics follow Levesque et al. (1988). The percentage volume of peat composition was estimated based on three main vegetative types of remains, lignosae (comprising woody parts or taxa with hard lignified tissues, especially stems), herbaceae (herbaceous plants), and muscinae (modern Bryophyta).

Background climate data

To test the climate forcing effect (the effect of the difference between sun energy absorbed by the Earth and energy radiated back into space, thus warming or cooling of climate) on vegetation, we used climate data from a transient simulation experiment with the ECBilt-CLIO-VECODE climate model, forced by annually changing values of orbital parameters, atmospheric CO_2 and CH_4 concentrations, ice sheet surface albedo (the proportion of sunlight that is reflected rather than being absorbed), topography and melt flux (Renssen et al. 2009). The ECBilt-CLIO-VECODE temperature reconstructions cover the world at 5.6° × 5.6° spatial resolution and monthly temporal resolution (Renssen et al. 2009). Local polynomial regression fitting (LOESS) with a span of 0.1 was used to estimate temperatures for those years analysed for pollen and other sedimentary proxies. The average modelled summer (May–August) and winter (December–February) temperatures for western Estonia were used. Temperatures were expressed as the difference from the pre-industrial mean simulated in the climate model (250–550 cal BP).

Pollen richness

Pollen richness is usually calculated by rarefaction with respect to established numbers of counted pollen grains (Birks and Line 1992). Andersen-transformed richness, by which the dominant tree taxa are down-weighted to reduce the bias from their high pollen production on the richness estimate, has shown higher correlations with vegetation richness than the traditional rarefied richness (Felde et al. 2016; Reitalu et al. 2019) and was therefore used in our study. The pollen sums of common tree taxa were multiplied by the Andersen transformation factors (Andersen 1970) and rarefaction was performed on the transformed sum. We also used the traditional rarefaction-based pollen richness estimate to compare with earlier pollen richness studies.

Statistical analysis

CONISS, temporally constrained hierarchical clustering (Grimm 1987) based on Bray–Curtis vegetation dissimilarity (Faith et al. 1987) was used to estimate stratigraphic zones in the pollen data. The broken stick method (Jackson 1993) was used to evaluate the number of significant stratigraphic clusters. Principal component analysis (PCA) with Hellinger-transformed pollen percentages was used for unconstrained ordination. Hellinger transformation together with PCA provides a Euclidean distance based method suitable for ecological data (Legendre and Gallagher 2001). The number of significant PCA axes was estimated based on the broken stick method. We used the envfit() function, which fits environmental factors onto an ordination (Oksanen et al.

2017), to investigate the association of pollen data with environmental variables and non-pollen palynomorphs. In addition, the envfit() function uses permutations to test the significance of each of the environmental variables in relation to the ordination, thereby providing an r^2 estimate (squared correlation coefficient) that reflects the strength of the association between the variable and the ordination axes.

In order to study which environmental parameters best explain the trend in pollen richness, we used linear regression analysis with the following explanatory parameters: LOI data (water, OM, MM, CC), humification, charcoal, the proportion of cultivated plants, sedimentation rate and modelled summer and winter temperatures. To clarify which of the explanatory variables significantly explained pollen richness in the core, we used a backward selection of variables in the multiple regression in which only significant variables ($p < 0.05$) remained in the model. The temporal autocorrelation of the residuals was tested using the autocorrelation function (ACF) from the nlme package (Pinheiro et al. 2019).

The community ecology package vegan (Oksanen et al. 2017), Quaternary science package rioja (Juggins 2017) and R environment v. 3.4.4 (R Core Team 2014) were used for the other statistical analyses.

Results

Chronology and lithology

The Kanna core consisted of homogeneous, highly decomposed peat and plant macrofossils. The bottom 5 cm of sediment was rich in coarse sand accompanied by organic material. The presence of calcareous tufa was observed on the top of the fen surface as well as in water pools and rivulets, but there were no visible traces of tufa within the sediment core.

The age-depth model for Kanna was constructed based on eight radiocarbon dates and three SFAP reference level derived ages (Table 1). The radiocarbon date at 40 cm (Poz-89179) was a clear outlier with a much older age than expected and was thus removed from the age-depth model. The date at 10 cm (Poz-99538) was ca. 40 years younger than suggested by SFAP and was also considered as an outlier. The dates at 25 and 40 cm (Poz-99538, Poz-99569) had reverse ages. The Poz-99538 date seems to be too old compared with the SFAP derived age and it suggests that there must be an about 1,000 year long hiatus in peat accumulation above 25 cm depth. That is however, not supported by the sediment lithology which shows continuous peat accumulation. Turney et al. (2000) reported that *Carex* macrofossils could have anomalously old radiocarbon ages and therefore Poz-99538 is considered as an outlier.

Based on the age-depth model (Fig. 2), the accumulation of peat at Kanna started ca. 9,200 cal BP and overall, it was generally uniform and continuous at a rate of 0.1–2.1 mm year^{-1}. The top 15 cm showed faster peat accumulation at 1.3–2.1 mm year^{-1}.

Physical properties of the peat

The sediment sequence contained on average 89.9% water, with four major water-based phases (Fig. 3). At the beginning of peat accumulation ca. 9,200 to 7,200 cal BP, water content is 90% on average and decreases around 7,200 cal BP. The second phase until 5,000 cal BP shows a decrease in water content reaching some of its lowest values. The maximum water content was found between ca. 5,000 to 3,000 cal BP, followed by a gradual drop to the present day. Organic matter (OM) values are on average 86.6% of the dry mass, and show an opposite trend to water content, except during the last 400 years, when there are the lowest (79.3%) and highest (91.2%) values. A decrease in OM occurs around ca. 7,000 cal BP. Mineral matter (MM) variability is 8–20% with a low variation from 8 to 11% occurring from 4,000 to 1,000 cal BP. The highest values of 20% MM occur ca. 50 to 80 cal BP and the highest variation of 8–20% is found during the last 100 years. The carbonate content (CC) in the sediment sequence is only 1.3% on average. The highest CC (3.6%) is at the top of the sediment core and tufa was also observed on the surface of the site during fieldwork. The period from 4,000 to 1,000 cal BP is a phase of comparatively high CC (1–2.5%), which coincides with the lowest MM content.

The average peat humification of Kanna fen is 22%, with the lowest values (17%) occurring during the first phase of the site's development between 9,000 and 8,000 cal BP. A gradual increase in humification began around 400 cal yrs BP, reaching > 30% in the top 10 cm of the core.

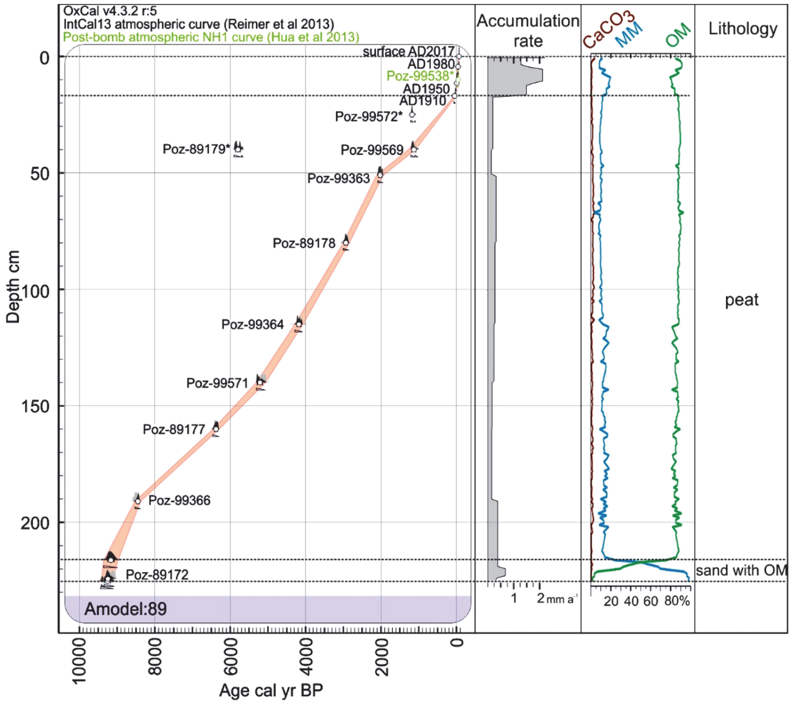
There is a notable peak in charcoal dust at around 2,500 cal BP and relatively high values up to 800 cal BP.

Pollen analysis results

Hierarchical clustering of pollen data and the broken stick model have distinguished three significant ($p < 0.05$) pollen stratigraphic (assemblage) zones, KAN1–3 in the pollen diagram from Kanna (Fig. 4, ESM).

During the earliest period from 9,200 to 7,200 cal BP (zone KAN1), the local landscape was colonized mainly by pine woods, with *Pinus* pollen representing 50 to 70% of the total. In contrast to other zones, pollen percentages of low growing perennial shrubs, *Calluna vulgaris*, *Ledum* and other Ericales, and of the deciduous shrub *Myrica gale* were high. This zone was characterized by a notable peak

Fig. 2 Age-depth graph of Kanna spring fen, based on ^{14}C dating and spherical fly ash particles (SFAP), accompanied by the peat accumulation rate, percentages of calcium carbonate, mineral matter, organic matter and peat lithology



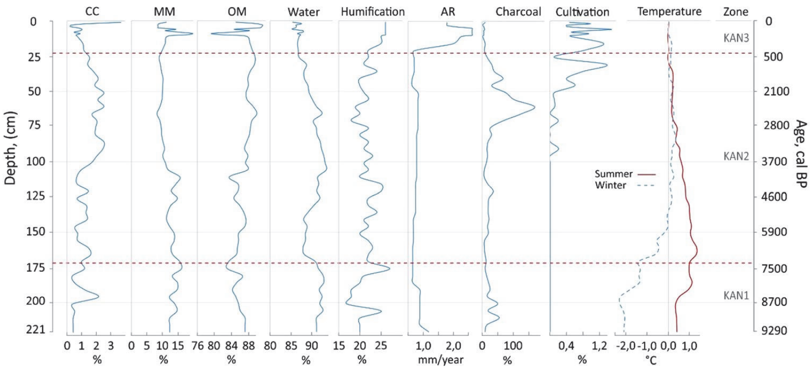


Fig. 3 Physical properties and background environmental conditions in Kanna spring fen. Sediment carbonate content (CC), mineral matter (MM), organic matter (OM), water content (Water) based on loss on ignition (%LOI). Peat humification, sediment accumulation rate (AR), charcoal, cultivation (proportion of cereal pollen). Temperature, average deviations of modelled summer (May–August) and winter (December-February) values from pre-industrial mean (Renssen et al. 2009), and stratigraphic zones based on hierarchical clustering of pollen data from the peat core

of *Sphagnum* spores, which together with *Tilletia sphagni* indicate that *Sphagnum* was present locally.

Zone KAN2 spans the longest time period from ca. 7,200 to 400 cal BP and is characterized by a rapid decline in *Pinus*, with pollen percentages down to 30%. Pine was replaced by deciduous trees characteristic of warmer conditions, such as *Alnus glutinosa/incana*, *Tilia cordata*, *Ulmus glabra/laevis* and *Quercus robur*. Pollen proportions of Ericales, *Calluna* and *Ledum* decrease and those of a variety of other pollen types increase, indicate a gradual replacement of these shrubs by herbaceous vegetation. The zone is characterised by the presence of various insect pollinated and calciphilous

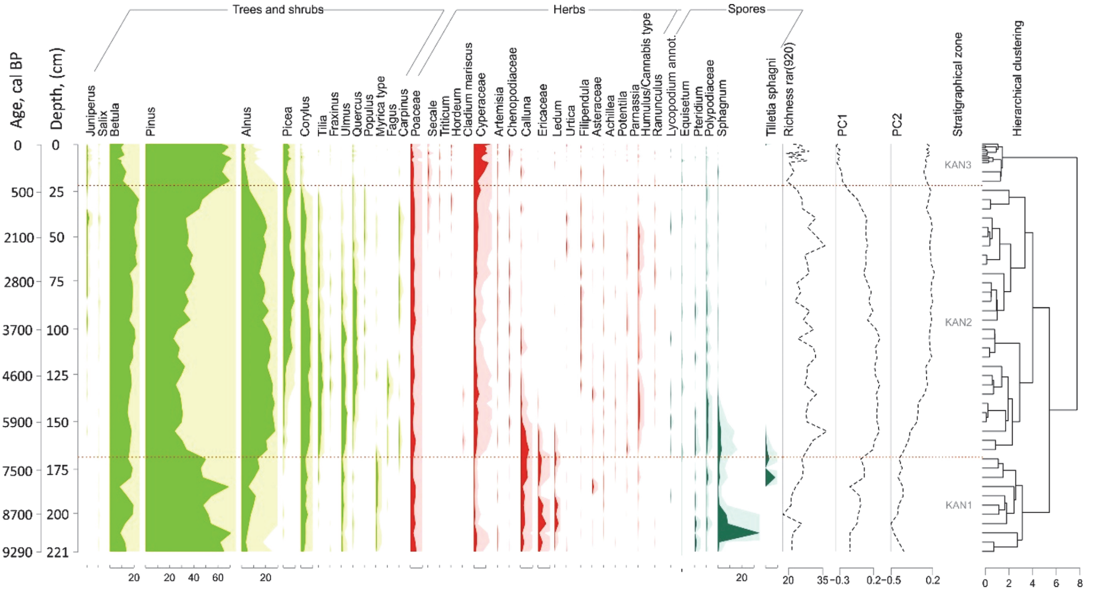


Fig. 4 Pollen diagram of the Kanna profile. Pollen percentages of selected taxa, spores, pollen richness rarefied to pollen sum of 920 grains per sample and first two axes of Principal component analysis PCA1 and PCA2 accompanied by zonation. The full pollen diagram is given in ESM

taxa such as *Potentilla* (most probably *P. erecta*) and *Parnassia palustris*. The first signs of cultivation associated with the appearance of cereal pollen around 3,500 cal BP appear here, followed by a gradual but variable increase in pollen types which indicate human impact.

Zone KAN3 (from ca. 400 to 0 cal BP) is characterized mainly by taxa indicative of human activity. *Pinus* pollen is dominant again, comprising 60% of total pollen. The peaks of *Juniperus* pollen indicate pasture in the landscape. The appearance of *Secale*, *Triticum* and *Hordeum* at the end of KAN2 indicates cereal growing and farming. A number of ruderal taxa, such as *Artemisia*, Chenopodiaceae and Apiaceae, attain their highest values here, accentuating evidence of human activity. Also, Poaceae pollen levels decrease slightly, while Cyperaceae increase sharply to the highest values among the non-arboreal pollen.

In the following text, these zones are referred to as KAN1—bog phase, KAN2—fen phase and KAN3—modern phase.

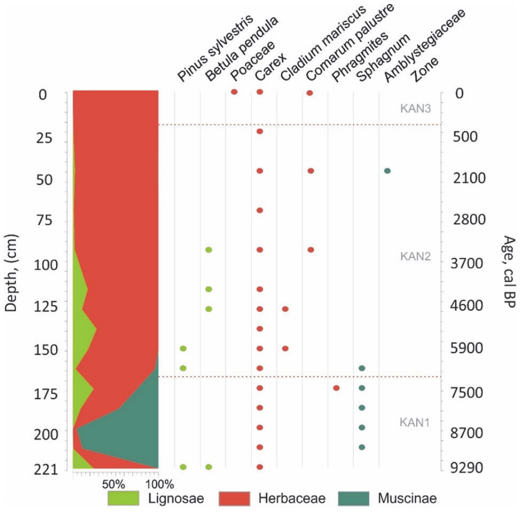


Fig. 5 Diagram of selected non-pollen palynomorphs (NPPs) from the Kanna fen sediment sequence expressed as % of pollen sum. The cluster zones are based on the zonation of the pollen data

Non-pollen palynomorphs (NPP)

The pollen slides from Kanna also revealed several different types of testate amoebae, fungi, zoological remains and charcoal (Fig. 5).

The earliest stratigraphic zone (bog phase, from ca. 9,200 to 7,200 cal BP), was characterized by peaks of various NPPs, most notably the peak of fungal hyphae. *Pinus* pollen together with dark-coloured hyphae was recorded only in this stage. This time period was rich in testate amoebae, especially testaceans of *Assulina muscorum*, *Arcella* type and *Trigonopyxia arcula*.

During the natural fen phase, (ca. 7,200 to 400 cal BP), testate amoebae are largely absent, except for *Centropyxis*. There is a noticeable peak of charcoal around 2,000 cal BP. Ascospores of *Gelasinospora, Podospora* and *Coniochaeta* and the good tree cover indicator *Trichocladium* (HdV-572) are also present. Fungal hyphae have relatively lower values than in the earlier phase.

Towards more recent time (modern phase, ca. 400 cal BP to present), testate amoebae increase, with the re-appearance of *Arcella* type and the highest values of *Centropyxis* type. Loricae of the rotifer *Habrotrocha angusticollis* are one of the most notable NPPs found from the last hundred years, coinciding with a rise in fungal hyphae.

Macrofossil analysis

The high level of peat decomposition limited the number of identifiable taxa found in the macrofossil analysis (Fig. 6). Based on this, the peat composition does not show high variability during its accumulation period and the three main phases which characterize local vegetation development can be recognised. The lower part of the core (the bog phase, ca. 9,200 to 7,200 cal BP) consisted mainly of *Sphagnum* moss peat including some *Carex* remains. *Sphagnum* peat was absent in the next zone (fen phase, ca. 7,200–400 cal BP), which was dominated by 80% herbaceous peat and ~20% wood remains. The herbaceous peat in this phase contained *Carex* spp. and *Cladium mariscus*; the wood consisted of *Pinus sylvestris* and *Betula pubescens*/*pendula*. The sediment of the modern phase (20–0 cm, ca. 400 cal BP to present) was comprised of herbaceous peat throughout, mainly composed of *Carex* spp. and with a presence of *Comarum palustre*.

Pollen richness

At the beginning of sediment accumulation in the early Holocene (ca. 9,200 cal BP), the pollen richness is relatively low, with an increasing trend (Figs. 4, 7). The highest pollen richness occurs from ca. 7,000 to 1,000 cal BP, during the natural fen phase. Throughout most of the period covered by the site, the richness is considerably higher than the average for Estonia (Fig. 7), but the rapid decrease in richness

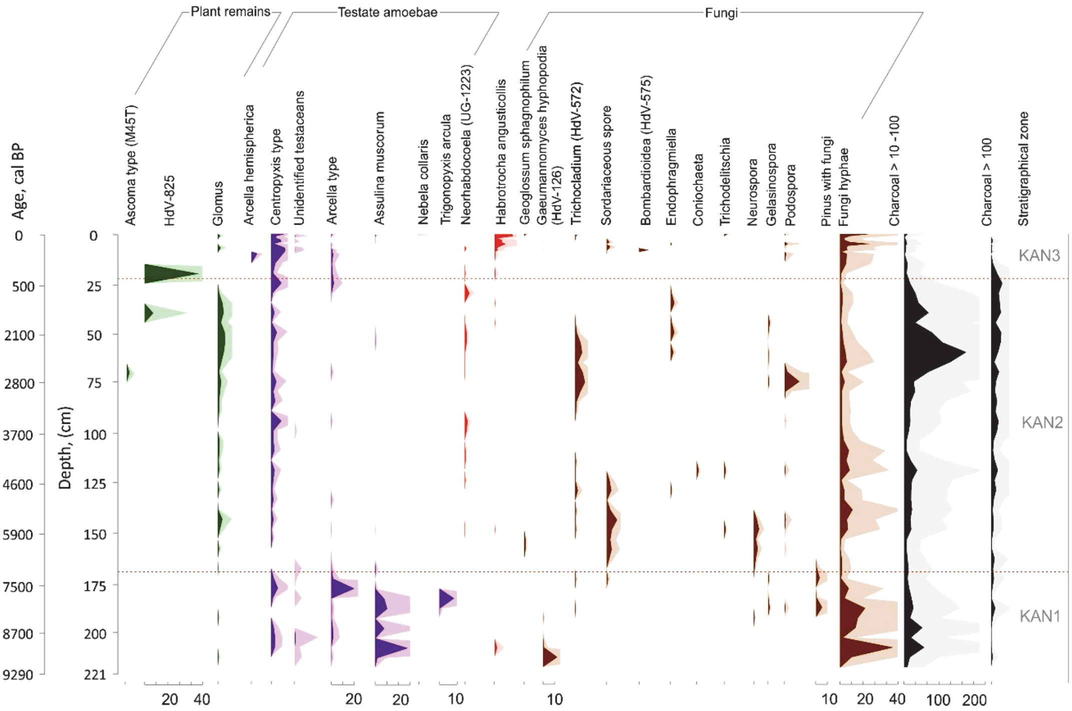


Fig. 6 Plant macrofossil diagram showing the local vegetation succession at Kanna. Three main peat types, lignosae (woody plants), herbaceae (herbaceous plants) and muscinae (mosses) are shown as % peat by volume, the taxa are shown as presence

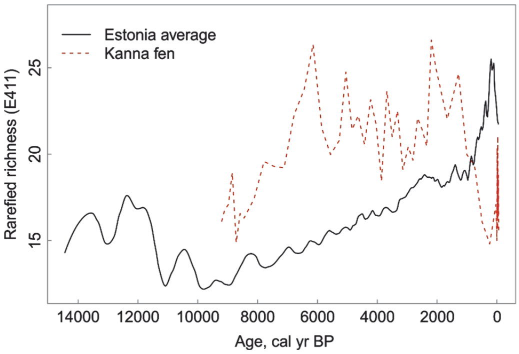


Fig. 7 Rarefied richness [pollen sum of 411−E(T411)] representing the average diversity in Estonia (Reitalu et al. 2015) and at Kanna

towards the present day is contrary to the general richness trend there.

The results of linear regression with backward selection show that pollen richness is significantly positively associated with winter temperature, summer temperature and the amount of charcoal dust (Table 2).

Principal component analysis (PCA)

The broken stick method shows two significant axes for the PCA which explain 52 and 24% of the total variation in the pollen data, respectively (Fig. 8). The results show that taxa such as *Pinus*, *Juniperus*, Cyperaceae and cultivated plants (*Secale*, *Triticum*, *Hordeum*) are positively associated with the first PCA axis, but most of the thermophilous taxa, *Corylus*, *Tilia*, *Ulmus*, *Quercus* and *Fagus*, are negatively associated. *Juniperus*, *Picea*, *Quercus*, Chenopodiaceae and *Parnassia* are positively associated with the second PCA axis, whereas the low-growing perennial shrubs *Calluna*, Ericales, *Myrica*-type and *Ledum* are negatively associated.

Of the environmental variables, organic matter (OM), and humification are positively associated with the first PCA axis, whereas carbonate content (CC), water content and mean summer temperature show negative associations (Fig. 9). The mineral matter (MM) and mean summer temperature are negatively associated with the second PCA axis. Positive associations with the second axis are shown by OM, CC and mean winter temperature. All the tested environmental variables have significant associations with pollen ordination ($p < 0.05$). The strongest associations with the PC axis are for mean winter temperature ($r^2 = 0.90$, $p < 0.001$), summer temperature ($r^2 = 0.73$, $p < 0.001$) and humification ($r^2 = 0.50$, $p < 0.001$).

The associations between pollen ordination and NPPs show that 14 NPPs are significantly associated with the PC axes (Fig. 9). Among the NPPs, testate amoebae, *Habrotrocha angusticolis*, *Centropyxis* type and fungal hyphae have a positive association with PC1, but charcoal, *Neurospora* and *Trichocladium* are negatively associated with it. *Assulina muscorum*, *Arcella*-type, the remaining testate amoebae and fungal hyphae show negative associations with PC2. *Habrotrocha angusticollis* ($r^2 = 0.31$, $p < 0.001$), *Centropyxis* ($r^2 = 0.39$, $p < 0.001$) and charcoal ($r^2 = 0.29$, $p < 0.001$) show the strongest associations with the PC axes.

Discussion

Our study provides a fine example of how a bog can change into a fen due to a unique combination of climatic, topographic and hydrological conditions. The geographically closest comparable published research describing such fen development and vegetation succession is from Apšuciems mire on the southeast Baltic coast of Latvia (Gałka et al. 2016), which developed as did our site, due to active water level changes, at Kanna in a depression on the slope of the Saaremaa upland around 9,200 cal BP.

The only comparable study related to calcareous fen development in Estonia is the unpublished work by Helle Mäemets and Kersti Kihno, in which two short cores (< 1 m) and one long one (2.5 m) were analysed for pollen and are mentioned in Ratas and Kokovkin (1989). This resulted in a pollen diagram for arboreal taxa in which non-arboreal taxa were noted only as presence or absence. Unfortunately, the original count data have been lost, thus impeding direct comparisons with our study. However, the beginning of sediment accumulation at approximately 9,000 cal BP is consistent

Table 2 Results of linear regression with Andersen-transformed pollen richness (E312) in 53 sediment samples in the Kanna core as the response variable

Variable	Estimate	t-value	*p* value	Model summary
Winter temperature	1.89 ± 0.42	4.49	< 0.001	Residual SE 2.96; F-statistic: 13.2; R2 = 0.41
Summer temperature	1.81 ± 0.42	4.27	< 0.001	
Charcoal (0–100 µm)	1.21 ± 0.42	2.90	0.006	

Only the significant ($p < 0.05$) variables after backward selection of the explanatory variables are shown. The explanatory variables were standardized to zero mean and unit variance. The residual temporal autocorrelation was not significant

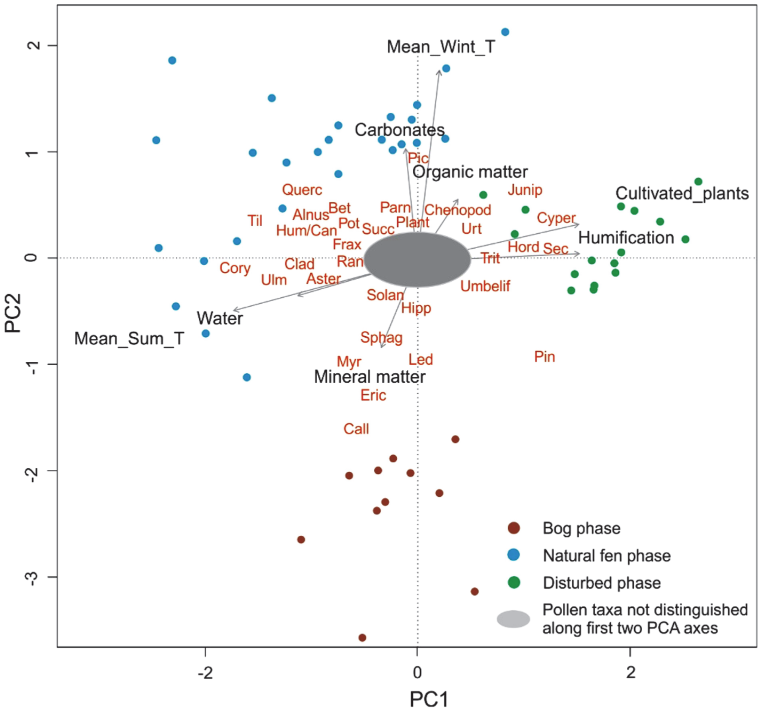


Fig. 8 Results of ordination by PCA, representing samples in clusters from the hierarchical clustering analysis; pollen taxa with selected environmental variables superimposed on the PCA plot. Aster, Asteraceae; Bet, *Betula*; Call, *Calluna vulgaris*; Chenopod, Chenopodiaceae; Clad, *Cladium mariscus*; Cory, *Corylus*; Cyper, Cyperaceae; Eric, Ericaceae; Frax, *Fraxinus*; Hipp, *Hippophae rhamnoides*; Hord, *Hordeum*; Hum/Cann, *Humulus/Cannabis*-type; Junip, *Juniperus*; Led, *Ledum*; Myr, *Myrica gale*; Parn, *Parnassia*; Pic, *Picea*; Pin, *Pinus*; Plant, *Plantago m/m*; Pot, *Potentilla*; Quer, *Quercus*; Ran, *Ranunculus*; Sec, *Secale*; Solan, *Solanum dulcamara*; Succ, *Succisa*; Sphag, *Sphagnum*; Til, *Tilia*; Trit, *Triticum*; Ulm, *Ulmus*; Umbelif, Apiaceae; Urt, *Urtica*

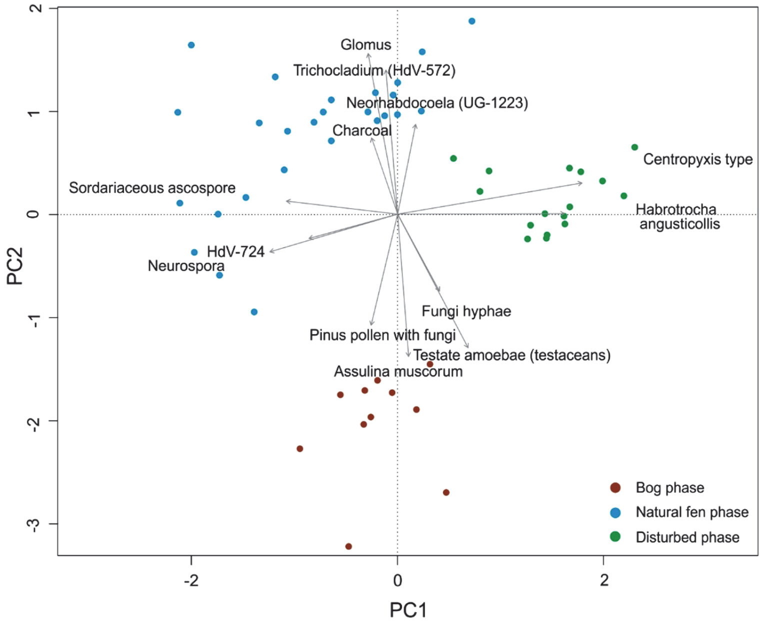


Fig. 9 PCA ordination of pollen data with samples grouped into clusters from hierarchical cluster analysis, where only significantly associated NPPs are superimposed as environmental variables

with our study. Although well-chosen plant macrofossils are considered reliable dating material (Hatté and Jull 2013), the age-depth model reconstruction for the top 40 cm of the Kanna core was complicated, as the samples close to the surface provided inconsistent dates. Having an outlier in a dating series is a common phenomenon, but fen environments can have complicating factors, such as surface flooding, periodic droughts, root intrusion or possible trampling by grazing animals, which might cause dates to deviate from the norm (Väliranta et al. 2014; Wolf and Cooper 2015). According to the date Poz-99538, there might be a hiatus in peat accumulation (Table 1), however, this possibility was dismissed since it disagreed with the SFAP-derived age. In addition, the hiatus would span 1,000 years, which is not supported by the sediment lithology. First, there is continuous peat accumulation and no corresponding discontinuity in other data as for example in mineralisation or erosion, like that recorded by Hájková et al. (2015). Secondly, there are no climatic reasons to suspect a hiatus, which would be more usual in the mid Holocene as a result of the warmer and dryer climate then (Rybníček and Rybníčková 1987; Ammann et al. 2013). In our case, the possible hiatus is during the period when the climate was getting wetter (Hammarlund et al. 2003).

Overall, the Kanna age-depth model appears to be reliable and fits with existing knowledge of vegetation and coastal development in this region.

Bog phase (ca. 9,200–7,200 cal yrs BP)

The beginning of sediment accumulation in the fen around 9,200 cal BP corresponds to the time of the former Initial Litorina Sea (Berglund et al. 2005), when the local water level at Kanna dropped to between 15 and 17 m a.s.l. (present level) (Saarse et al. 2009). This decrease in the water level and loss of water contact between the depression on the slope and the Initial Litorina Sea resulted in the emergence of an isolated water body. The isolation and increasing role of precipitation then led to the development of ombrotrophic vegetation (fed by precipitation rather than ground water) there, as suggested by the pollen and spore assemblage including *Calluna vulgaris*, other ericaceous taxa and the great abundance of *Sphagnum* (Fig. 4). It is a typical scenario with the *Sphagnum* mosses forming the main part of the ombrotrophic peat, as in a raised bog (Clymo 1963), and it fully agrees with the results of the macrofossil analysis (Fig. 5), demonstrating that at the beginning of its accumulation the peat was comprised mainly of *Sphagnum* moss (up to 80%). Analysis of NPPs also suggests ombrotrophic conditions from the abundant presence of the testate amoebae *Assulina muscorum*, *Arcella*-type and *Trigonopyxis*, while *A. muscorum* is regarded as typical of the early stages of raised bog formation (Mazei and Bubnova 2007). The pollen of calciphilous plants is recorded in low numbers, so the role of calcium rich groundwater is not clear, considering that the depression in which the sediment accumulation started is lower than the point from which spring water escapes. It has been shown that peat moss can acidify its surroundings by taking up cations, including calcium, and by releasing hydrogen ions (Clymo 1963), and this effect might have reduced the impact of calcium rich groundwater.

The loss on ignition results suggest an increasing input of mineral rich water at around 8,500 cal BP, coinciding with the lowest values of peat humification (Fig. 3). The humification index has also been used to interpret past changes in regional climate, especially changes in wetness (Chambers et al. 2011b). The increase in water content corresponds to the time of the rise in the level of the former Litorina Sea, caused by an increase in ocean water mass due to the final melting of the Laurentide Ice Sheet (Berglund et al. 2005). As the bog surface wetness is believed to be affected primarily by precipitation and temperature (Sillasoo et al. 2007), the increase in carbonate content and low humification level around 8,500 cal BP in Kanna could be attributed to an increase in groundwater discharge caused by such a rise in the level of the Litorina Sea.

Since the beginning of mire development around 9,200 cal BP and throughout the bog phase, the pollen richness is relatively low. Bogs are usually characterized by low but very distinct biodiversity (Lachance and Lavoie 2004). In addition, a potentially slow spread or delay in the spread of vegetation to land that had recently emerged from the sea could also be associated with low pollen diversity (Giesecke et al. 2012; Matthias et al. 2015).

Bog to fen transition, natural fen phase and early human impact (ca. 7,200–400 cal yrs BP)

The results of hierarchical clustering suggest changes in the vegetation as a transition, starting around 7,200 cal BP. The first 2,000 years of the second stratigraphic zone (KAN2) can be considered a transition phase between bog and fen and are characterized by the inherent properties of both phases. Declining levels of *Sphagnum* and ericaceous taxa, as well as an increase in various herbs such as Cyperaceae, *Potentilla*, *Parnassia* and *Ranunculus* suggest a change from ombrotrophic to more minerotrophic conditions that coincided with higher summer temperatures (Renssen et al. 2009) and further decreasing water levels in the Baltic Sea (Saarse et al. 2009). Although pinpointing the causes of the change is difficult, we can speculate that desiccation of the bog during a phase of warmer and drier climate led to an increasing role of mineral-rich surface water that started to flow through the mire. Hájková et al. (2012a) showed in her study that a similar change from bog to fen was related to bog surface desiccation due to a climatically-caused unstable water regime, resulting in peat surface layer decomposition and an increase in shrub and tree cover. Macrofossil analysis from Kanna shows that 30% of the peat in this phase was composed of woody material, suggesting that the surface of the site was drier and the peat was thin enough for woody plants to grow on it (Fig. 5). A decrease in water content (Fig. 3) and disappearance of most of the testate amoebae (Fig. 6) also suggest drier conditions.

Myrica gale growing in fens has been associated with an oceanic climate and open mires with slightly acidic and relatively shallow peat (Skene et al. 2000). The decrease in *Myrica* in the transitional phase at Kanna can be related to a decrease in *Sphagnum* which caused changes in pH, or to increasing woodland cover. Today *Myrica* still grows on the margins of Kanna and abundantly on both fen and bog margins in the western part of Estonia. The appearance of *Cladium* and an increasing carbonate content (Fig. 3) agree with the specific environmental conditions reported for *Cladium mariscus* in fens, shallow water and high calcium content (Rodwell 1995). These records of *Cladium* correspond to a time when it was more widespread throughout Europe (Salmina 2004; Hájková et al. 2013) and they are consistent with findings from the southeast Baltic coast (Gałka et al. 2016).

The transition phase exhibits a rapid increase in pollen richness, with the highest values around 6,000 cal BP. This features characteristics of both bog and fen phases, which probably accounts for the high local vegetation diversity. Low diversity at the beginning of the Holocene and a steady subsequent increase have been recorded in a regional study of several sites in Estonia and northern Latvia, and attributed to warmer and/or drier conditions (Fig. 7; Reitalu et al. 2015). Linear regression confirms the climatic effect on the pollen richness of Kanna, with a positive association for both modelled mean winter and summer temperatures (Table 2). The period from ca. 7,500 to 4,000 cal BP is associated on Saaremaa with rapid land emergence from the sea (Poska and Saarse 2002), resulting in the availability of new habitats and arrival of new plants, and therefore an increase in biodiversity.

Around 4,000 cal BP the site probably already had the characteristics of a fen and running surface water. A high abundance of *Comarum palustre* and *Parnassia palustris,* both typical of open seepage areas, was recorded together with the pollen of other insect-pollinated plants such as *Epipactis palustris*, *Linum* and *Iris*-type. An abundance of herbaceous plants has been shown to lead to increased biomass, which, in turn, leads to increased soil organic matter (Weil and Brady 1985), as demonstrated by our loss on ignition results. At the same time, the increase in biomass caused a decrease in soil minerals, which serve directly and indirectly as both sources and sinks of essential plant nutrients (Hawkesford et al. 2012). In general, from ca. 4,000 to the last 1,000 cal BP, the low variability in organic and mineral matter suggests a relatively stable fen environment.

The fen phase exhibits relatively high pollen richness and high variability. The pollen richness values from the bog and fen phases are similar to present-day diversity in bogs and mineral-rich fens. The greater richness during the fen phase is due to the increase in pH caused by an increase in calcium concentration, thereby allowing the coexistence of many calciphilous plants (Tahvanainen 2004; Rozbrojová and Hájek 2008) and relating to the large number of such taxa found in northern Europe (Zobel et al. 2011).

The first evidence of human activity here is indicated by the appearance of cultivated plants, with the first cereal grains appearing ca. 3,500 cal BP. (Figure 3) Earlier evidence of cereal cultivation in the region, from Vedruka and Pitkasoo mires, has been dated to ca. 4,200–4,000 cal BP (Poska and Saarse 2002). An abundance of *Juniperus communis* pollen, a light demanding shrub and indicator of more open vegetation at this time could be related to increasing pasture in the landscape. High charcoal presence in the sediments between 3,000 and 1,000 cal BP (Fig. 3) coincides with the evidence of cereal growing and suggests the use of fire in landscape management for slash and burn agriculture, rather than natural fires. Earlier studies suggest that the use of fire in landscape management on Saaremaa started ca. 4,500 cal BP (Poska and Saarse 2002). Our results indicate that the early agriculture caused no visible disturbance to fen development, probably because the fen is relatively far, > 500 m from the closest suitable agricultural areas.

Modern phase (ca. 400 cal yrs BP until present day)

The last 400 years in the development of the fen are characterized by a change in vegetation composition. This phase is dominated by *Pinus* pollen, with low values of pollen from thermophilous taxa, an increase in the ruderal plants Chenopodiaceae, *Artemisia*, and *Plantago*, as well as a rapid increase in Cyperaceae (Fig. 4).

The re-emergence of NPPs such as testate amoebae, *Arcella*-type and an increase in *Centropyxis*-type suggests an increase in surface wetness (Fig. 6). However, the relatively low values of carbonates and an increase in humification (Fig. 3) suggest a decrease in calcium-rich groundwater and drier conditions. Furthermore, the humification index might be misleading, as more recent environmental change can cause later-stage peat degradation. An increase in surface wetness and a rise in water level during the last 1,000 years is evident in some regional studies of fens and mires (Charman et al. 2007; Sillasoo et al. 2007; Lamentowicz et al. 2015; Gałka et al. 2016). However, the evidence is inconclusive whether there was an actual increase in surface wetness at Kanna or not.

The top part of the sediment core which covers the last 100 years is characterized by the highest variability in most of the physical properties of the peat, organic, mineral, calcium carbonate contents and humification. This high variability might reflect disturbances directly at or near the site, for example those connected with drainage systems dug in the middle of the 20th century to improve farming and forestry production or related to livestock grazing.

According to historical maps (Maa-Amet, Estonian Land Board 2018), the first improvement works close to the fen were undertaken in the 1940s to straighten the river Vedruka ca. 900 m to the west. Peat extraction from the bog at Vedruka ca. 2 km west of Kanna began in 1940 (Eesti elu 1940). A complex drainage system in the area between this bog and Kanna fen already existed in 1959. The sensitivity of peatland ecosystems and the effects of changes in environmental conditions caused by land use changes such as drainage have been studied widely (Landry and Rochefort 2012; Urbanová et al. 2012; Gałka et al. 2016; Glina et al. 2016; Stivrins et al. 2017). The profound effects of drainage on peatland biogeochemistry can cause vegetation changes that are seen in differences in organic matter quality and decomposition rate. It has been shown that a lowering of the water level increases the thickness of the aerobic surface layer and thus the peat decomposition rate (Minkkinen 1999; Landry and Rochefort 2012; Urbanová et al. 2012), and this effect might explain the increasing humification levels at the top of our core. A relatively slow groundwater flow is essential for fen systems, as it prevents erosion and stimulates iron and calcium carbonate precipitation (Middleton et al. 2006). This would account for the decrease in carbonate and the rapid decrease in organic matter, as a lowered water table exposes previously accumulated organic matter to aerobic decomposition.

A rapid decrease in pollen richness is evident during the modern phase, in contrast to both the regional richness trend noted by Reitalu et al. (Figure 7; 2015) and the landscape scale richness change in Vedruka (Poska and Saarse 2002). The changes in pollen deposition could reflect vegetation changes only within the wetland environment but not in the surrounding landscape (Waller et al. 2017) and these could be of local origin, caused by changes in the fen vegetation and environment. It bears pointing out that the present-day vegetation at Kanna is regarded as typical spring fen vegetation for western Saaremaa and is considered highly species rich. Pollen richness values from modern moss and trap samples were used to compare them with the richness from the modern phase KAN3, in order to test whether the decrease in pollen richness in sediments could be caused by decomposition. This comparison indicated no significant difference, suggesting that pollen decomposition is not the reason (Fig. 10).

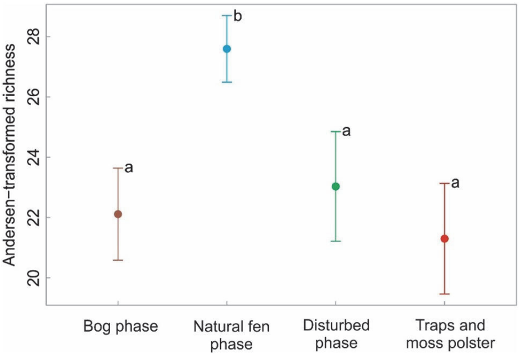


Fig. 10 Andersen-transformed pollen richness in Kanna, comparison between different stages of fen development and modern pollen samples from moss polsters and Tauber traps. Letters a and b denote a statistical significance in the difference between the groups, in which the natural fen phase is significantly different from the other phases

The decrease in groundwater flow and accompanying changes in fen vegetation might be also attributed to changes during the natural succession of the fen. The increase in peat thickness and the corresponding rise of the bog surface could have started to cover and impede groundwater escape. The groundwater flow might have decreased over higher surfaces, thereby reducing the relative abundance of calciphilous forb taxa and increasing the abundance of Cyperaceae, most probably *Schoenus ferrugineus*, which is dominant in the present-day vegetation. A high local abundance of Cyperaceae would decrease the probability of detecting rarer, usually insect-pollinated, forb taxa due to pollen representation bias (Odgaard 1999). However, the reasons for the increase in Cyperaceae pollen are still unclear.

Another possible factor affecting the fen vegetation is grazing by domestic livestock. The fen has probably been grazed at least since the 19th-20th centuries, but precise details and the intensity of this use as pasture are unclear. The remains of pasture fences are still visible in the landscapes of several nearby fen areas. Intense cattle grazing and trampling can cause damage to the fen system and its vegetation (Stammel et al. 2003: Bobbink et al. 2006) and can even change the ecological function of these systems (Sánchez et al. 2017). Trampling by cattle can affect peat subsidence, change bulk density, reduce the amount of biomass productivity, alter its structure and accelerate decomposition of organic matter (Sjögersten et al. 2011; Chimner et al. 2017). Grazed mires in Britain show an increase in native arboreal pollen towards the surface horizons, owing to suppression of flowering by local graminaceous plants, including Cyperaceae (Chambers et al. 2011a). These findings are inconsistent with our results. Despite the decrease in the pollen percentages of Poaceae during the last 1,000 cal yrs

BP, this period featured a rapid increase in Cyperaceae and lower arboreal pollen values than in earlier zones. Certain coprophilous fungi associated with grazing, such as *Podospora* (Cook et al. 2011), *Sordaria* sp. (Krug et al. 2004) and *Trichodelitschia* (Ebersohn and Eicker 1992), were recorded in the samples, but their occurrence was sporadic and did not reliably indicate intense grazing activities (Fig. 6).

To better understand the effect of grazing and/or drainage on fen vegetation and diversity would require sites to be studied where these particular management methods do not overlap. Palaeoecological studies of other similar fens in the vicinity would allow evaluation of the whole pattern of decreasing diversity and provide better understanding of the reasons for these changes.

Implications for conservation

Calcareous spring fens by definition require mineral-rich springs (Rodwell 2016), which are the main feature of these biotopes and the origin of their biodiversity, and which should be the main conservation question. Although drainage and peat extraction works are several hundred metres from Kanna fen, their impact on sediment properties and vegetation composition is noticeable. This is proof that in order to conserve spring fens for the future it is essential to preserve not only their physical features within their boundaries but also their wider surrounding and their hydrological systems. Such actions would require a maintenance strategy for the whole area and efforts to stabilize the water level with the help of existing drainage systems might be needed to ensure the persistence of these diversity hotspots. Knowledge of the fen environment and the response of its taxa to past climatic changes provides information for the future that can be useful for conservation purposes.

Conclusions

Our investigation is the first highly detailed palaeoecological study of a calcareous spring fen in northern Europe. The study presents a mire development from ca. 9,200 cal BP that does not follow the typical mire succession. The ombrotrophic conditions which followed the Ancylus Lake regression favoured the development of a spring fen fed by mineral-rich calcareous groundwater around 7,200 cal BP due to a climatically and tectonically caused lowering of the overall water table. Our results suggest that the main changes in mire development, vegetation community and pollen richness in the past closely followed the changes in climatic conditions.

The establishment of a fen between ca. 7,200 and 5,000 cal BP was accompanied by exceptionally high pollen richness, which lasted through most of its history, decreasing only during the last 400 years. The higher than average local pollen richness is related to the large number of calciphilous herbaceous pollen taxa growing there as a result of the maintainance of stable conditions throughout the Holocene. The reasons for the vegetation change and decrease in pollen richness during the last 400 years are not clear from our investigation, but seem to be related partly to water level changes possibly resulting from the drainage activities 500 m down the slope below the fen. Today there are many plants growing on the fen and in its close vicinity which are considered relicts from former climatic periods or are neoendemic; the growth of these taxa is also related to the long history of stability at the fen (Hájek et al. 2011).

Our study further affirms the high value of calcareous fens for the conservation of biodiversity in northern Europe. The fen environment and vegetation has been shown to be strongly related to past climatic changes, indicating that fens are also highly likely to be affected by ongoing climate change.

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Modern Pollen–Plant Diversity Relationships Inform Palaeoecological Reconstructions of Functional and Phylogenetic Diversity in Calcareous Fens

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Predicting the trajectory of ongoing diversity loss requires knowledge of historical development of community assemblages. Long-term data from palaeoecological investigations combined with key biodiversity measures in ecology such as taxonomic richness, functional diversity (FD), phylogenetic diversity (PD) and environmental factors expressed as Ellenberg indicator values (EIVs) could provide that knowledge. We explored the modern pollen–plant (moss polster pollen vs. surrounding vegetation) diversity relationships for herbaceous and woody taxa in calcareous fens from two different regions in Estonia, NE Europe. Associations of taxonomic richness, vegetation composition, FD (including functional alpha diversity and trait composition), PD and EIVs in modern pollen vs. plant data were studied with correlation analysis, Procrustes analysis and linear regression models. To test their potential use in palaeoreconstructions, diversity measures were applied on pollen data from Kanna spring fen reflecting fen vegetation development over the last nine millennia and diversity changes through time were studied using generalized additive models. Results showed significant pollen–plant richness correlations for herbaceous taxa at vegetation estimate scales up to 6 m radius and Procrustes analysis showed significant compositional associations at all plant estimate scales (up to 100 m). Woody taxa had no significant pollen–plant richness correlations but composition relationships were significant at plant estimate scales of 6–100 m. Traits that were best reflected by pollen data (both in terms of trait composition and functional alpha diversity) among woody and herbaceous taxa were seed number, clonality, SLA and LDMC. PD of herbaceous species was reflected by pollen data. Among the EIVs, Ellenberg L and T were significantly reflected by pollen data for both woody and herbaceous communities. Palaeoreconstruction from Kanna fen indicates that trends of woody taxa are mostly related to long-term changes in climate while diversity variables of herbaceous taxa closely follow autogenic processes within the fen. We suggest that pollen-based diversity estimates should be calculated separately for woody and herbaceous taxa as they clearly represent different spatial scales. Present study suggests that linking sedimentary pollen data with FD, PD and EIVs provides possibilities to examine long-term trends in community assembly and ecosystem processes that would be undetectable from traditional pollen diagrams.

Keywords: pollen–plant relationships, calcareous spring fens, functional diversity, phylogenetic diversity, Ellenberg indicators, Holocene, palynological diversity

INTRODUCTION

Identifying the drivers underlying biodiversity changes is among the key research questions both in ecology (Vellend et al., 2017) and palaeoecology (Birks et al., 2016b). Biodiversity can be measured at different organizational levels – from genetic diversity to taxonomic (species) diversity, to landscape diversity. Coupling these measures with community functional diversity (FD), which reflects the type, scope, and abundance of functional traits in communities provides a link between species diversity and ecosystem functioning (Tilman, 2001; Lavorel and Garnier, 2002; Díaz et al., 2007). In addition, phylogenetic diversity, which estimates the phylogenetic relatedness among the coexisting species (Faith, 1992) connects local community assembly and evolutionary processes (Gerhold et al., 2015, 2018). The concepts of functional and phylogenetic diversity are of central interest in a large number of contemporary ecological studies of land plants (e.g., Cadotte et al., 2009; Cavender-Bares et al., 2009; Purschke et al., 2013; Díaz et al., 2016). In palaeoecology, plant functional types have been used for several decades to enable the transformation of pollen records to biomes or land-cover types for comparison with climate models (e.g., Prentice et al., 1996; Fyfe et al., 2010; Davis et al., 2015). The more detailed studies of functional and phylogenetic aspects of palaeo communities are relatively rare (e.g., Lacourse, 2009; Reitalu et al., 2015; Brussel et al., 2018; Carvalho et al., 2019; Jabłońska et al., 2019) and have demonstrated the great potential of functional and phylogenetic palaeodiversity to contribute to a better understanding of processes underlying long-term patterns of community assembly. For example, Brussel et al. (2018) showed that long-term fire frequency variations may drive directional selection for fire–adapted plant community attributes.

In palaeoecology, sedimentary pollen analysis is one of the main tools for reconstructing changes in past vegetation and plant diversity in the late Quaternary (Berglund and Ralska-Jasiewiczowa, 1986; Birks and Birks, 2006; Gaillard et al., 2008; Reitalu et al., 2015). However, interpreting pollen data in terms of past plant diversity is not straightforward because of the low taxonomic resolution of pollen data and interspecific variation in pollen production and dispersal (Odgaard, 1999; Liu et al., 2014; Birks et al., 2016a; Carvalho et al., 2019). To clarify the pollen–plant relationships and to aid the pollen-based biodiversity reconstructions, modern pollen assemblages acquired from moss polsters, pollen traps, and lake surface sediments have been compared with detailed information of the surrounding vegetation (Bunting and Hjelle, 2010; Meltsov et al., 2011, 2012; Matthias et al., 2015; Felde et al., 2016; Julier et al., 2018; Reitalu et al., 2019). Several studies have demonstrated a positive association between modern pollen richness and plant richness (Meltsov et al., 2011; Matthias et al., 2015; Felde et al., 2016; Reitalu et al., 2019). Pollen of woody taxa is expected to be produced in greater quantities, to travel larger distances and to reflect broader spatial scales than the pollen of herbaceous and/or insect-pollinated taxa (Meltsov et al., 2011; Felde et al., 2016; Reitalu et al., 2019). In the present study, we will, therefore, examine the woody and herbaceous species/pollen taxa separately.

Carvalho et al. (2019) have highlighted the importance of using modern pollen–plant relationships also for functional palaeodiversity. They showed in modern pollen–plant study from fen peatland that some leaf traits (C and N content) were better reconstructed from pollen data than others (specific leaf area and leaf dry matter content). The choice of traits for analyzing functional diversity is often debated and depends on the research system, hypotheses and data availability (Lavorel and Garnier, 2002). In the current study, we have focused on the commonly used traits in plant functional ecology that could be assumed to be relevant for shedding light to the past plant communities. The chosen traits reflect different aspects of plant life history related to vegetative growth [clonality, plant height, specific leaf area (SLA), leaf dry matter content (LDMC)], reproduction (seed size and number) and biotic interactions (mycorrhizal type). In palaeoecological context, plant height, SLA, LDMC, seed size and mycorrhizal type can be assumed to be related to long-term climate variability and indicative of niche differentiation during favorable climatic conditions (Lacourse, 2009; Reitalu et al., 2015; Knight et al., 2020). Clonality, plant height, seed number and mycorrhizal type can be assumed to be associated with plant establishment in the harsh conditions of novel habitats (Ye et al., 2014; Pither et al., 2018) and with waterlogging in wetlands (Jabłońska et al., 2019).

There is a wide array of measures and several conceptual frameworks for estimating the functional and phylogenetic aspects of community assembly (see overviews in Vellend et al., 2011; Garnier et al., 2016). The functional structure of the community (functional diversity *sensu lato*, FD) can be characterized by average trait values and by measures estimating the variation in trait values (functional diversity *sensu stricto* or functional alpha diversity) (Garnier et al., 2016). Community weighted mean (CWM) trait values are widely used for evaluating links between community dynamics and ecosystem processes (Lavorel et al., 2008; Muscarella and Uriarte, 2016; Duarte et al., 2017). Functional alpha diversity (FDa) reflects the variability of traits among the coexisting species and allows to differentiate between functional divergence and convergence (Mason et al., 2005; de Bello et al., 2010; Laliberté and Legendre, 2010).

While stochastic effects also influence patterns of functional trait variation, selection and adaptation to changing environment will lead to non-random patterns. Environmental changes are assumed to select for or against species with certain traits and result in functional convergence (species being more similar in their traits than expected by random) (Pillar et al., 2009). Competition can be assumed to lead to functional divergence due to niche differentiation (species being less similar in their traits than expected by random) (Purschke et al., 2013). Phylogenetic diversity (PD) reflects the variability of phylogenetic distances among the coexisting species and helps to differentiate between phylogenetic divergence (coexisting species are phylogenetically more distant than expected by random) and phylogenetic convergence (coexisting species are phylogenetically more similar than expected by random) (Grime, 2006; Vellend et al., 2011). In the case of phylogenetically conserved traits, FDa and PD should show similar patterns but trait variation could also be large within phylogenetic lineages (Prinzing et al., 2008). In the current study, we follow the example of Reitalu et al. (2015) and use three measures to characterize the functional and phylogenetic structure of community assembly: (1) functional composition representing the community weighted mean trait values (CWMs), (2) functional alpha diversity (FDa) reflecting the variability of traits among the coexisting species, (3) phylogenetic diversity (PD) reflecting the variability in distances between species/taxa in a phylogenetic tree. We test the applicability of these measures for pollen-based biodiversity reconstructions.

In addition to CWM, FDa, and PD, we will use Ellenberg indicator values (EIVs) (Ellenberg et al., 1991) to characterize plant/pollen assemblages in terms of their environmental tolerances. EIVs provide an understanding of environmental differences between sites where environmental conditions cannot be directly measured, such as in palaeoecological reconstructions (Kuneš et al., 2011; Reitalu et al., 2015; Felde and Birks, 2019).

To study palaeoecological changes in biodiversity, calcareous spring fens are suitable environments – they are recognized as hotspots of biodiversity (Bedford and Godwin, 2003; Hájková et al., 2015) and provide continuous sediment archives that preserve proxy records for biodiversity and environmental reconstructions. Calcareous fens are of ecological interest to both palaeo- and contemporary ecologists as they provide data of recent and long-term vegetation changes (Almendinger and Leete, 1998; Hájková and Hájek, 2003; Grootjans et al., 2006; Blaus et al., 2019; Carvalho et al., 2019; Jabłońska et al., 2019). Human activities such as artificial drainage, agricultural practices, and eutrophication have negatively influenced the directional development of calcareous spring fens leading to a gradual disappearance of characteristic species or habitats (Stammel et al., 2003; Topiæ and Stanèiæ, 2006; Osadowski et al., 2018). There are several palaeoecological studies of calcareous fens in Europe (e.g., Pidek et al., 2012; Hájková et al., 2012, 2015; Gałka et al., 2018; Jamrichová et al., 2018; Blaus et al., 2019; Jabłońska et al., 2019) but none of them have investigated modern pollen-plant diversity relationships. The current study of modern pollen-plant diversity from spring fens provides valuable information for palaeo reconstructions of fen vegetation by examining the functional and phylogenetic aspects of fen biodiversity offering a new angle on the development of these unique environments.

We focus on modern pollen–plant diversity relationships in spring fens from two different regions in Estonia: southern Estonia and Saaremaa Island in western Estonia. Pollen data is derived from moss polsters and plant cover data is estimated from the surrounding vegetation. We compare taxonomic richness, vegetation composition, FDa, trait CWM, PD and EIVs in modern pollen and plant data (**Supplementary Figure S1**). We aim to test the following hypotheses:

(1) Pollen-based richness and composition estimates of woody and herbaceous taxa are positively associated with corresponding plant-based estimates but at different spatial scales;
(2) Pollen- and plant-based CWM, FDa, PD and EIV estimates are positively correlated both in woody and herbaceous taxa;
(3) Pollen–plant diversity relationships do not differ between study areas (southern Estonia and western Estonia).

Further, we will use the information from the modern pollen–plant diversity relationships and apply the CWM, FDa, PD, and EIVs that have significant modern pollen–plant correlations to sedimentary pollen data (**Supplementary Figure S1**). Using existing well-dated pollen dataset from Kanna spring fen in western Estonia (Blaus et al., 2019), we will reconstruct the changes in different diversity components over the 9000-year history of the Kanna fen. Kanna fen developed first as a small bog and a shift to minerotrophic fen started ca 7000 years ago (Blaus et al., 2019). We expect to find high values of CWM of traits related to survival in nutrient-poor habitats (clonality, LDMC, mycorrhizal type) and tendency toward functional convergence due to environmental filtering in the initial bog phase of the mire development. In the minerotrophic fen phase during the mid-Holocene warm period, we expect to find high values of CWM of traits related to competitive abilities (SLA, plant height, seed size) and a tendency toward functional divergence due to niche differentiation. Among the Ellenberg indicator values, we expect the reaction (R), nutrient availability (N) and temperature (T) values to show the highest rate of change through the fen development.

MATERIALS AND METHODS

Study Area

Pollen and plant data were collected from 34 calcareous fens in Estonia. Of the 34 sites, seven open and seven forested sites are located in southern Estonia (South region), with ten open and eight forested sites located in Saaremaa Island (West region) (**Figure 1**). The sites distributed between the two regions were located at least 2.5 km apart but the open and forested fens were sampled relatively close to each other (60 to 300 m apart). The terrain in the South region is predominantly dome-shaped consisting of undulating hillocky dead-ice landforms covered with forest and grasslands. Between hillocks, there are wet meadows, lakes and patches of mires

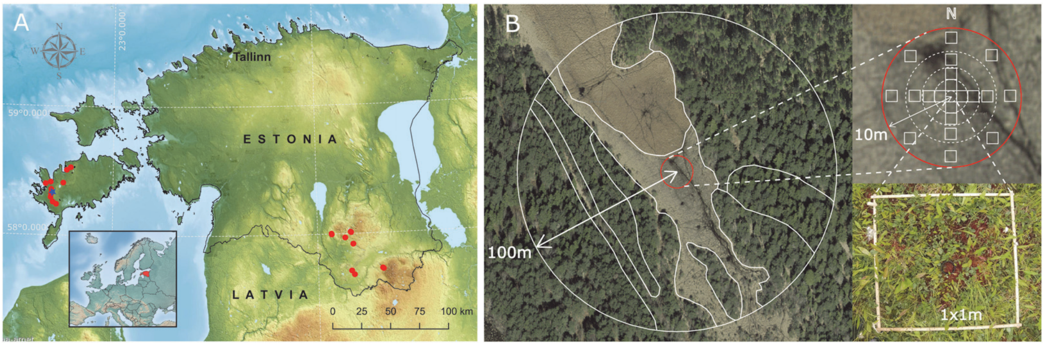

FIGURE 1 | Study area and sampling scheme. **(A)** Red dots indicate the sampled spring fens in southern Estonia and Saaremaa Island. Blue star marks the location of a Kanna spring fen used for sediment pollen based reconstructions. **(B)** The schematic overview of vegetation survey strategy modified from Bunting et al. (2013).

(transitional mires, bogs, fens, alder fens). About 70% of the region is covered with boreonemoral forest dominated by *Pinus sylvestris, Picea abies, Betula pubescens,* and *Alnus glutinosa.* Saaremaa is the largest island in Estonia, located in the Baltic Sea. The island is composed of Silurian carbonate rocks, primarily limestone, that are covered by glacial sediments reworked by fluvial geomorphology during the development of the Baltic Sea (Saarse et al., 2009). Over 40% of the island is covered with forests, predominantly pine forests (*Pinus sylvestris*), mixed forests and broad-leaved (deciduous) trees (e.g., *Quercus robur*) are found. Sandy soils (Podzols), peatland soils (Histosols), waterlogged soils (Gleysols) and lessive soils (Luvisols) comprise most of the soil cover in southern Estonia, whereas Limestone rendzinas (Rendzic Leptosols) and calcareous soils (Calcaric Regosols) are typical in western Estonia (Reintam et al., 2005). Both study areas are regions with the densest calcareous spring fen network in Estonia. The fens in West region in Saaremaa, have relatively uniform vegetation, dominated by *Schoenus ferruginaeus*, *Carex davalliana* and *Molinia caerulea*, while the fens in South region are more variable in species composition but usually dominated by *Carex* spp., *Molinia caerulea*, *Phragmites australis*.

Pollen Data

Moss polster samples (size of 5 cm in radius) were collected to determine the modern pollen assemblage from each of the fen sites ($n = 34$). The moss samples consisted of a relatively wide range of species, most abundant being *Calliergonella cuspidata*, *Plagiomnium ellipticum, Scorpidium cossonii, Campylium stellatum, Sphagnum subnitens.* In the majority of sites, the mosses did not form tense tussocks but the structure was relatively loose. For pollen analysis, only the green (living) upper part of the mosses was collected. Moss sample collection was synchronized with vegetation inventories. All the sampling and preservation of moss polsters followed the Crackles Bequest Project protocol (Bunting et al., 2013). For diversity reconstructions, we used sediment pollen assemblages from 53 sedimentary samples of Kanna spring fen (Blaus et al., 2019).

Both modern (polster) and historic (sediment) pollen samples were treated with HCl and 10% KOH followed by standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986; Faegri and Iversen, 1989). Both moss and sediment samples were examined under a light microscope at magnifications of 250, 400, and 1000x. Approximately 1000 terrestrial and aquatic pollen grains per moss polster and sediment pollen sample were counted (min = 920; max = 1115), spores of vascular plants were also counted.

The potential of pollen data to reconstruct vegetation proportions (and vegetation diversity) is hampered by interspecific differences in pollen production and dispersal causing over-representation of some taxa and under-representation of other taxa in pollen assemblages (Birks et al., 2016a). To reduce the influence of high pollen producers, we used Andersen's correction factors (Andersen, 1970) to downweight the dominant pollen taxa – a method that has been shown to improve the pollen-plant diversity relationships in earlier studies (Felde et al., 2016; Reitalu et al., 2019). All the pollen-based diversity estimates were, therefore, calculated on Andersen-transformed pollen counts.

Pollen data was divided into woody taxa (including trees and shrubs) and herbaceous taxa (including grasses and dwarf shrubs from the Ericaceae family) prior to the diversity calculations. Spores of pteridophytes are included in diversity calculations but for simplicity, we refer to the dataset as "pollen data" in the article.

Vegetation Data

Vegetation survey around each moss sample was carried out at the end of the flowering season during the second half of July and August (2017 and 2018). Survey timing and vegetation recording methodology followed Crackles Bequest Project protocol (Bunting et al., 2013), which is designed to produce vegetation abundance estimates in different distance classes in concentric areas around the pollen sample. Although vegetation mapping was conducted relatively late, only a few spring-flowering ephemerals (e.g., *Anemone*) might have been overlooked. At each site, vegetation was recorded within a 100 m radius around the moss sample (**Figure 1**). Within a 10 m radius, the vegetation was described in detail in five concentric areas at radii of 0.5, 1.5, 3, 6, and 10 m. In each 10 m area, twenty-one 1 × 1 m quadrats were systematically placed: one quadrat on top of the moss sample, four quadrats positioned at each cardinal direction at 1, 2.25, and 4.5 m from the central moss polster, and eight quadrats at 8 m distance from the center (**Figure 1**). In each 1 × 1 m quadrat, the percentage cover of all vascular plants was recorded. Additionally, species not occurring in the quadrats but within the circles were recorded. Between 10 and 100 m, vegetation types were mapped by using orthophoto maps (incl. infrared orthophoto maps) and field-work observations. The vegetation types were delimited keeping in mind the pollen perspective – for example, single trees and shrubs in open fen areas were mapped as separate entities because their role in pollen signal is potentially high (Bunting et al., 2013). Species composition of each vegetation type in 100 m radius was characterized in the field. For woody taxa, the percentage cover of each species was estimated. For herbaceous taxa, the Braun-Blanquet cover-abundance scale was used (Braun-Blanquet, 1964). The abundances were then translated to cover estimates within each vegetation type as follows: ±0.01%; 1 – 5%; 2 – 10%; 3 – 25%; 4 – 50%; 5 – 75%.

Altogether, plant cover estimates were calculated for nine different radii; 0.5, 1.5, 3, 6, 10, 25, 50, 75, and 100 m. For the radiuses up to 10 m, the plant cover estimates were averaged from the quadrats belonging to the particular radius. For the radiuses 25, 50, 75, and 100 m, the cover of each species was calculated from species cover estimates in different vegetation types weighted by the area of the vegetation type within the radius (**Figure 1**).

Similarly to pollen data, plant data was divided into woody taxa (including trees and shrubs) and herbaceous taxa (including grasses and dwarf shrubs from the Ericaceae family) prior to the diversity calculations.

Pollen–Plant Richness and Compositional Relationships in Different Radii

In order to clarify which spatial scale of vegetation is best reflected by modern pollen, we used plant cover estimates of nine different radii (0.5, 1.5, 3, 6, 10, 25, 50, 75, and 100 m) and plant richness of woody and herbaceous species was calculated for each radius. In addition to richness estimates, we used Principal Component Analysis (PCA) with Hellinger-transformed plant cover data (Legendre and Gallagher, 2001) to characterize the vegetation composition. PCA was performed separately for woody and herbaceous plant species in each radius. PCA ordinations of pollen data and plant data for two radii (6 m for herbaceous species and 100 m for woody species) are given in **Supplementary Figure S2**. Pollen richness estimates and PCA ordinations of Hellinger-transformed woody and herbaceous pollen percentages were used for comparison with corresponding plant estimates in different radii. Pollen-plant richness relationships in different radii were studied with the help of Pearson's correlation coefficients. Pollen–plant compositional relationships were analyzed with the help of Procrustes analysis (Gower, 2001) that introduces uniform scaling and rotation to minimize the squared differences between pollen-based and vegetation-based ordinations. The Procrustes symmetric sum of squares was used as "Procrustes correlation" to quantify the pollen–plant compositional relationship. We used the bootstrap method to provide confidence intervals for Pearson's correlation coefficients and Procrustes correlations (Davison and Hinkley, 1997).

The R environment (version 3.4.4) (R Core Team, 2018) was used for the analyses with packages "vegan" (Oksanen et al., 2017) and "boot" (Canty and Ripley, 2019) for ordination analyses and bootstrapping, respectively.

Functional Diversity and Ellenberg Indicators

To calculate the functional trait composition (CWM) and functional alpha diversity (FDa), we used nine traits that reflect different aspects of plant life history: clonality, height, specific leaf area (SLA), leaf dry matter content (LDMC), seed size, seed number, mycorrhizal type. For mycorrhizal type, we used the affiliation of plant species in three plant mycorrhizal types: arbuscular mycorrhiza (AM), ectomycorrhiza (EM) and ericoid mycorrhiza (ERM). Traits, the sources and availability of trait data and the functional significance of different traits are summarized in **Table 1**. Trait availability was the lowest for LDMC (only 40% of the species) and for SLA (62%), however, trait values were available for the most dominant taxa and we chose to include them in functional diversity calculations. Pteridophytes were included in trait assignments (except for seed weight and number).

Assigning trait values to pollen types that have only one species (for example, *Pinus* pollen type only includes *P. sylvestris* in Estonia) was straightforward. To calculate trait values for pollen types that included several different species the average trait values were calculated from the species recorded in our vegetation survey (for example, *Potentilla* pollen type includes *P. anserina*, *P. erecta*, *P. reptans*). Averages were also used for mycorrhizal types. In case one species can form two types of mycorrhizal associations, it is used in both estimates. Averaged trait values for pollen types are given in **Supplementary Table S1**.

Functional alpha diversity and CWM trait values were used to express FD. Species cover estimates and Andersen-transformed pollen percentages were used as weights for CWM calculations in plant and pollen data, respectively. "Functcomp" function in the "FD" R package (Laliberté et al., 2014) was used to calculate CWMs. FDa was calculated as an abundance weighted standardized effect size of mean pairwise distance (SESmpd) according to de Bello et al. (2016) for individual traits as well as all traits combined. Negative SESmpd indicates functional convergence and positive SESmpd indicates functional divergence; values ≤ -2 and ≥ 2 indicate significant ($P < 0.05$) convergence and divergence, respectively (Gotelli and Graves, 1996). All diversity measures were calculated separately for herbaceous and woody taxa.

TABLE 1 | Plant traits used to examine functional composition (CWM) and alpha diversity (FDa) of pollen and plant communities.

Trait	Source	Definition and functional significance	Trait availability (% of species/pollen)
Seed weight (g)	Kühn et al., 2004; Liu et al., 2008	Related to dispersal distances and seed nutrient provision strategy, larger seeds have a better chance to establish as seedlings but generally shorter dispersal distances (Kleyer et al., 2008).	78/87
Height (m) (AH)	Kleyer et al., 2008	Correlated with life span and time to maturity, reflecting species' ability to compete for light (Westoby et al., 2002).	86/99
Leaf dry matter content (mg/g) (LDMC)	Kleyer et al., 2008	The ratio of leaf dry mass to fresh mass, an indicator of plant resource use strategy. High LDMC reflects conservation of resources usually in unproductive environments (Garnier et al., 2001)	40/45
Specific leaf area (mm^2/mg) (SLA)	Kleyer et al., 2008	The ratio of leaf area to leaf dry mass. Responsive to light and moisture levels, related to drought stress (Cornelissen et al., 2003).	62/73
Seed number	Kleyer et al., 2008	Related to regeneration strategies, usually inversely associated with seed size (Saatkamp et al., 2018).	70/84
Clonality	Kühn et al., 2004	Derived from "plant reproduction type" with the original qualitative trait coded as follows: "mostly vegetatively, rarely by seed" = 0.9, "by seed and vegetatively" = 0.5, "mostly by seed, rarely vegetatively" = 0.1, "by seed" = 0. Reflects plant ability to spread vegetatively. Clonal structures can also serve as storage organs (Cornelissen et al., 2014).	100/100
Arbuscular mycorrhiza (AM)	Hempel et al., 2013; Chaudhary et al., 2016; Bueno et al., 2019	Association between plants and fungi defined by the presence of arbuscules in root cortex cells (Brundrett and Tedersoo, 2018). Most widespread among herbaceous plants. Related to acquisition of soil resources, mainly phosphorus (Brundrett, 2009).	98/100
Ectomycorrhiza (EM)	Hempel et al., 2013; Chaudhary et al., 2016; Bueno et al., 2019	Association between plants and fungi defined by the presence of a Hartig net and mantle (Brundrett and Tedersoo, 2018). Dominant mycorrhizal type in temperate and boreal forest ecosystems, related to acquisition of soil resources, mostly nitrogen (Brundrett, 2009).	98/100
Ericoid mycorrhiza (ERM)	Hempel et al., 2013; Chaudhary et al., 2016; Bueno et al., 2019	Formed between plants in the family Ericaceae and a diverse group of soil fungi. Represents adaptation to harsh, acidic and nutrient poor soils such as in bogs and heathlands (Cairney and Meharg, 2003).	98/100

In addition to the functional diversity, community weighted EIVs of light (L), temperature (T), continentality (K), moisture (F), pH reaction (R) and nitrogen or nutrient availability (N) were tested with modern pollen-plant relationships. EIVs were calculated as community weighted mean values similarly to CWM trait values described above.

Phylogenetic Diversity

Phylogenetic diversity (PD) is based on the phylogenetic relationship amongst the coexisting species in the community and is represented by a phylogenetic tree (Brocchieri, 2016). To estimate PD, we calculated the phylogenetic tree from the latest megaphylogeny for vascular plants in the "V.PhyloMaker" R package (Jin and Qian, 2019). Similarly to FDa, PD was expressed as the standardized effect size of mean pairwise distance (SESmpd). The mean pairwise distance was estimated across the whole phylogenetic tree by averaging all species pairwise distances (Pavoine and Bonsall, 2010). SESmpd was calculated by comparing the observed community mpd to the null distribution of randomized communities with equal species richness using the null model "taxa.labels," implemented in the "picante" R package (Kembel et al., 2010). SESmpd was calculated separately for woody and herbaceous species, and additionally for only angiosperms in both woody and herbaceous groups. Negative values of SESmpd indicate phylogenetic clustering (i.e., the coexistence of closely related species), whereas positive values indicate over-dispersion (i.e., the coexistence of distantly related species) (Webb et al., 2002). When pollen taxa included more than one species, we randomly chose one representative species from the list of species in our vegetation survey, for example, Primulaceae was represented by *Primula farinosa*.

Pollen-Plant Functional and Phylogenetic Diversity Comparisons

Based on our results of richness and vegetation composition analyses in different radii (**Figure 1**) and published literature on the source area of pollen for the herbaceous (Hjelle, 1998; Bunting, 2003; Bunting and Hjelle, 2010) and woody species (Broström et al., 2005; Mazier et al., 2008), we used two radii – 6 m for herbaceous species and 100 m for woody species – to test the modern pollen–plant functional and phylogenetic diversity and EIV relationships. To test for significant pollen-plant associations of CWM, FDa, PD, and EIV measures we used correlation analyses. Prior to the correlation tests, we tested for the normal distribution of the variables and several variables were log-transformed to achieve normality (**Tables 2–5**). Pearson's correlation coefficient was used when both variables were normally distributed. Alternatively, Kendall's Tau coefficient was used. To control for the effect of multiple tests (52 correlation tests altogether), we used Benjamini and Hochberg (1995) correction approach.

To test the influence of the region (West and South) on the pollen–plant diversity relationships, linear regression models were fitted for all pollen–plant diversity associations (CWM, FDa, PD, and EIV) with pollen diversity (pollenD) as the response variable and corresponding plant diversity (plantD), region (Reg) and their interaction term (plantD:Reg) as explanatory variables. The full model was given as: pollenD $\sim$ plantD + plantD:Reg. Backward selection with the function "stepAIC" [and with $k = 4$ (the multiple of the number of degrees of freedom used for the penalty)] in the "MASS" R package (Venables and Ripley, 2002) was used to clarify which combination of predictors significantly explained pollen richness. Assumptions for using linear models were tested. In some cases, outlier(s) were excluded in order to meet the assumptions for linear modeling (**Supplementary Figure S3**).

Sediment Pollen-Based Reconstructions

Finally, we applied the different diversity metrics (richness, CWM, FDa, PD) and EIVs tested in modern pollen–plant data to Kanna spring fen pollen sequence (53 pollen samples). Kanna spring fen is located in Viidumäe Nature Reserve (22.096721 °E; 58.325031 °N) in the western part of Saaremaa Island (**Figure 1**). The peat accumulation in Kanna began 9.2 ka (calibrated kilo annum before present). The age-depth model is based on 11 AMS radiocarbon dates and dates from spherical fly ash particles, peat accumulation was generally uniform and continuous (Blaus et al., 2019). Blaus et al. (2019) separated three main stages of the Kanna fen development: bog phase (9.2–7.2 ka) characterized by ombrotrophic conditions; fen phase (7.2–0.4 ka) characterized by minerotrophic conditions; and "recent phase" characterized by shifts in dominant fen taxa, possibly caused by human impact. These three development phases were also used in the current study to examine the functional (FDa, CWM), PD and EIV shifts associated with major changes in Kanna fen development. We used the diversity metrics which showed significant correlations between modern pollen and plant data (**Tables 2–5**) for reconstructions. Generalized additive models (GAM) with the 95% confidence intervals were used to fit the relationships of each diversity variable with time using the "mgcv" R package (Wood, 2011).

RESULTS

Pollen–Plant Richness and Compositional Relationships

The results of Pearson's correlations with bootstrapped 95% confidence intervals showed significant positive correlations

TABLE 2 | Correlation test results for pollen- and plant-based community weighted mean (CWM) trait values (functional trait composition).

Trait	Log	Correlation coefficient	*p*-Value/BH *p*-Value	LM results
Woody taxa				
AM		**r = 0.59**	**0.000/0.001**	**PlantD + Reg**
EM		τ = 0.21	0.086/0.135	PlantD
Clonality	log(pol), log(pla)	**r = 0.42**	**0.013/0.027**	**PlantD + Reg**
Seed weight	log(pol), log(pla)	r = 0.28	0.111/0.166	PlantD*Reg
Height		**r = 0.41**	**0.017/0.033**	**PlantD**
LDMC		**τ = 0.54**	**0.000/0.000**	**PlantD + Reg**
Seed number	log(pol), log(pla)	**r = 0.57**	**0.000/0.002**	**PlantD + Reg**
SLA	log(pol)	**r = 0.85**	**0.000/0.000**	**PlantD + Reg**
Herbaceous taxa				
AM		τ = −0.33	0.005/0.013	PlantD*Reg
EM		τ = 0.10	0.443/0.536	–
ERM		**τ = 0.51**	**0.000/0.001**	**–**
Clonality		r = −0.08	0.670/0.741	Reg
Seed weight	log(pla)	r = −0.15	0.410/0.521	–
Height	log(pla)	r = 0.36	0.034/0.061	PlantD
LDMC		**r = 0.56**	**0.001/0.002**	**PlantD**
Seed number	log(pol), log(pla)	**r = 0.40**	**0.018/0.035**	**PlantD**
SLA		**r = 0.66**	**0.000/0.000**	**PlantD*Reg**

Plant CWMs were calculated at 100 m for woody taxa and at 6 m for herbaceous taxa. Trait abbreviations are clarified in ***Table 1****. Column "Log" indicates for which variables plant (pla) and/or pollen (pol) data were log-transformed prior to the correlation test. When the tested variables were normally distributed, Pearson's correlation coefficient (r) was used, alternatively Kendall's Tau (τ) was used. Original p-Value and the Benjamini-Hochberg corrected p-Value (BH p-Value) are given. Results with BH p-Value < 0.05 for correlation are marked bold. Linear models (LM) results show whether corresponding plant diversity (PlantD), region (Reg) and their interaction (PlantD*Reg) were significant ($p < 0.05$) predictors of pollen diversity.*

TABLE 3 | Correlation test results for pollen- and plant-based functional alpha diversity FDa estimates.

Trait	Log	Correlation coefficient	*p*-Value/BH *p*-Value	LM results
Woody taxa				
AM		**$\tau = 0.33$**	**0.006/0.014**	**Reg**
EM		$r = 0.34$	0.046/0.080	PlantD*Reg
Clonality		**$\tau = 0.39$**	**0.001/0.003**	**PlantD**
Seed weight	log(pla)	$r = 0.02$	0.904/0.930	Reg
Height		$\tau = 0.10$	0.426/0.528	–
LDMC		$r = -0.03$	0.870/0.923	–
Seed number		**$r = 0.66$**	**0.000/0.000**	**PlantD**
SLA		**$r = 0.54$**	**0.001/0.003**	**PlantD + Reg**
All traits		**$r = 0.60$**	**0.000/0.001**	**PlantD**
Herbaceous taxa				
AM		$\tau = -0.20$	0.097/0.148	Reg
EM		$\tau = 0.14$	0.262/0.349	–
ERM	log(pol), log(pla)	**$r = 0.56$**	**0.001/0.002**	**PlantD**
Clonality		**$r = 0.43$**	**0.012/0.027**	**PlantD**
Seed weight		$\tau = -0.11$	0.377/0.489	Reg
Height	log(pol), log(pla)	$r = 0.10$	0.575/0.665	–
LDMC		$r = 0.38$	0.028/0.052	PlantD + Reg
Seed number		$\tau = -0.01$	0.930/0.930	–
SLA	log(pol)	**$r = 0.41$**	**0.016/0.032**	**PlantD*Reg**
All traits		$r = -0.02$	0.917/0.930	Reg

*Trait abbreviations are clarified in **Table 1**. Plant FDa was calculated at 100 m for woody taxa and at 6 m for herbaceous taxa. Column "Log" indicates for which variables plant and/or pollen data were log-transformed prior to the correlation test. When the tested variables were normally distributed, Pearson's correlation coefficient (r) was used, alternatively Kendall's Tau (τ) was used. Original p-Value and the Benjamini-Hochberg corrected p-Value (BH p-Value) are given. Results with BH p-Value < 0.05 for correlation are marked bold. Linear models (LM) results show whether corresponding plant diversity (PlantD), region (Reg) and their interaction (PlantD*Reg) were significant (p < 0.05) predictors of pollen diversity.*

TABLE 4 | Correlation test results between pollen and plant based phylogenetic diversity.

Trait	Log	Correlation coefficient	*p*-Value/BH *p*-Value	LM results
Woody taxa				
All		$\tau = 0.23$	0.053/0.089	–
Angiosperms		$\tau = 0.06$	0.638/0.721	–
Herbaceous taxa				
All	log(pol), log(pla)	**$r = 0.63$**	**0.000/0.003**	**PlantD*Reg**
Angiosperms		$r = 0.20$	0.262/0.349	–

*Plant PD was calculated at 100 m for woody taxa and at 6 m for herbaceous taxa. Column "Log" indicates for which variables plant and/or pollen data were log-transformed prior to the correlation test. When the tested variables were normally distributed, Pearson's correlation coefficient (r) was used, alternatively Kendall's Tau (τ) was used. Original p-Value and the Benjamini-Hochberg corrected p-Value (BH p-Value) are given. Results with BH p-Value < 0.05 for correlation are marked bold. Linear models (LM) results show whether corresponding plant diversity (PlantD), region (Reg) and their interaction (PlantD*Reg) were significant (p < 0.05) predictors of pollen diversity.*

for herbaceous taxa at the scales of vegetation estimate up to 6 m ($r = 0.42$–0.47, **Figure 2**). For woody taxa, the pollen-plant richness correlation was not significant at any of the vegetation estimate scales. Compositional relationships assessed by Procrustes' analysis showed positive associations for herbaceous taxa at all vegetation estimate scales. For woody taxa, the Procrustes correlations were significantly positive at the scales of 6 to 100 m.

Linear regression model showed that for herbaceous taxa both plant richness ($t = 4.26$, $p < 0.001$) and region ($t = -5.02$, $p < 0.001$) were significant predictors of pollen richness (determination coefficient $R^2 = 0.5$). Pollen richness increased with increasing plant richness in both regions and region South had significantly higher pollen richness than region West (**Figure 3**). In contrast, for woody taxa, the regression model did not indicate any significant variables describing pollen richness (**Supplementary Figure S1b**).

Pollen-Plant Functional and Phylogenetic Diversity Comparisons

Correlations between pollen–plant CWM traits of woody taxa showed significant positive pollen–plant associations for SLA, seed number, AM, LDMC, clonality and plant height (**Table 2**). Linear regressions for CWMs of woody taxa indicated that both plant-based CWM estimate and region (South vs. West)

TABLE 5 | Results of correlation tests between pollen-plant based Ellenberg indicators (EIVs) of light (L); temperature (T); continentality (K); moisture (F); soil pH reaction (R); nutrient availability (N) for woody and herbaceous plants.

Trait	Correlation coefficient	*p*-Value/BH *p*-Value	LM results
Woody taxa			
L	***r* = 0.72**	**0.000/0.000**	**PlantD + Reg**
T	***r* = 0.59**	**0.000/0.001**	**PlantD**
K	τ = 0.22	0.075/0.122	–
F	**τ = 0.41**	**0.001/0.002**	**PlantD + Reg**
R	***r* = 0.50**	**0.003/0.007**	**Reg**
N	*r* = 0.21	0.224/0.315	PlantD*Reg
Herbaceous taxa			
L	**τ = 0.66**	**0.000/0.000**	**PlantD + Reg**
T	**τ = 0.34**	**0.004/0.010**	**PlantD*Reg**
K	τ = 0.17	0.174/0.251	–
F	τ = −0.03	0.814/0.882	Reg
R	τ = −0.08	0.536/0.634	–
N	**τ = 0.39**	**0.001/0.003**	**PlantD**

*When the tested variables were normally distributed, Pearson's correlation coefficient (r) was used, alternatively Kendall's Tau (τ) was used. Original p-Value and the Benjamini-Hochberg corrected p-Value (BH p-Value) are given. Results with BH p-Value < 0.05 for correlation are marked bold. Linear models (LM) results show whether corresponding plant diversity (PlantD), region (Reg) and their interaction (PlantD*Reg) were significant (p < 0.05) predictors of pollen diversity.*

were significant predictors of pollen CWM (**Table 2** and **Supplementary Figure S3**). However, the interaction term of the region and plant CWM was not significant. For herbaceous taxa, pollen and plant CWM traits were significantly positively correlated for four traits: ERM, SLA, LDMC and seed number. For the herbaceous CWM of LDMC and seed number, the plant-based estimate was the only significant predictor of pollen-based CWM estimate (**Table 2**). For SLA, the pollen-plant CWM relationship differed significantly between the regions.

Pollen and plant functional alpha diversity (FDa) of woody taxa was significantly positively correlated for four traits: seed number, SLA, clonality and AM (**Table 3**). Linear models for FDa of woody taxa showed that for seed number and clonality, plant estimate was the only significant predictor of pollen diversity, for SLA and clonality, region was also significant (**Table 3** and **Supplementary Figure S3**). The correlation between pollen and plant FDa calculated across all traits was significantly positive for woody taxa and the association did not depend on the region. Herbaceous taxa showed positive significant FDa correlation for three traits: ERM, clonality and SLA. Linear regressions showed that for ERM and clonality, corresponding plant-based diversity estimate was the only significant predictor, for SLA the pollen-plant relationship differed between the regions (**Table 3**).

Phylogenetic diversity (PD) was significantly positively correlated between pollen and plant data only for herbaceous taxa, the significant correlation disappeared when pterophytes were excluded from the calculation (**Table 4**). Linear regression indicated that the slope of herbaceous pollen-plant PD relationship differed between the regions (**Table 4**). Woody taxa did not show significant PD correlations.

The Ellenberg indicator values (EIVs) based on woody taxa were significantly positively correlated between pollen- and plant-based estimates for the indicators of light (L), temperature (T), soil reaction (R) and moisture (F) (**Table 5**). Linear regressions showed that for woody taxa pollen-based T estimate, plant-based T was the only significant predictor, pollen-based L and F were significantly associated with corresponding plant-based estimate and region (**Table 5**). Ellenberg R estimate based on woody pollen taxa was significantly associated only with the region. EIVs based on herbaceous taxa were significantly positively correlated for L, T and nutrient content (N). Linear regressions showed that for herbaceous pollen-based N estimate, plant-based N was the only significant predictor, for L and T region was also significant (**Table 5** and **Supplementary Figure S3**).

Reconstructions in Time

Pollen richness of both woody and herbaceous taxa was the lowest in the beginning of the mire development (9-8 ka) and increased between 8 and 6 ka (**Figure 4**). Richness of herbaceous taxa was more or less stable until present day but richness of woody taxa decreased during the last 2 ka.

Community weighted mean values of AM, SLA and LDMC showed relatively similar trends for woody and herbaceous taxa through the fen development – AM and SLA had their maximum values between 6 and 2 ka and LDMC was the lowest during the same period (**Figure 5**). Plant height, seed number and clonality had contrasting trends through time for woody and herbaceous taxon groups. For woody taxa, clonality was the highest and height was the lowest between 7 and 2 ka. For herbaceous taxa, clonality was the lowest around 7 ka and the plant height had its maximum between 6 and 2 ka. Herbaceous seed number and ERM were the highest in the beginning of the study period (9-7 ka) (**Figure 5**).

Functional alpha diversity was the highest in the beginning of the study period for several traits: AM and clonality for both woody and herbaceous taxa, seed number and ERM for herbaceous taxa and SLA for woody taxa (**Figure 6**). During the middle of the study period, the FDa values of several traits decreased notably indicating a shift from functional divergence toward functional clustering. FDa values were close to or above 2 indicating significant functional divergence for seed number, AM and ERM in herbaceous taxa and for SLA and AM in woody taxa. The tendency toward functional convergence was detected only for woody taxon clonality.

Phylogenetic diversity showed relatively little change through time (**Figure 7**). The highest PD based on woody taxa was shown for the beginning of the study period (9-7 ka) when PD was close to or above 2 indicating phylogenetic divergence. When gymnosperms were excluded from the PD calculation, the values dropped drastically and indicated phylogenetic convergence throughout the study period (SESmpd < -2). PD of herbaceous angiosperms increased around 7 to 6 ka.

Ellenberg indicator valuess based on woody taxa indicated that moisture (F), light (L), and continentality (K) were higher during the beginning of the study period and close to the present-day and

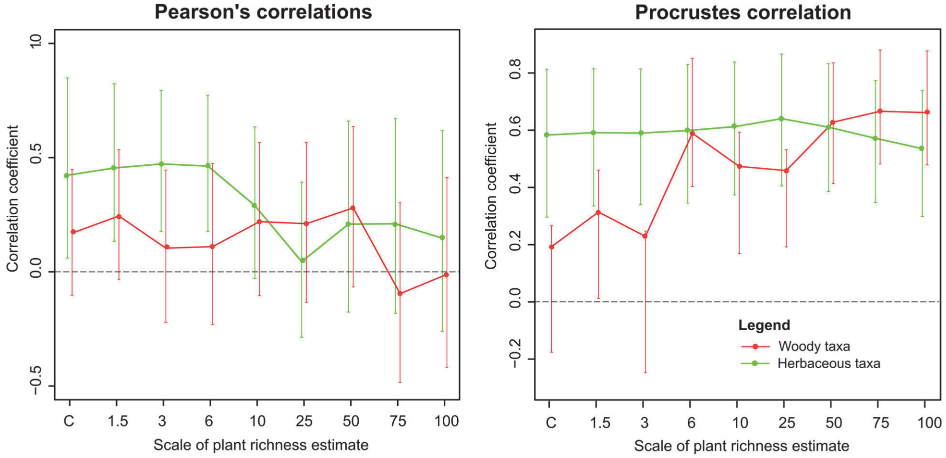

FIGURE 2 | Pollen–plant richness and composition correlations. *Y*-axis: the values of Pearson's correlation coefficients (for richness on the left) and Protest correlations (for vegetation composition on the right). *X*-axis: the radius of plant estimate. Vertical lines indicate bootstrapped 95% confidence intervals for the correlations.

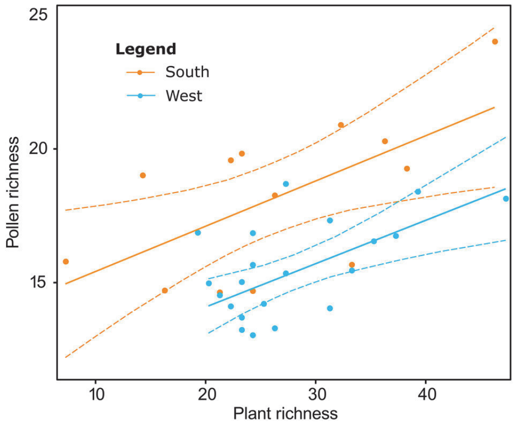

FIGURE 3 | Association between pollen-based and plant-based herbaceous richness showing the influence of a geographical region [South (orange) vs. West (blue)]. Herbaceous plant richness at 6 m scale is used. Linear model with backward selection of variables indicates that plant richness ($t = 4.26$, $p < 0.001$) and region ($t = -5.02$, $p < 0.001$) are significant predictors of pollen richness (determination coefficient $R^2 = 0.5$).

had the lowest values between 6-5 ka. For herbaceous taxa, the same indicators show little change or slight increase toward the present-day. The R for herbaceous taxa showed a strong increase from 7 to 5 ka, R for woody taxa increased during the same period but the change was less pronounced. Nutrient availability (N) increased according to both woody and herbaceous taxa between 7 and 5 ka but the N-value based on woody plants decreased and N-value based on herbaceous taxa stayed more-or-less stable from 5 ka until the present.

DISCUSSION

The use of sedimentary pollen to reconstruct functional and phylogenetic diversity is a relatively novel approach with previous studies focusing mainly on functional trait composition (community weighted mean trait values) (e.g., Reitalu et al., 2015; Brussel et al., 2018; Carvalho et al., 2019; van der Sande et al., 2019). In addition, Reitalu et al. (2015) calculated sedimentary pollen based functional alpha diversity and phylogenetic diversity that allow to study convergence and divergence patterns in community assembly. Our study adds to the evidence from modern pollen-plant studies of functional aspects (Carvalho et al., 2019) that both functional composition and alpha diversity can be studied using sedimentary pollen data and have the potential to provide valuable knowledge on palaeo-environments in addition to the conventional methods. However, not all studied variables had significant pollen-plant associations highlighting that uncritical use of different diversity metrics in pollen-based reconstructions may be misleading.

Taxonomic Diversity

Modern Pollen–Plant Richness and Composition

We hypothesized that modern pollen richness and composition reflect vegetation richness and composition, and that this relationship is dependent on plant group (woody vs. herbaceous) and spatial scale. The results partly supported our predictions showing that pollen richness of herbaceous taxa in moss polster samples best reflects herbaceous vegetation richness within 0.5–6 m radius and pollen-plant compositional relationship

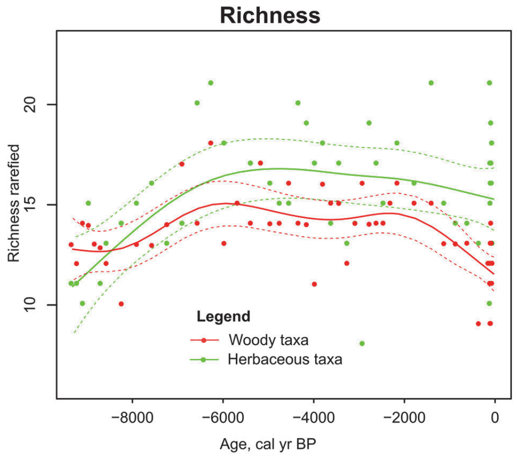

FIGURE 4 | Sedimentary pollen based richness in Kanna spring fen. Generalized additive model of herbaceous taxa (green line) and woody taxa (red line) in time. Dashed lines enclose the 95% confidence intervals of trend lines.

for herbaceous taxa was significant at all scales (**Figure 2**). The positive richness association existed in both study areas (**Figure 3**). This adds to the growing evidence that pollen taxonomic diversity is positively associated with the surrounding plant diversity (Urrego et al., 2011; Meltsov et al., 2012; Jantz et al., 2014; Matthias et al., 2015; Birks et al., 2016a; Mourelle and Prieto, 2016; Reitalu et al., 2019). In pollen analytical studies, the scale of the vegetation reflected in pollen sites is expressed as the relevant source area of pollen (RSAP). The RSAP is the area beyond which the pollen–plant correlation does not improve (Sugita, 1994). Our results for herbaceous taxa agree with existing studies from moss polsters where the RSAP of non-arboreal (non-woody) taxa is in the range of 0.5 – 10 m (Hjelle, 1998; Bunting, 2003; Bunting and Hjelle, 2010). When the RSAP calculation involves woody taxa, the RSAP estimations from the moss polsters are in the range of 300 – 400 m (Broström et al., 2005; Mazier et al., 2008) exceeding the scale of our vegetation survey. The lack of significant richness correlation for woody taxa in our study may be caused by the fact that our study radius was too small. However, the forests in the study regions are relatively uniform and increasing the radius would not add many new woody species. Pollen richness of woody taxa has been shown to be strongly positively associated with woody plant richness in a broad-scale study across entire N Europe (Reitalu et al., 2019) where the number of tree species varied from 3 to 80. In the current study, the richness of woody plant species varied from 11 to 22 and we can surmise that the variation in woody plant richness is too small to be reflected by the pollen data. However, the compositional relationship between pollen-plant data of woody taxa was significant at scales of 6 – 100 m radius indicating that vegetation composition of woody taxa is reflected by the pollen data.

While palaeo-diversity is traditionally calculated for all taxa combined (see overview in Birks et al., 2016a), our results support the studies suggesting to look at the diversity of wind-pollinated and insect-pollinated taxa (Meltsov et al., 2011) or at woody and herbaceous taxa separately (Carvalho et al., 2019; Reitalu et al., 2019). To conclude, dividing woody and herbaceous taxa in pollen-based diversity estimates improves our understanding of spatial scales reflected in palaeo-diversity reconstructions. Woody and herbaceous plants clearly form different functional groups (Díaz et al., 2016), and analyzing their diversity separately allows for better comparisons with contemporary plant ecological studies.

Sediment Pollen Based Richness Reconstruction

The richness of both woody and herbaceous taxa was relatively low in the beginning of the fen development from 9.2 to 7.2 ka and increased to the highest levels by ca 6 ka. Similar trend of increasing palynological richness in the beginning of the Holocene can be observed in other studies from Saaremaa (Poska and Saarse, 2002) and in the entire region (Reitalu et al., 2015). Palaeoecological studies from N Europe often show an increase in pollen richness during the last 2 or even 4 ka, associated with human-induced landscape opening (Birks and Line, 1992; Berglund et al., 2008; Reitalu et al., 2015). In the current study, herbaceous richness was relatively stable and woody richness decreased during the last millennia. Based on the modern pollen-plant correlations, herbaceous pollen richness from the fen samples is most likely to reflect local within-fen richness changes and taxa associated with agricultural activities and landscape opening coming from outside the fen are less likely to contribute. The decline in the richness of woody species is most likely a reflection of climate-driven decrease in broadleaved trees and increase in pine dominance that today has established a relatively homogeneous forest cover in the landscape.

Functional Diversity

Modern Pollen–Plant Relationships

We documented significant positive pollen-plant correlations for six CWM traits for woody taxa and for four CWM traits for herbaceous taxa (**Table 2**). Functional alpha diversity (FDa) had significant positive associations for five traits in woody taxa and for three traits in herbaceous taxa (**Table 3**). Woody taxa might show stronger relationships because fewer species are included in each pollen type, and when trait values for pollen types are calculated by trait averaging more information is lost for herbaceous species. In our dataset, the only woody pollen type including large number of species is *Salix* but for herbaceous taxa many pollen types have comparatively large numbers of species (e.g., Asteraceae $n = 27$; Cyperaceae $n = 51$; Poaceae $n = 41$; Orchidaceae $n = 17$). Similarly to our study, the modern pollen-plant study from fens in England showed that trait averaging for herbaceous pollen types might reduce the pollen-derived trait variability (Carvalho et al., 2019). Trait averaging is likely to have a stronger effect on the FDa (measured as mean trait distance between species/taxa in a community) than on the CWM that is already a result of averaging. FDa is particularly difficult to assess for taxon-trait combinations where the trait variation

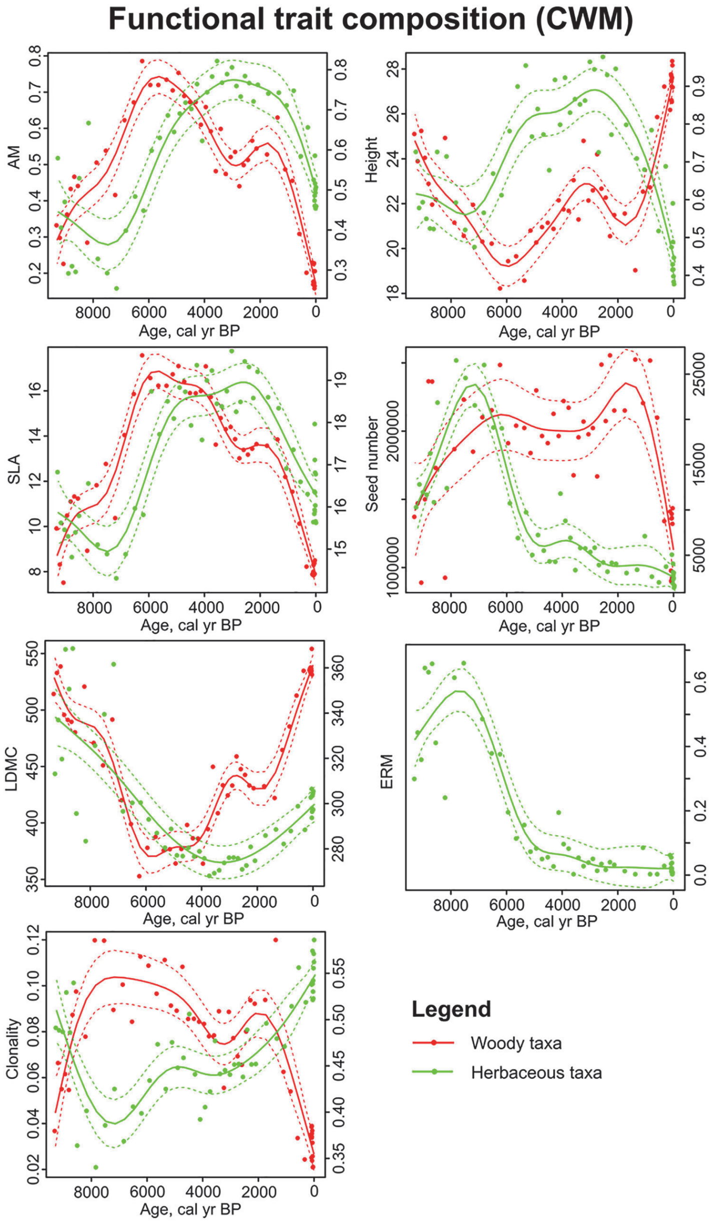

FIGURE 5 | Sedimentary pollen based reconstructions of functional trait composition (CWM) in Kanna spring fen. Generalized additive models in relation to time for woody (red line) and herbaceous taxa (green line). Red and green dashed lines enclose the 95% confidence intervals of trend lines. Traits of herbaceous taxa is plotted on the secondary y-axes. Abbreviations of trait names are explained in **Table 1**.

within pollen taxon is large (for example AM and plant height in Cyperaceae) leading to significant effects of trait averaging in pollen data. Even though mycorrhizal type, plant height and seed weight can be expected to be associated with waterlogging and nutrient stress in fen systems (Jabłońska et al., 2019), our modern pollen-plant analyses indicate that pollen might not be the best

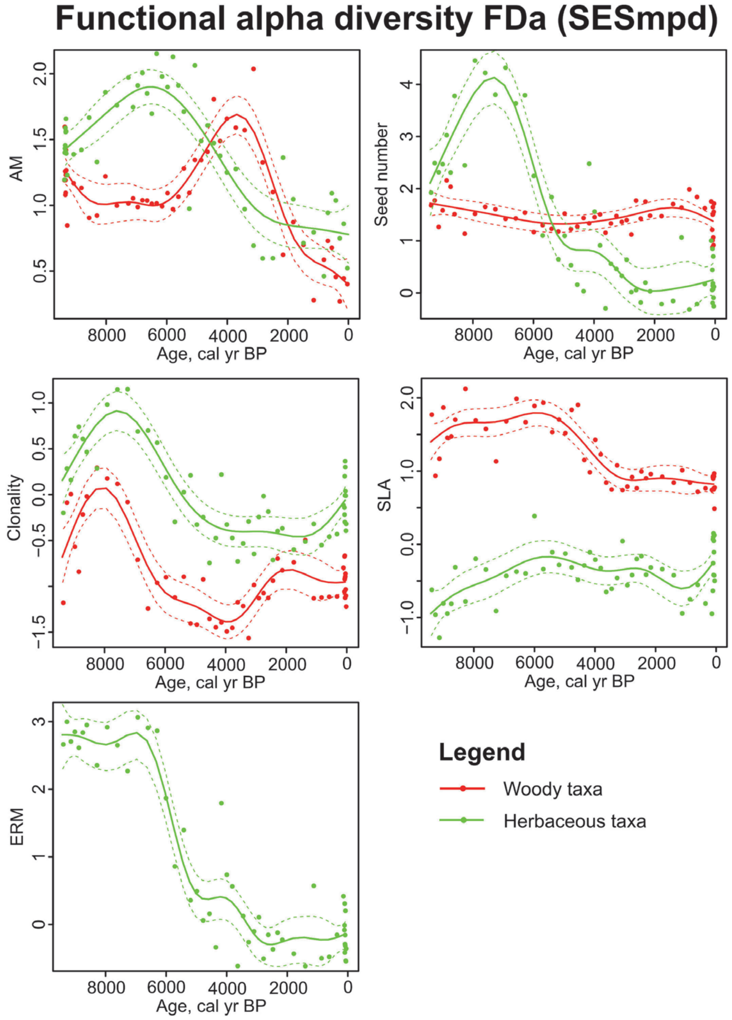

FIGURE 6 | Sedimentary pollen based reconstructions of functional alpha diversity (FDa) in Kanna spring fen. Generalized additive models in relation to time for woody (red line) and herbaceous taxa (green line). FDa is expressed as a standardized effect size of mean pairwise distance (SESmpd). Red and green dashed lines enclose the 95% confidence intervals of trend lines. Abbreviations of the trait names are explained in **Table 1**.

proxy to reconstruct the long-term changes in these traits. Plant macro remains (Felde and Birks, 2019; Jabłońska et al., 2019) or sedaDNA (Parducci et al., 2014) may give better taxonomic resolution. Another possible reason for the lack of significant correlation in modern pollen-plant data is related to short gradients within the study area, for example, EM associations are characteristic to the majority of present-day Estonian woody taxa and the CWM of EM varied between 0.8 and 1. Similarly to the missing woody taxon richness association, we can surmise that the variation is too small to be reflected by the pollen data and modern pollen-plant studies across larger geographic extent and longer diversity gradients would improve our understanding of the pollen plant diversity associations (Davis et al., 2013).

The diversity estimates that showed significant pollen-plant associations for woody taxa can be assumed to be associated with climate change (mycorrhizal type, clonality, height, LDMC, SLA), disturbance (height, clonality, seed number) and competitive strength (mycorrhizal type, height, clonality, SLA) (Cornelissen et al., 2003; Brundrett and Tedersoo, 2018). The woody taxon functional diversity – reflecting the landscape-scale changes – can therefore be used to reconstruct trait responses to climate change and long-term human disturbances and

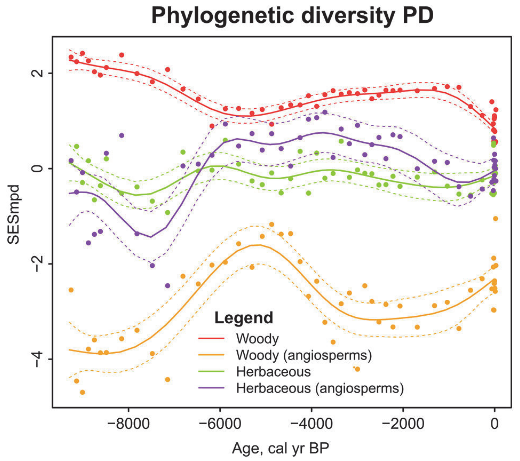

FIGURE 7 | Sedimentary pollen based reconstruction of phylogenetic diversity (PD) in Kanna spring fen. Generalized additive models in relation to time. Dashed lines enclose the 95% confidence intervals of trend lines.

to quantify the role of competition for woody community assembly (Reitalu et al., 2015). As herbaceous pollen diversity mostly reflects change in local fen community, we can expect traits to respond to waterlogging and nutrient stress (SLA, LDMC, clonality) (Jabłońska et al., 2019), changes in soil reaction (ERM), disturbance by drainage (seed number) and to indicate competition within the fen community (clonality, SLA) (Cornelissen et al., 2003).

We hypothesized that the pollen–plant diversity relationships do not differ between the study areas (southern Estonia and western Estonia). This was true for most of the functional diversity estimates – out of the traits that had significant pollen-plant correlations, the interaction with region was only significant for herbaceous SLA (**Tables 2–3**). The region effect on SLA is most likely the result of small variation in SLA in the fens of western region while in the southern region, there is much longer gradient in the SLA (**Supplementary Figures S3k,ab**). For the majority of traits, pollen-plant association was similar in both regions giving assurance that the diversity estimate can be used in palaeoreconstructions.

Sediment Pollen Based Functional Diversity Reconstruction

Woody taxa

The trait composition (CWM) of woody taxa showed low clonality, low proportion of AM associations, low SLA, and high LDMC during the first millennia of Kanna site development (9.2-7 ka) (**Figure 5**). Both SLA and LDMC have been widely used to reflect species' response to soil fertility and climate change (Cornelissen et al., 2003; Laughlin et al., 2010) with SLA being positively and LDMC negatively associated with soil fertility and warmer climate. After the ice retreated, Saaremaa was under the waters of the Baltic Ice Lake and the highest parts of the island emerged after the drainage of the lake at about 10.3 ka (Poska and Saarse, 2002). The peat in Kanna site began to accumulate right after the site emerged from the water due to land uplift (Blaus et al., 2019) and the beginning of vegetation development represents establishment of the pioneer communities. Early site development was dominated by *Pinus sylvestris* (Blaus et al., 2019) that is a good example of species with resource conservation strategy by reducing water loss as an adaptation to nutrient-poor environments through low LDMC (Qin and Shangguan, 2019). Clonality, which is associated with abiotic stress (Klimeš et al., 1997; Ye et al., 2014), reached maximum around 8 ka. However, the variation in clonality of woody plants is relatively small and is likely to be mainly associated with encroachment by clonal shrubs like *Salix* and *Myrica* in the wet depressions.

Most of the trait CWMs showed relatively rapid turnover during 8-6 ka and the period between 6 and 4 ka is characterized by the highest SLA and AM values and the lowest LDMC for the entire period. These responses are likely to be associated with fundamental trade-offs related to nutrient conservation, nutrient acquisition and turnover (Wright et al., 2004), that in turn reflect warmer and drier climatic conditions during the mid-Holocene (Hammarlund et al., 2002) when favorable conditions for expansion of thermophilous tree species existed in Estonia (Saarse and Veski, 2001; Sillasoo et al., 2007). High CWM of AM coincides with immigration of some AM associated species e.g., *Ulmus gabra* (Thomas et al., 2018) and *Fraxinus excelsior* (Seven and Polle, 2014) and the trends are in line with findings that show correlation between warmer temperature and general AM fungal activity (Compant et al., 2010; Hempel et al., 2013). Around 2 ka, CWM of SLA and AM declined rapidly coinciding with climate cooling in the area (Hammarlund et al., 2002) and spruce (*Picea abies*) expansion in Saaremaa (Saarse et al., 1999). Overall, the trait CWM changes of woody taxa in our study area are compatible with reconstructed biome dynamics for Northern Europe based on plant functional types (Davis et al., 2015).

The FDa values of woody plants were above zero for most of the traits except clonality (**Figure 6**). Although most of the values were below significant trait overdispersion, there was a strong overall tendency toward niche differentiation in AM, seed number and SLA, especially in the beginning of the study period. This pattern is most likely associated with the many fundamental functional differences between gymnosperms and angiosperms (Brodribb et al., 2012) allowing for their long-term coexistence.

Herbaceous taxa

Between 9 and 7 ka Kanna fen developed as a small bog with a high abundance of Ericaceae species, presence of Poaceae and Cyperaceae (Blaus et al., 2019) with a shift to minerotrophic fen starting around 7 ka. For the "bog phase" of the mire development, we expected to find trait composition indicative of low productivity and adaptations to acidic conditions. In accordance with the expectations, our results indicated high values for ERM, seed number, LDMC, clonality and low values for SLA and plant height (**Figure 5**). Several of the traits have been hypothesized to mitigate nutrient scarcity in wetlands

(LDMC, mycorrhizal type, clonality) (Moor et al., 2017; Jabłońska et al., 2019) and to be associated with waterlogging gradient (LDMC, SLA) (Violle et al., 2011; Baastrup-Spohr et al., 2015; Jabłońska et al., 2019). The "bog phase" was characterized by high proportion of Ericaceae taxa (that have low SLA, high LDMC and ERM) that are typical for nutrient poor and acidic soils (Cairney and Meharg, 2003).

Substantial changes in fen plant CWM traits during 7-5 ka coincide with the site transition to minerotrophic fen environment caused by the unique combination of climatic, topographic and hydrological conditions (Blaus et al., 2019). The "fen phase" of the mire development is characterized by increased water, calcium carbonate and organic matter content and occurrence of fen habitat specialists (e.g., *Potentilla erecta, Parnassia palustris*) as well as by high palynological richness (Blaus et al., 2019). High SLA and low LDMC during the fen phase are in good accordance with earlier studies showing that high SLA and low LDMC are associated with increase in soil reaction (Bartelheimer and Poschlod, 2015), in water and nutrient content (e.g., Díaz et al., 2004; Ordońez et al., 2010; Moor et al., 2015), anoxia (Klimkowska et al., 2019), organic matter accumulation (Nieder and Benbi, 2008), and species richness (Violle et al., 2011). High values for AM during the fen phase suggest similarly to Ramírez-Viga et al. (2018) that AM associations have an important role in wetlands.

After 2 ka, herbaceous CWM decreased for SLA and seed number but increased for LDMC and clonality. This functional change is related to the increasing proportions of Cyperaceae and the decline in the abundance of forbs that characterizes the "recent phase" of Kanna fen development (Blaus et al., 2019). Decreasing SLA and increasing LDMC have been associated with drier conditions in wetlands (Baastrup-Spohr et al., 2015). Jabłońska et al. (2019) showed that the importance of tussock-forming species with small clonal spread increased in fens prior to the termination of fen phase (and development of bog or mire woodland) and the reported functional changes might be an early "warning" for nature conservation. The actual reasons behind the recent functional changes and increase in Cyperaceae are rather unclear and it is difficult to draw a border between local and larger scale processes. Even if the changes are autogenic or successional these processes are usually following to allogenic disturbances (Bodini and Klotz, 2009). Besides, some studies have shown that climate induced hydrological changes in wetlands might have greater impact on plant community changes compared to autogenic processes (Wilcox, 2004; Dieleman et al., 2014).

Functional alpha diversity of ERM and seed number showed significant functional divergence (**Figure 6**). In grassland communities, functional divergence has been associated with niche differentiation at fine scales (within one square meter and less) where herbaceous species interact (de Bello et al., 2013). At larger spatial scales (within habitat patches), the functional divergence is likely a result of fine-scale within-habitat environmental heterogeneity where species with different traits occur side by side (de Bello et al., 2013; Bergholz et al., 2017). In addition to Ericaceae and other bog indicators, several typical fen species (*Potentilla*, *Parnassia*, *Cladium mariscus*) were present in low numbers in Kanna fen initial phase pollen samples (Blaus et al., 2019) and most probably grew on the edges of the small bog leading to the functional divergence pattern in the pollen signal.

Phylogenetic Diversity

Pteridophytes and gymnosperms, being evolutionarily distant from angiosperms, have a strong impact on the phylogenetic structure of the vegetation (e.g., Massante et al., 2019). Modern pollen-plant PD associations in our study were also strongly influenced by pteridophytes (especially ferns) and gymnosperms. Pollen-plant PD correlation was significant for herbaceous taxa but only when pteridophytes were included in the calculation (**Table 4**). Ferns and their spores were closely related between vegetation and pollen samples, meaning that if ferns were present in vegetation their spores occurred frequently in the moss polster.

Results of PD reconstruction in Kanna fen exhibited significant clustering (phylogenetic convergence) of woody taxa throughout the 9.2 ka when gymnosperms were excluded from the PD calculation but overdispersion (phylogenetic divergence) was evident when gymnosperms were included in the reconstruction (**Figure 7**). This pattern is consistent with the study of Reitalu et al. (2015) who showed that gymnosperms significantly increased the phylogenetic overdispersion. Massante et al. (2019) found that woody taxa are phylogenetically overdispersed at high latitudes compared to low latitudes, because after originating in the tropics, specific and distant lineages of woody taxa, i.e. gymnosperms, were able to adapt and survive extinctions in cold temperate conditions. The slight decrease in overdispersion in woody taxa in the mid-Holocene is probably caused by climate changes that shaped PD by colonization of broad-leaved species (Eiserhardt et al., 2015). Weakening of the clustering of woody angiosperms at the same time supports the studies that identify overdispersion as related to warm and nutrient-rich conditions (Cavender-Bares et al., 2004; Spasojevic and Suding, 2012). These favorable conditions for plant growth most probably weaken the effect of environmental filtering for specific phylogenetic clades with adaptations for extreme environmental conditions, and allow species from distant lineages to coexist.

The PD of angiosperm herbaceous taxa followed the main phases of Kanna fen development (**Figure 7**). During the ombrotrophic stage (ca. 9-7 ka), the PD of herbaceous angiosperms tended toward phylogenetic clustering, most probably influenced by the high abundances of different Ericaceae species (Blaus et al., 2019). Clustering has been observed for species pools of relatively young habitats (Lososová et al., 2015), and could be related to site emergence from the sea and extreme environmental conditions. Clustering has commonly been explained as a result of environmental filtering, since closely related species are usually expected to be ecologically similar (Webb et al., 2002). In particular, low nitrogen and soil reaction 9.2 ka might have led to environmental stress and filtering the lineages not adapted to particular conditions (González-Caro et al., 2014). However, the functional diversity reconstructions showed functional over-dispersion for several traits during the same period, indicating that the functional-phylogenetic diversity relationships are more complex.

The fen phase (ca. 7-2 ka) was characterized by relatively high PD as a result of phylogenetically distinct species co-occurring together, and may depend mechanistically on climate as shown by Svenning et al. (2015). This stage coincides with the increase in summer temperatures (Renssen et al., 2009) and the maximum of palynological richness (**Figure 4**). Empirical studies have justified that PD typically covaries with species richness at different scales (Mace and Purvis, 2008; Mooers et al., 2008; Kluge and Kessler, 2011), reflecting patterns of species migration and diversification (Forest et al., 2007). PDs of both herbaceous and woody taxa showed a slight decrease toward the present day, likely in response to the increase in Cyperaceae within the fen, and decline of broad-leaved taxa in the surrounding landscape, respectively. The decline also coincides with decreasing pollen richness. In contrast, Reitalu et al. (2015) showed a decrease in PD in spite of the increase in pollen-derived richness associated with human impact, particularly, the facilitated increase in ruderal communities. To conclude, PD can be reconstructed from pollen data at least to some extent, it has a different dynamic in time among the plant growth forms and our example shows that period of high taxonomic richness in the natural fen system is also characterized by high PD.

Ellenberg Indicator Values

The applicability of Ellenberg indicator values (EIVs) for different habitat types and in different regions in Europe has evoked considerable discussion in plant ecological literature (e.g., Schaffers and Sýkora, 2000; Diekmann, 2003; Smart and Scott, 2004; Williams et al., 2011; Bartelheimer and Poschlod, 2015). EIVs have been widely used in different mire systems to study a wide range of hypothesis (e.g., Cornwell and Grubb, 2003; Williams et al., 2011; Andersen et al., 2013; Gawenda-Kempczyńska, 2016; Klimkowska et al., 2019) and our findings add to those studies by showing the indicators that could be applied on sediment pollen and therefore could be used to interpret historical environmental gradients.

In current study, we found significant positive pollen-plant correlations for woody taxon EIVs of light (L), temperature (T), humidity (F), and soil reaction (R) (**Table 5**). Diekmann (2003) points out that short environmental gradients and within-sample heterogeneity may lead to unreliable EIV results. Because pollen samples of woody taxa are "sampling" vegetation from a relatively large area, results from heterogeneous study areas may be misleading as they can only provide average values for the entire area.

For herbaceous taxa significant pollen-plant associations were found for EIVs of light (L), temperature (T) and nutrient availability (N) (**Table 5**). Humidity (F) and soil reaction (R) that are recognized as main drivers of plant species diversity and composition of spring fen ecosystems (Hájková and Hájek, 2003; Sekulová et al., 2011) did not show significant pollen-plant associations. Our modern pollen-plant sampling scheme was designed to include open and overgrown fens but did not include large gradients of pH and humidity. The mean pH was 6.5 ± 0.7 and only three sites had pH < 6. Spring fens have relatively constant water availability, therefore moisture levels are high and do not vary much between the fens. The lack of positive pollen-plant associations for F and R may, therefore, be related to the relatively short gradient lengths in these indicators (cf. Diekmann, 2003). Ellenberg R has been shown to be relatively weakly associated with pH in wetlands (Williams et al., 2011) and might be better associated with calcium content (Schaffers and Sýkora, 2000). Our results showing significant pollen-plant correlations for L and N are promising as both indicators have

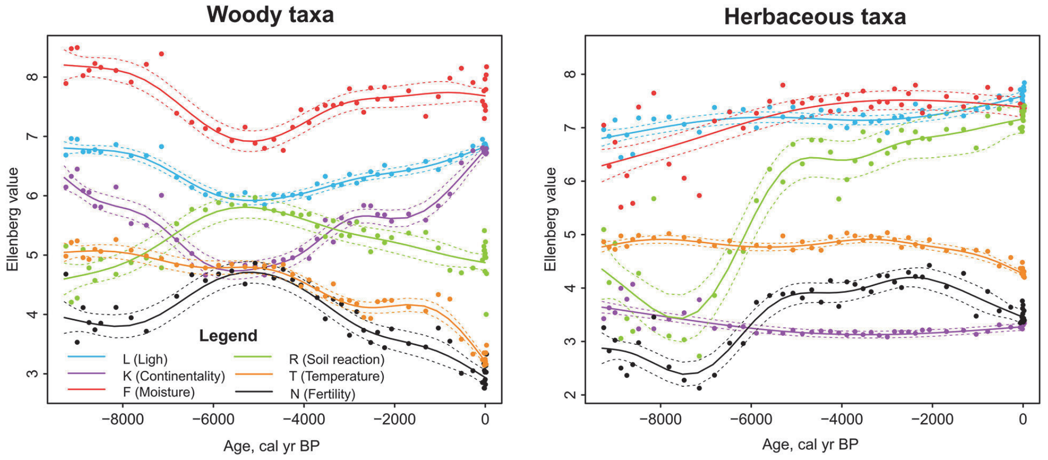

FIGURE 8 | Sedimentary pollen based reconstructions of Ellenberg indicator values (EIVs) in Kanna spring fen. Generalized additive models in relation to time. Dashed lines enclose the 95% confidence intervals of trend lines.

been shown to be significantly associated with major gradients in fen species composition (Kotowski and van Diggelen, 2004; Andersen et al., 2013) and have great potential for pollen-based palaeoreconstructions from fens.

The reconstruction of EIVs from Kanna sediment pollen shows that the beginning of site development is characterized by low Ellenberg values of N and R (**Figure 8**) – which is in line with functional characteristics of both woody and herbaceous taxa and with earlier interpretations of site development history (Blaus et al., 2019). Indicators of L, F and K revealed by woody taxa were relatively low from 7 to 3 ka coinciding with mid-Holocene thermal maximum (Davis et al., 2003) agreeing with the studies reporting dryer climatic conditions during the mid-Holocene (Hammarlund, 2003; Seppä and Poska, 2004). The opposite trends in R and L in the mid-Holocene support the results showing negative R and L correlations in forest, mostly because acido-tolerant but light-demanding species are outshaded by closed forest canopy (Diekmann, 2003).

From the herbaceous EIV reconstructions, R and N showed an increase between 7 and 5 ka (**Figure 8**) corresponding to the period when minerotrophic conditions developed in the fen. Ellenberg R has been shown to be well correlated with fen calcium carbonates (Schaffers and Sýkora, 2000) while Ellenberg N reflects biomass or fertility (Hill et al., 2000; Schaffers and Sýkora, 2000; Diekmann, 2003). Our results agree well with Bartelheimer and Poschlod (2015) who showed that N is positively associated with SLA and plant height among herbaceous species. High N coincides with high pollen richness and with high phylogenetic diversity of herbaceous taxa.

Temperature reconstructions from pollen data based on modern pollen calibration datasets are widely used in Quaternary palaeoecology (e.g., Seppä and Poska, 2004; Salonen et al., 2012). Our results together with earlier studies (e.g., Kuneš et al., 2011; Reitalu et al., 2015; Felde and Birks, 2019) indicate that there is also potential for reconstructing long-term changes in soil reaction (calcium content), fertility, moisture and light.

CONCLUSION

In a modern pollen-plant study from Estonian calcareous fens, our results suggest that while pollen of herbaceous taxa in fens reflects vegetation at local fen scale, the pollen of woody taxa is likely to reflect larger landscape scale forest vegetation. Dividing woody and herbaceous taxa in pollen-based diversity estimates improves our understanding of spatial scales reflected in palaeodiversity reconstructions. Woody and herbaceous plants clearly form different functional groups (Díaz et al., 2016), and analyzing their diversity separately allows for better comparisons with contemporary plant ecological studies.

Correlations between pollen- and plant-based estimates of functional and phylogenetic diversity indicated that pollen data reflected the functional and phylogenetic aspects of plant communities reasonably well. For most of the indicators pollen-plant association did not differ between the two study regions. However, not all tested variables exhibited positive modern pollen-plant associations. The CWM values were better reflected in pollen data than the FDa values based on mean pairwise distances between taxa in a sample. The interpretation of functional variables that have large variation within pollen types may be difficult because information is lost by averaging trait values for pollen types. Testing for various pollen–plant diversity associations in our dataset may have been partly hindered by relatively short gradients in diversity variables and we, therefore, encourage further studies of modern pollen–plant diversity relationships not only from fens but across various environments to help to increase the reliability of interpreting historical processes from sedimentary pollen data.

Reconstructions of different diversity aspects in Kanna spring fen through 9.2 ka of fen development showed that diversity of woody taxa was closely related to the main climate changes with the mid-Holocene warm period having contrasting functional and phylogenetic diversity values compared to both early- and late-Holocene. The largest changes in the FD and PD of herbaceous taxa were related to the bog-fen transition around 7 ka. Our results show that climate and other abiotic processes have considerably influenced community FD and PD through the 9.2 ka. FDa of both woody and herbaceous taxa indicated functional divergence for several periods of community development where coexisting taxa were less similar in their traits than expected by random.

To conclude, pollen-based functional and phylogenetic diversity estimates and EIVs provide valuable knowledge in addition to the conventional pollen analysis. The use of different diversity metrics helps to achieve a better understanding of environmental effects on different strategy mechanisms of plants and to better interpret long-term processes affecting community assembly in various palaeoenvironments.

DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the Dryad data repository the Dryad Digital Repository (doi: 10.5061/dryad.wstqjq2hh).

AUTHOR CONTRIBUTIONS

AB and TR were the principal conceivers of the manuscript with the study design and conceptual idea by TR and the leading of writing by AB, with the input from all authors. AB and TR conducted the fieldworks of modern vegetation and pollen sample data collection and performed the data analysis. JM provided the script for phylogenetic analysis. IH compiled mycorrhizal type data. PG, IH, JM, and SV reviewed the manuscript and contributed significantly with the comments and valuable insights. All authors contributed to the article and approved the submitted version.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2020.00207/full#supplementary-material

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Publication III

Blaus, A., Reitalu, T., Poska, A., and Veski, S., (2020). Mire development trajectories and related biodiversity changes over the last 10,000 years in western Saaremaa, Estonia. *Manuscript.*

Mire development trajectories and related biodiversity changes over the last 10 000 years in western Saaremaa, Estonia

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ABSTRACT

Mires are important habitats for their biodiversity but also vulnerable and clearly responding to climate changes and increasing human impact. Their sensitivity to temperature and groundwater level changes is causing the loss of habitat specialist species, overgrowing and habitat diminishing from the landscapes. Understanding mire development trajectories and related biodiversity changes in the past is highly important for the conservation planning of these threatened habitats. Present study uses data from modern pollen samples to study differences in pollen signal in different mire types (open and forested fens and bogs) and to clarify indicator pollen taxa for these mire types. The results from modern pollen samples allow to better interpret the sediment records and biodiversity changes in six mires in western Saaremaa, Estonia. Palynological richness and phylogenetic diversity as well as Ellenberg indicator values in different mire development phases are compared throughout the 10-thousand-year history of Saaremaa mires. We show that herbaceous pollen taxa allow to separate between forested fens, open fens and bogs and indicator pollen taxa can be associated with these habitats. The pollen of woody taxa is more related to landscape-scale and regional patterns and is not associated with local mire development. We show how mire development patterns that began around 10 000 years ago on Saaremaa, are linked to changes in groundwater level associated with different Baltic Sea stages. These fluctuations and calcareous bedrock are likely the main determinants of the fen type and environmental conditions at site initial development stages. Large differences in the timing of fen-bog transitions and periods of forest encroachment in mires suggest differences in mire responses to climatic changes and highlight the importance of local conditions and autogenic changes. We show that in general, fen phases of the mire development show higher local herbaceous richness and phylogenetic diversity than bog phases. Fen phases are characterized by higher Ellenberg values of R, N and F and by lower values of L and T than the bog phases of the same mires. Our results indicate that local pollen signal from mires adds valuable information to peatland development reconstructions allowing to separate between different mire types and to reconstruct past diversity and local environmental changes.

Keywords: Mires, Fen-Bog succession, Biodiversity, Palynology, Peatland, Phylogenetic diversity, Ellenberg indicator values

1. INTRODUCTION

Mires or peatlands host unique biodiversity, are important carbon sinks and provide many other crucial ecosystem services (Kimmel and Mander, 2010; Peterka et al., 2017, Harenda et al., 2018). The ecological and environmental significance of mires has been widely emphasized (e.g. Wu and Roulet, 2014; Hanis et al., 2015; Swindles et al., 2019). Global peatland distribution is uneven and approximately 95 % are concentrated in temperate climatic regions - from the middle to high latitudes, due to the generally cold-humid or mild-humid climate, which is suitable for peat accumulation (Treat et al., 2019; Xu et al., 2018). Different mire types like ombrotrophic bogs and minerotrophic fens diverge in their hydrological regimes and characteristic vegetation. However, their development trajectories can be very closely related and changes in allogenic and autogenic processes might result in the transition from one to another. Therefore, the boundaries between fens and bogs are not always clear and easily defined (Hughes and Dumayne-Peaty, 2002;

Väliranta et al., 2017). Classical mire development scenario begins with minerotrophic fen that develops into ombrotrophic bog - so called "fen-bog succession" (Hughes and Barber, 2003). However, in exceptional cases, opposite development has been recorded (Barber and Hughes, 1995; Hájková et al., 2012a; Blaus et al., 2019).

Bogs, which are usually poor in overall species richness compared to fens are habitats for several specialist species of high conservation interest, especially the bogs that are rich in ponds and flushes (Fontaine et al., 2007; Beadle et al., 2015). Natural fen systems harbor some of the most diverse plant communities in mid and high latitudes with many relict and endangered species. However, their biodiversity strongly depends on fen type, determined by nutrient availability (poor-rich fen gradient), hydrological regime and overgrowing by shrubs and trees (Hájková and Hájek, 2003; Locky and Bayley, 2006; Jabłońska et al., 2011). Evolutionarily, peatlands are relatively ancient habitats associated to Late-Tertiary (ca. 20 Mya), that are characterized by overdispersed phylogenetic structure with coexisting species belonging to distant phylogenetic lineages (Lososová, et al., 2015).

Degraded state of mires leads to a loss of characteristic diversity, reduced ecosystem multifunctionality (Robroek et al., 2017) and turns them into greenhouse gas emitters, particularly releasing carbon dioxide (CO_2) and methane (CH_4) (Couwenberg et al., 2011; Hooijer et al., 2012). High plant diversity is a cornerstone to maintain ecosystem services and almost any species has a significant impact on ecosystem functioning and services in different contexts (Isbell et al., 2011). For example, Robroek et al. (2017) showed that overall carbon-related sink functions are promoted by high diversity in mire communities. The biodiversity of mires is threatened by climate changes and the gradual but systematic habitat loss caused by anthropogenic land-use transformation all over the world (Koch and Jurasinski, 2015; Hughes et al., 2016; Sun et al., 2016; Chimner et al., 2017, Jurasinski et al., 2020). The ongoing climate change is believed to strongly influence the different types of mires in northern hemisphere with warmer climate accelerating fen-bog succession (Väliranta et al., 2017) and leading to overgrowing with woody vegetation (Pinceloup et al., 2020). Anthropogenic disturbances in open mires often accelerate habitat overgrowing with trees and shrubs (Barry et al., 2008; Sundberg, 2011). Scenarios of increasing woody vegetation through reduction of light availability trigger community changes of herbaceous species and bryophytes, reduce biodiversity and disrupt natural habitat functionality (Hooijer et al., 2006; Parish et al., 2008). Peat-related industries add another threat to mire habitats across many regions, including northern Europe. Exploitation of peatlands for industrial resources such as fuel, gardening, building materials, have transformed many peatlands beyond the recognition (Rotherham, 2020). To better understand future development trajectories and restore the degraded mires and their biodiversity requires an understanding of the historical development of these systems from different perspectives (Dobrowolski et al., 2019; Carvalho et al., 2019, Blaus et al., 2020; Jurasinski et al., 2020). Peatlands are regarded as natural archives storing information about past vegetation change, climate and other environmental changes and studying the plant remains (pollen, plant macroremains, sedimentary DNA) in the peat provides valuable historical perspective for biodiversity research and nature conservation (Davies and Bunting, 2010; Parducci et al., 2014; Greiser and Joosten, 2018).

Environmental gradients play an important role in determining plant community changes and species diversity patterns (Bedford et al., 1999; van der Hoek et al., 2004; Locky and Bailey, 2005). Wetness, light conditions, reaction (pH), temperature and nutrient availability have been mentioned as important environmental factors and drivers (or consequences) of peatland succession (Tuittila et al., 2007; Laine et al., 2018; Blaus et al., 2020). It is not always possible to measure the relevant environmental parameters and environmental indicator values such as Ellenberg indicators (EIVs) are, therefore, a useful tool in plant ecology and palaeoecology (Diekman, 2003; Felde and Birks, 2019, Blaus et al., 2020).

Sedimentary pollen data together with other proxies from peatland palaeoenvironments, have been used to infer wide range of knowledge. These studies provide information about mire development, such as long-term plant succession (fen-bog succession), climatic, environmental, and hydrological changes (Booth and Jackson, 2003; Jakab and Sümegi, 2010; Lamentowicz et al., 2019; Dobrowolski et al., 2019; Marcisz et al., 2020) and help to advise peatland conservation (Lavoie et al., 2003; McCarroll et al., 2016). However, the sedimentary pollen studies from mires are often focussing on the development of upland plant communities surrounding the mires and the pollen signal from within the mires is often regarded as "noise". Yet, the pollen signal in small sedimentary basins has been shown to reflect the local plant diversity and gives the possibility to study the changes within the mire (Carvalho et al., 2019; Blaus et al., 2020). More reliable palaeoecological interpretations can be obtained by using modern pollen-vegetation studies that help to inform the interpretation of the sediment cores in different spatiotemporal scales (Meltsov et al., 2011; Gosling et al., 2017; Carvalho et al., 2019; Blaus et al 2020). In the current study, we use modern surface pollen data and indicator taxon analysis to study the pollen signal from bogs and open and forested fens to better recognize and interpret mire stages and site openness in palaeodata.

Saaremaa Island provides a dense network of fen and bog habitats. Moreover, it is located in the Baltic region, which is characterized as being rich in specialist and relict species (Horsáková et al., 2018), therefore it is a good place to study different aspects concerning fen and bog systems, and their diversity. Palaeoecology and palaeogeography of Saaremaa since its emergence from the sea after the Last Ice Age ca 10000 years ago is relatively thoroughly studied (Saarse and Königsson, 1992; Veski, 1996; Poska and Saarse, 2002; Saarse et al., 2009). However, these studies are mainly focussing on shore displacement, regional or landscape-scale climate and evironmental changes and human impact - but the peatland development itself with its plant community shifts and diversity changes has not been in the centre of attention.

The current study brings together existing pollen data from six mires (both present day fens and bogs) in western Saaremaa. We study the pollen signal of woody taxa separately from herbaceous taxa (cf. Blaus et al., 2020). We expect the woody taxa to show regional changes and to be relatively similar among the peatlands, but herbaceous taxa to show varying vegetation and diversity changes depending on the local conditions within each peatland. The aim of the present study is to examine the changes in community composition and taxonomic and phylogenetic diversity related to fen-bog successions using pollen data. We use indicator species analysis to infer indicator pollen taxa for open and forested fens and for bogs to better understand the mire succession dynamics through the Holocene in western Saaremaa. More specifically, we address the following questions:

1) Can pollen signal separate between open and forested fens and bogs?
2) Have presently open peatlands been open throughout the Holocene?
3) Do mire succession and related environmental changes follow similar paths in different study sites?
4) Are the richness and phylogenetic diversity changes related to mire succession consistent among the studied mires?

2. MATERIALS AND METHODS

2.1. Study area

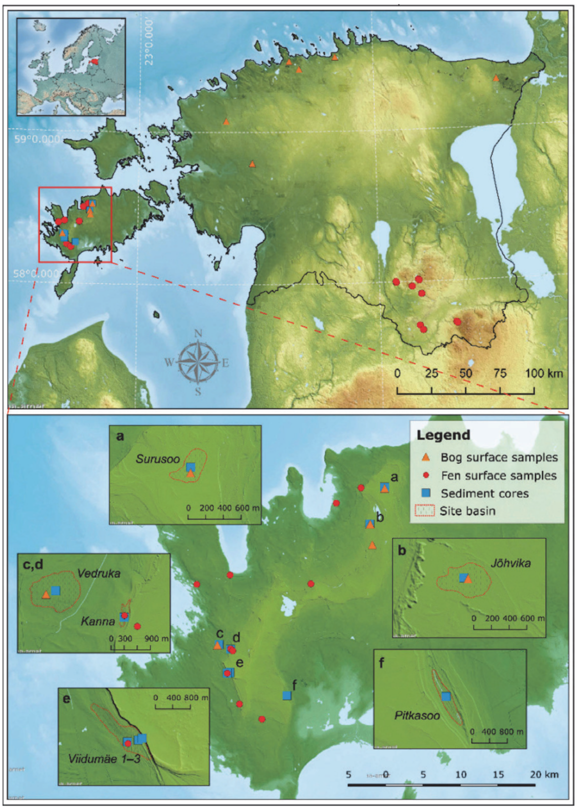

Figure 1. *Study area and insets of more detailed physiogeographic locations of studied sites: modern fen surface samples (red dots), modern bog surface samples (orange triangles) and sediment cores (blue squares).*

Our study comprises eight sediment cores from six peatlands in the western part of Saaremaa, of those, three are currently ombrotrophic bogs (Vedruka, Jõhvika, Surusoo), two are minerotrophic, base-rich fens (Viidumäe, Kanna) and one (Pitkasoo) is a drained mire with topsoil removed in 1960s (Fig. 1, Table 1). In the context of peatland development in Saaremaa it is important to emphasize the impact of water level changes in the Baltic Sea, an important factor initiating peatland development and shaping the present-day landscape and settlement distribution. The island has been significantly affected by the Baltic Sea basin water level changes caused by postglacial isostatic land uplift and the eustatic sea level changes. The highest part of the island (54.5 m a.s.l.), West Saaremaa Upland, started to emerge during Yoldia Sea (11.7-10.7 ka [calibrated *kiloannum* before present]) after the drainage of the Baltic Ice Lake (Saarse et al., 2009). The coastal formations of the Ancylus Lake (10.7-9.8 ka) are located between 35-25 m a.s.l. and the coastal formations of the Litorina Sea (9.8-4.5 ka) between 20.5 and 15.5 m a.s.l. (Saarse et al., 2009).

Table 1. *Sites discussed in the paper and their overall characteristics with the references on previous studies.*

Site	Coordinates	Description	Current status	Height (m.a.s.l)	Size (ha)	Depth (cm)	No of dates	No of samples	Modelled age in core bottom (ka)	Dominant species/current species cover	Pollen analyst	Publications
Pitkasoo	58.295756°N 22.082993°E	Ancylus Lake lagoon on SE slope of the West Saaremaa Upland.	degraded fen	25	24	306	7	73	10.52±0.15		Ivan Lundvall	Saarse and Königsson, 1992; Königsson et al., 1998; Poska and Saarse, 2002
Kanna	58.325031°N 22.096721°E	Coastal escarpment of Ancylus Lake on W slope of the West Saaremaa Upland	fen	29-31	5	221	11	53	9.27±0.09	*Schoenus ferrugineus, Carex panicea, C. hostiana, Phragmites australis, Molinia caerulea, Menyanthes trifoliata*	Ansis Blaus	Blaus et al., 2019, 2020
Surusoo	58.526016°N 22.422991°E	Above the Ancylus Lake shoreline. Shallow basin at the watershed area.	bog	43.1	112	229	15	62	10.83±0.39	*Calluna vulgaris, Eriophorum vaginatum, Pinus sylvestris, Empetrum nigrum, Vaccinium oxycoccos*	Siim Veski	Veski, 1996; Poska and Saarse, 2002
Vedruka	58.330069°N 22.061581°E	Litorina Sea terrace surrounded by abraded ridges.	bog	21.5	95	415	12	87	8.34±0.38	*Calluna vulgaris, Pinus sylvestris, Drosera rotundifolia, Empetrum nigrum, Eriophorum vaginatum, Rubus chamaeomorus, Andromeda polifolia*	Anneli Poska	Poska and Saarse, 2001
Jõhvika	58.484422°N 22.387027°E	In marginal area of the West Saaremaa Upland.	bog	32.5	10	200	5	25	9.65±0.29	*Calluna vulgaris, Pinus sylvestris, Ledum palustre, Vaccinium oxycoccos, V. vitis-idea, Empetrum nigrum, Phragmites australis*	Kersti Kihno	Hansson et al., 1996
Viidumäe 1	58.296566°N 22.088447°E	On the slope of Ancylus Lake coastal escarpment, depression between coastal ridges.	fen	32	0.6	80	1	8	3.39±0.04	*Molinia caerulea, Juncus subnodulosus, Filipendula ulmaria, Cirsium oleraceum, Myrica gale*	Kersti Kihno	Ratas and Kokovkin, 1989
Viidumäe 2	58.296293°N 22.086580°E	Depression between coastal ridges.	fen	30	1	100	1	10	2.99±0.05	*Molinia caerulea, Juncus subnodulosus, Schoenus ferrugineus, Myrica gale*	Kersti Kihno	Ratas and Kokovkin, 1989
Viidumäe 3	58.295756°N 22.082993°E	Litorina Sea coastal lagoon.	fen	24	2	170	2	17	7.58±0.06	*Schoenus ferrugineus, Phragmites australis, Potentilla erecta, Primula farinosa, Myrica gale*	Helle Mäemets	Ratas and Kokovkin, 1989

2.2. Data sources

The sedimentary pollen and spore data were gathered from existing published studies (Table 1), only the results of Viidumäe pollen study are published in a local project report (Ratas and Kokovkin, 1989). In all the studies, the sampling strategy followed similar methods and the cores were collected with the Russian type sediment corer. The pollen preparation and analyses in all sites followed the standard procedures (Erdtman, 1963; Berglund and Ralska-Jasiewiczowa, 1986; Fægri and Iversen, 1989). Based on the existing conventional and accelerator mass spectrometry (AMS) radiocarbon dates from each site, the chronologies were modelled and calibrated using the OxCal 4.2.4 deposition model (Bronk Ramsey 2008, 2009) and the IntCal13 calibration curve (Reimer et al., 2013). The modelled weighted average (WA) ages and associated standard errors at a 95.4% probability are used, expressed as "ka" - thousands of years (*kiloannum*) before present (where present equals to 1950). In addition to the existing dates, AMS radiocarbon dates were obtained from the bottom samples of Viidumäe 1 (Poz-123515; 3160 ± 30 BP) and 2 (Poz-124455; 2865 ± 30 BP) where the dates were previously missing. On average, ca 1000 terrestrial pollen grains were counted with minimum of 245 and maximum of 1434. Spores of sporophytes were counted alongside with pollen. In case of Viidumäe, the original pollen counts have been lost and the percentage data exists for trees and presence/absence data for herbaceous taxa. Viidumäe sites 1-3 were, therefore, omitted from analyses that required pollen abundance estimates.

For the modern pollen data, we used moss polster pollen data from open (n=17) and forested fens (n=16) in Saaremaa and southern Estonia from Blaus et al. (2020), where ca. 1000 pollen grains per sample were counted. The modern pollen data for the bogs was compiled from the topmost samples of 11 existing pollen studies from Estonian bogs (Koff, 1990; Hansson et al., 1996; Kihno, 1996; Kimmel et al., 1996; Poska and Königsson, 1996; Veski, 1998; Poska and Saarse, 1999, 2002, 2006) (Fig. 1), that have a varying pollen sum per sample (min=308, max=1673).

2.3. Pollen diversity and pollen-based Ellenberg indicator values (EIVs)

Pollen diversity was expressed as taxonomic richness (palynological richness) and as phylogenetic diversity. For palynological richness, we used rarefaction analysis (Birks and Line, 1992) limited to the minimum pollen sum (245) among all the samples in order to standardize the sampling effort. Palynological richness was calculated for woody and herbaceous taxa separately. To calculate phylogenetic diversity (PD), we used the latest megaphylogeny of vascular plants in the R package "V.PhyloMaker" (Jin and Qian, 2019). To reduce the influence of high pollen producers, we used Andersen's correction factors (Andersen, 1970) to downweigh the dominant pollen taxa (c.f. Felde et al., 2016; Reitalu et al., 2019). Andersen-transformed pollen percentages were used as weights in PD calculation. PD was calculated as standardized effect size of mean pairwise distance (SESmpd) using the averaging of all species pairwise distances across the whole phylogenetic tree (Pavoine and Bonsall, 2010). To calculate the SESmpd, we then compared the mean pairwise distances with equally species rich randomized communities in the "picante" R package (Kembel et al., 2010). PD was calculated separately for woody and for herbaceous taxa. Because inclusion of phylogenetically distant groups can have a large effect on PD (e.g. Massante et al., 2019), we calculated PD both for all taxa (including seedless vascular plants and gymnosperms) and for angiosperms only.

To characterize the environmental changes in the mires, we calculated community weighted means of Ellenberg indicator values (EIVs). Ellenberg indicator values (Ellenberg et al., 1991) are a numerical system that classifies species according to their ecological preferences (habitat niches) and thus allows to study different environmental gradients (Diekman, 2003; Bartelheimer and Poschold, 2016). To use it with pollen data we first calculated average indicator values for pollen taxa that include more than one species and then used Andersen transformed pollen percentages to estimate community weighted mean EIVs (cf. Blaus et al., 2020). We used the following EIVs: light availability (L), nutrient availability (N), moisture (F), temperature (T) and soil reaction (R).

2.4. Numerical analyses

Indicator value method (IVM) (Dufrene and Legendre, 1997; Dai et al., 2006) was used to determine the pollen taxa associated with the open and forested (overgrown) fens and with bogs. The indicator value is calculated based on “specificity” - taxon abundance in specific habitat and “fidelity” – taxon predominance in the habitat. The analysis was done with the R program version 3.6.1 (R Core Team 2019) using the “indval” function from the "labdsv" package (Roberts, 2006), only taxa with the significance level $p<0.05$ were selected.

Random forest classification method was used to test how well modern pollen data can separate between bogs, open and forested fens. “Random forest” is a classification method that is based on large number of individual decision trees (Breiman, 2001). We used “randomForest” R package (Liaw and Wiener, 2002) to create the classification models and their result output is given as a confusion matrix (Appendix 1). The models were processed with 500 classification trees and the number of variables tried at each split were 20 and 10, for herbaceous and woody taxa, respectively.

To analyze the overall trends in modern pollen data and in stratigraphical pollen data, we used principal component analysis (PCA). Pollen percentage data was Hellinger-transformed prior to the PCA. Hellinger transformation is a routinely used standardization method in community ecology (Legendre and Gallagher, 2001).

Cluster analysis with temporally constrained hierarchical clustering (CONISS) (Birks and Gordon, 1985) based on Bray-Curtis vegetation dissimilarity (Faith et al., 1987) was used to classify the stratigraphical pollen data. Broken stick method (Bennett, 1996) was used to assess the number of significant clusters. R-package “rioja” (Juggins, 2017) was used for cluster analysis.

To study the relationships between diversity estimates (richness and PD) and environmental gradients (EIVs), Pearson’s correlation tests were used. In order to account for site differences in correlation, we calculated “partial correlations” by first performing a linear regression with diversity as response variable and “site” as explanatory variable and thereafter used the residuals from the regression to calculate the correlations with EIVs. Benjamini and Hochberg (BH) adjusted p-values for multiple comparisons of correlations (Benjamini and Hochberg, 1995) were used to assess the correlation significance.

Generalized additive models (GAM) were used as a smoothing function for the palynological richness, PD and EIV reconstructions through time (Wood, 2017). To test whether diversity estimates and EIVs differed significantly between fen and bog phases, we used the four sites which had both fen and bog phases (Vedruka, Kanna, Jõhvika and Surusoo). We used linear mixed effects (LME) models with Site as random factor, temporal autocorrelation function included and “Fen vs Bog” as explanatory variable.

3. RESULTS

3.1 Classification and patterns of modern surface samples

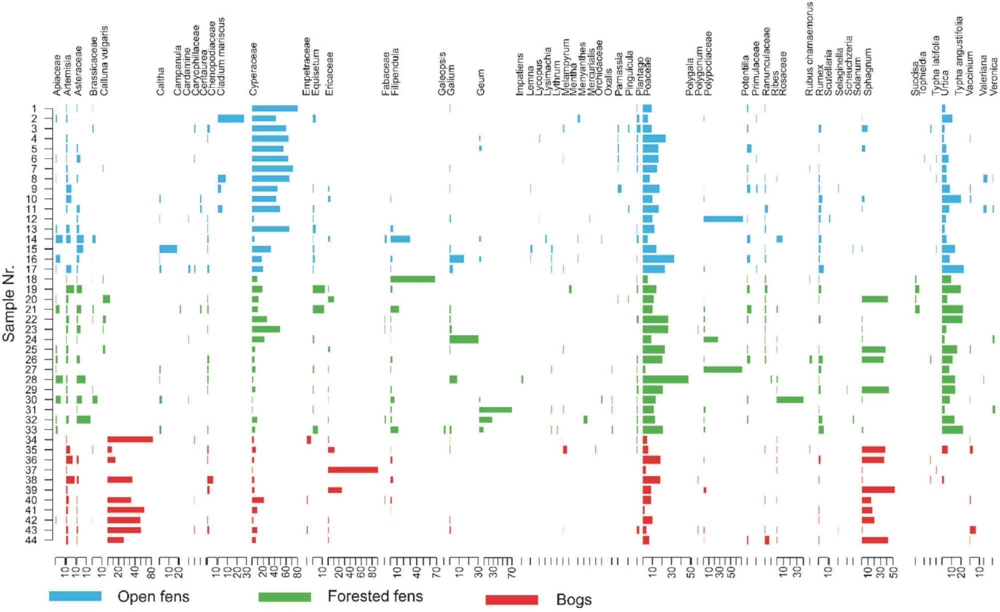

Figure 2. *Pollen/spore percentages of dominant herbaceous taxa in the modern surface samples from the open and forested fens and from the surface bog samples. Percentages of spores are expressed in relation to pollen sum.*

Pollen/spore percentages of herbaceous taxa indicate that the difference between bogs and fens is clearer than the difference between open and forested fens (Fig. 2). However, pollen of Cyperaceae dominate open fen samples (approx. 60-80%) together with *Cladium mariscus*, *Caltha* and *Parnassia.* Cyperaceae pollen is clearly less abundant in forested fens and *Filipendula* and *Geum* appear in higher abundances. *Calluna vulgaris* is clearly dominating bog samples (up to 80%) with some input of other Ericaceae pollen and *Sphagnum* spores. In addition, some forested fen samples have relatively high abundance of *Sphagnum* spores comparable to bog samples.

Results of Random Forest classification show that herbaceous taxa are more reliable to classify open fens, forested fens and bogs (Appendix 1). The error rate estimates show that 25 % of points are misclassified using herbaceous taxa but the error rate reaches 52% for woody taxa. When based on herbaceous taxa, bogs are classified with smallest classification errors (17%), classification errors of open and forested fens based on herbaceous taxa are 29% and 27%, respectively.

Table 2. *List of pollen/spore taxa associated to open fen, forested fen and bog habitats based on modern pollen samples and indicator value method (IVM) for both herbaceous and woody taxa. Only taxa with significance levels p< 0.05* are given.*

Taxa	Habitat type	Indicator value (IV)	*p*-value	Frequency (F)
Cyperaceae	Open fen	0.659	0.002	44
Parnassia	Open fen	0.322	0.015	7
Primulaceae	Open fen	0.235	0.032	4

Frangula	Forested fen	0.324	0.009	6
Prunus	Forested fen	0.292	0.014	6
Oxalis	Forested fen	0.266	0.010	4
Succisa	Forested fen	0.266	0.016	4
Sorbus	Forested fen	0.247	0.036	7
Sphagnum	Bog	0.785	0.001	27
Calluna vulgaris	Bog	0.743	0.001	15
Ericaceae	Bog	0.625	0.005	17
Vaccinium	Bog	0.369	0.013	10
Empetraceae	Bog	0.25	0.029	3

Indicator value method (IVM) exhibits 3-5 statistically significant ($p<0.05$) predictors of specified habitats (Table 2). Based on the IVM results Cyperaceae is recognized as the main indicator of open fen habitats with IV=0.659, p=0.002, even though Cyperaceae is present in all samples (F=44). Although relatively rare in modern samples, *Parnassia* and Primulaceae (F=7 and F=4, respectively) contribute as indicators of open fen habitats. No dominant indicator can be associated with forested fen habitats and taxa such as *Oxalis* and *Succisa* together with woody taxa *Frangula*, *Prunus* and *Sorbus* have similar indicator values (IV between 0.25 and 0.32). *Sphagnum* and *Calluna vulgaris* have highly significant indicator values for bog habitats (IV 0.79 and 0.74, respectively). Additionally, Ericaceae, *Vaccinium* and Empetraceae contribute to bog classification.

Results of PCA of modern pollen data suggest that woody taxa do not differ between open fens, forested fens and bogs with no clear PC axes associations (Fig 3). Whereas herbaceous taxa reasonably well demonstrate how specified habitats vary with respect to species composition on PCA ordination. Axis 1 explains 26% of variation and accounts for fen-bog gradient, whereas Axis 2 explaining 15%, is associated with open-forested fen gradient.

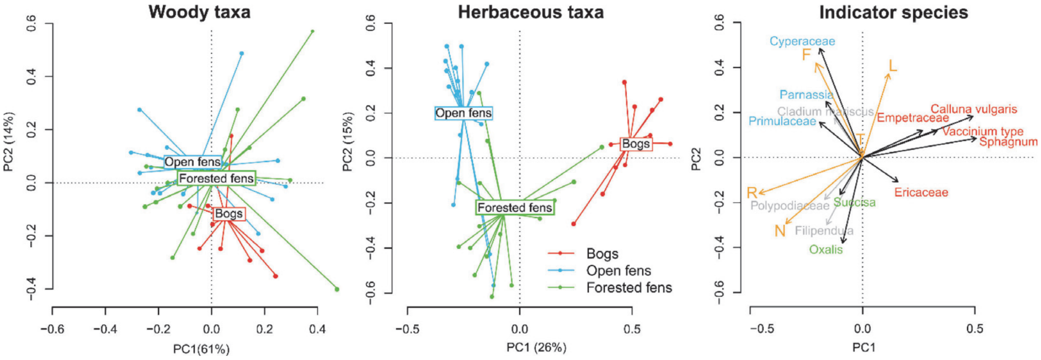

Figure 3. *PCA of fen and bog surface sample data separately for woody taxa (left) and herbaceous taxa (middle). Rightmost panel shows fitted indicator species and environmental gradients on PCA of herbaceous taxa. Taxa are colored according to the associated habitats: open fens (blue) forested fens (green), bogs (red), based on IVM. Environmental indicator values (R - reaction, N - nutrient availability, T - temperature, L - light and F - moisture) are in orange. Grey indicates the species that have strong association with these habitats based on PCA analysis but where not recognized by IVM.*

Fitted indicator species on herbaceous PCA are in line with the results of Indicator value analysis showing that Cyperaceae, *Parnassia* and Primulaceae are associated with open fens, *Succisa* and *Oxalis* with forested fens, but *Calluna vulgaris*, Empetraceae, *Vaccinium* and

Sphagnum with bogs, whereas Ericaceae are in-between bogs and forested fens. In addition, PCA ordination of herbaceous taxa shows that *Cladium mariscus* is associated with open fens, Polypodiaceae and *Filipendula* to forested fens; however, these taxa were not highlighted by the IVM.

3.2. Classification and patterns of sediment pollen data

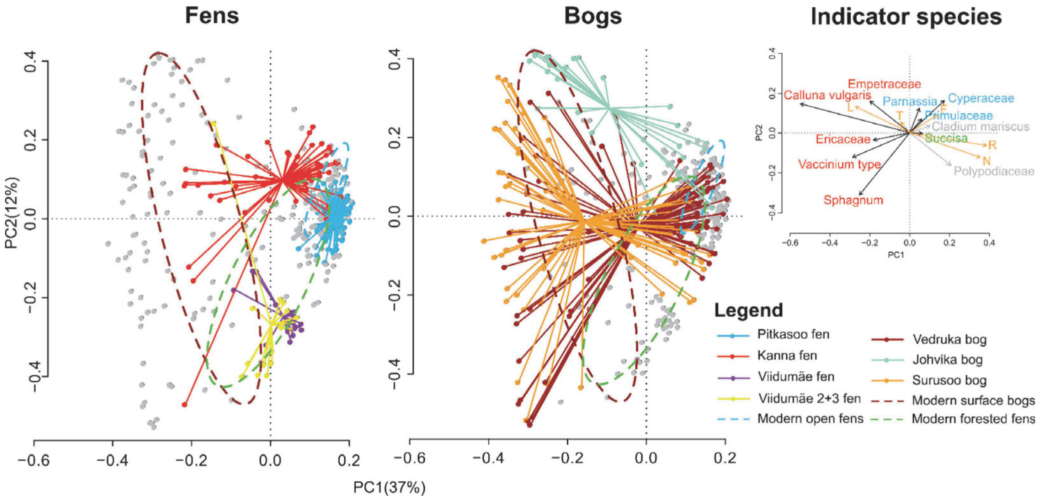

***Figure 4**. PCA of herbaceous taxa from sedimentary pollen records with highlighted present-day fens (on the left) and present-day bogs (in the middle). Dashed ellipses indicate the ordination space occupied by samples from modern bogs, open and forested fens (ellipsoids exhibit 95% confidence intervals). In the right upper corner, indicator species are shown colored according to the associated habitats: bogs (red), open fens (blue) forested fens (green), grey highlights the species that have strong association with modern PCA axes but where not recognized by indicator analysis*.

PCA results of sediment pollen data (Fig. 4) show that the first ordination axis is associated with the fen-bog gradient with fen samples at the right side on the PCA plot and most of the bog samples occupying the left side of the ordination plot. Both fen and bog samples are stretched vertically along PCA axis 2. Indicator species along axis 2 are *Sphagnum* in one end and *Calluna vulgaris* with *Empetrum* in the other end. Modern day bog and fen samples have strong Axis 2 association but are situated in opposite directions.

3.3. Trajectories of mire development

Implemented time trajectories on the PCA of herbaceous taxa allow to track the changes and the development of the individual sites (Fig. 5). Results show that different sites have experienced different magnitude of vegetation turnovers. First PCA axis is associated with fens on the positive end of axis and bogs in the negative end (Fig. 4). Hence, Pitkasoo has been a fen since the beginning of the sediment accumulation with very little change in vegetation composition. Surusoo and Jõhvika have developed as fens in the beginning of the site development but have experienced turnovers towards the bog type habitat. Vedruka and Kanna sites have had similar properties at the beginning of their origin but have relatively different pathways to the current state. Viidumäe site is somewhat different compared to others, and according to modern day samples (Fig. 4), occupies the space of modern forested fens. In general, according to the PCA, present-day bogs have experienced greater vegetation change than present-day fens.

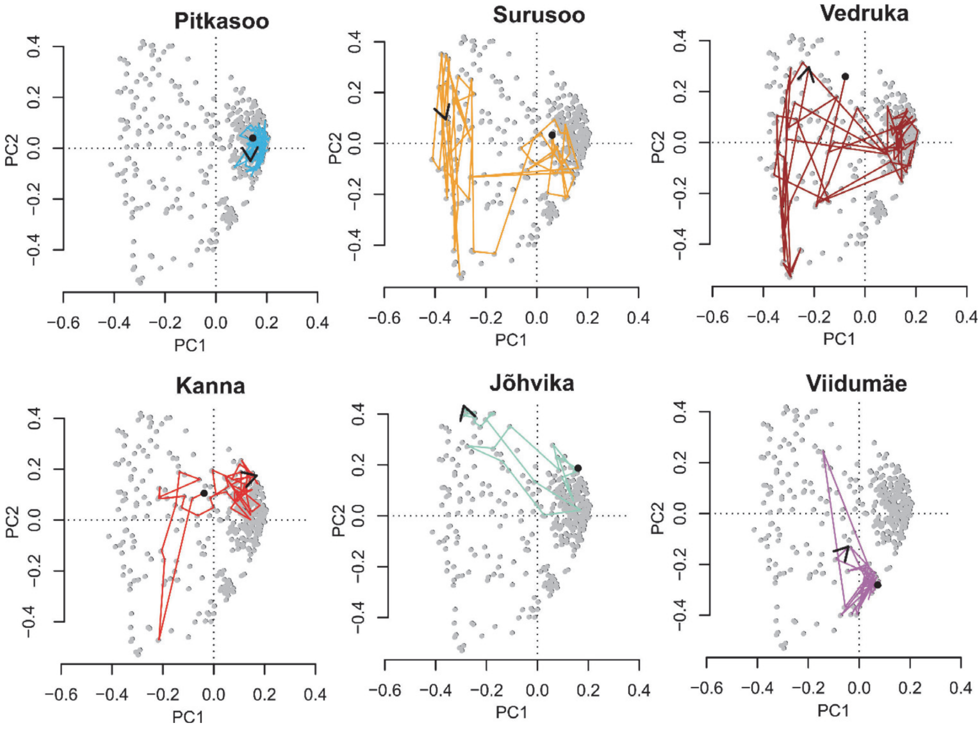

Figure 5. *PCA ordination of sediment data for herbaceous taxa with time trajectories. The black dot indicates the beginning of site development and the arrowhead indicates the topmost sample. The PCA axes are the same as on Figure 4.*

3.4. Vegetation turnovers

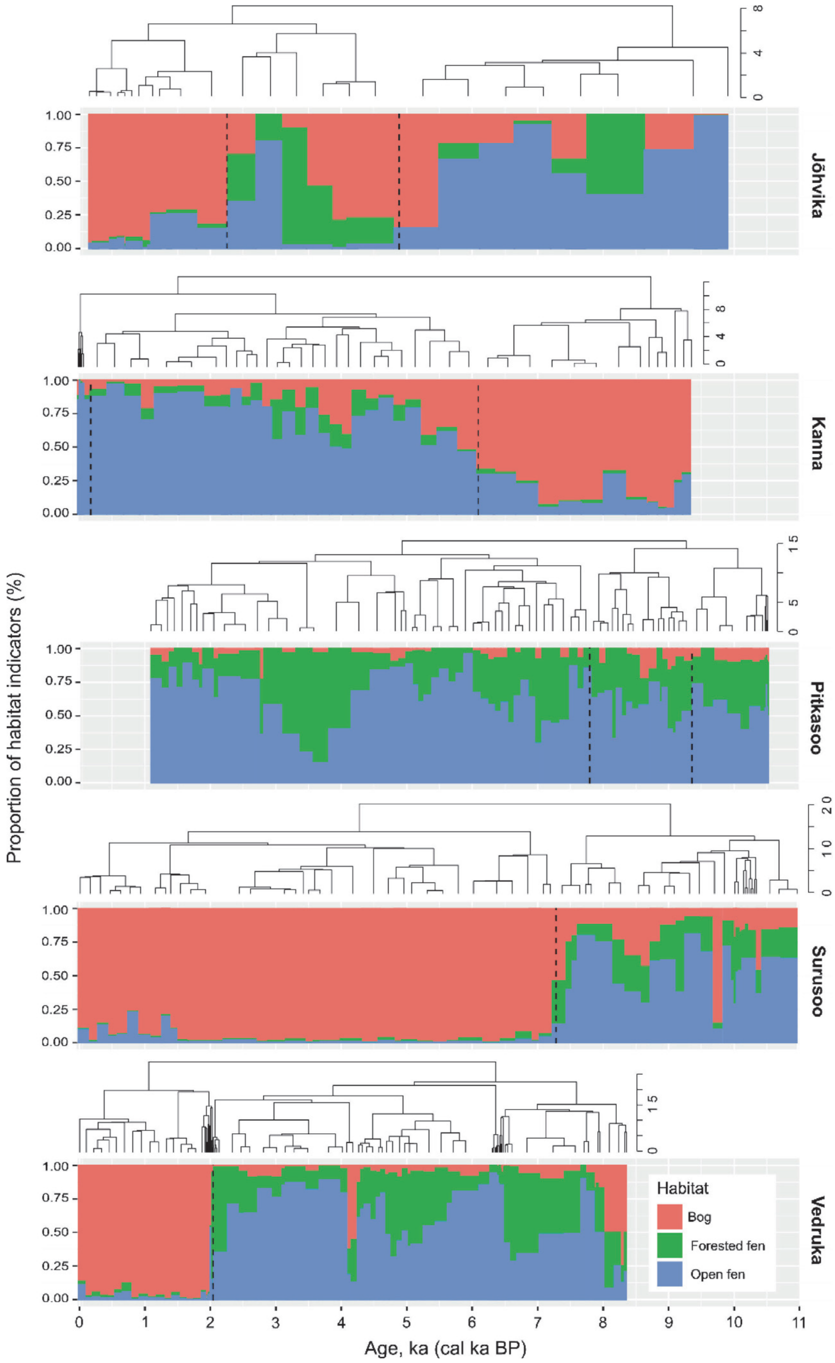

Figure 6. *Abundances of different habitat indicators throughout the development of sites and constrained hierarchical clustering based on herbaceous taxa with borders of significant clusters (black dashed lines). Proportion of habitat types is calculated based on indicator taxa recognized by IVM and PCA.*

Indicator species grouped according to associated habitats - bog, forested and open fen, plotted against the time show clear variation among the sites (Fig. 6). Similarly to the results of PCA, the vegetation composition in Pitkasoo is relatively stable in time compared to other sites. Rapid (in less than 500 years) shifts of plant communities from open fens to bog type habitats occur in Surusoo, Vedruka and Jõhvika sites but at different times - around 7.5 ka in Surusoo, around 2 ka in Vedruka and around 5 ka in Jõhvika. Reverse scenario can be seen in Kanna where plant communities associated with bog habitat dominated for the first 3000 years of the site development and community composition changes towards open fen have happened gradually over relatively long time period. High proportion of taxa associated with forested fens can be seen in Jõhvika and Pitkasoo between 3000 and 4000 years ago. In general, mire type turnovers coincide well with the hierarchical clustering classification borders, except for Pitkasoo, where indicator species are not associated with cluster borders. Changes in woody taxa abundances are shown in Appendix 2.

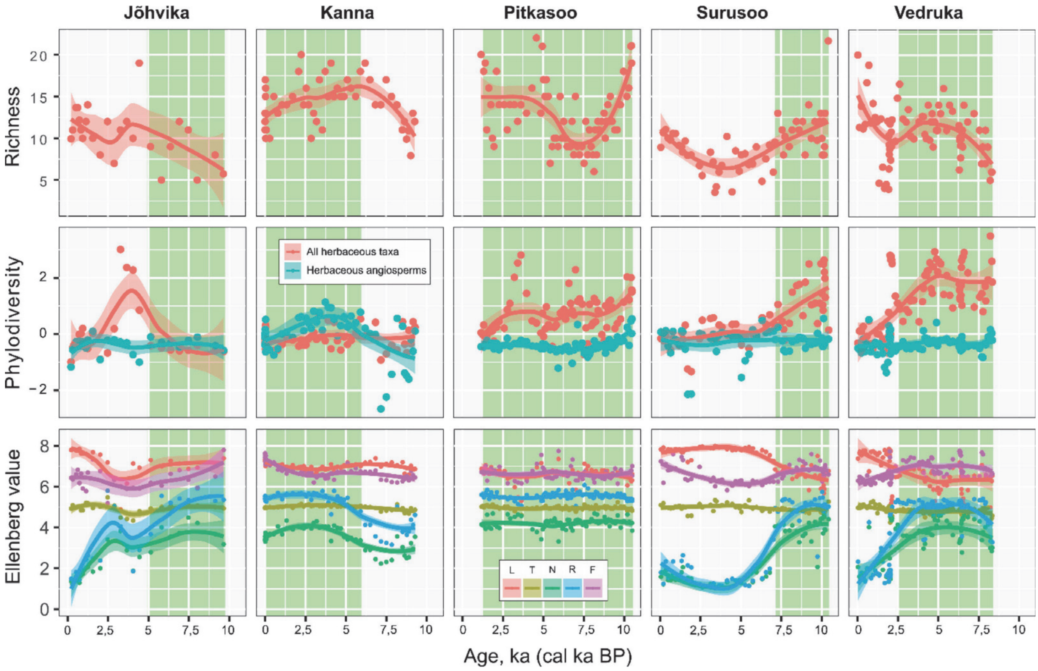

Figure 7. *Palynological richness, phylodiversity and EIV trends of herbaceous taxa through the development of sites. Green background indicates fen stage based on cluster analysis and indicator taxa. EIVs are given as: L – light availability, T – temperature, N - nutrient availability, R - reaction, and F - moisture).*

3.5 Changes in diversity and EIVs

Both Pitkasoo and Surusoo that developed earlier compared to other sites, show the highest herbaceous richness levels in the beginning of the site development, a progressive richness decrease with minima around 7.5 ka for Pitkasoo and around 4 ka for Surusoo and a gradual increase of richness towards the present day (Fig. 7). In contrast, Vedruka, Kanna and Jõhvika have the lowest palynological richness at the beginning of site development with gradual increase up to ca 5 ka. Vedruka and Jõhvika both show richness decreases around 2.5 ka, with further increase up to the present day, whereas in Kanna there is a slight decrease towards modern day.

The highest PD when calculated on all herbaceous taxa is at the beginning of site development for Pitkasoo, Surusoo and Vedruka, PD decreases gradually for Pitkasoo and Surusoo until the present day, while in Vedruka PD began to decrease ca 3000 years later. For all three sites, PD is close to significant phylogenetic divergence (SESmpd ~ 2) at the beginning of the site development. In Kanna, the PD of all herbaceous taxa is relatively stable throughout the site development and close to random. In Jõhvika, the PD is the lowest at the beginning of the site development and has maximum values around 3.5 ka. When seedless vascular plants are excluded from PD calculation, most sites have more-or-less similar and random PD throughout the site development, only in Kanna, there is a tendency towards functional convergence in the beginning of the site development.

From the EIVs, N and R values show the largest variation reflecting changes in community shifts with N and R both being relatively low during bog phases and relatively high during the fen phases (Fig. 7). Ellenberg T does not vary through the site development in any of the sites. Ellenberg L and F are also relatively stable through the development of the sites, however, there is a tendency of L being higher and F being lower during the bog phases compared to the fen phases.

LME models show that all tested herbaceous diversity estimates and EIVs differ significantly between fen and bog phases (Table 3). Fen phases have higher diversity (richness and both PD estimates), higher values of R, N and F but lower values of L and T than bog phases.

Palynological richness of woody taxa shows relatively uniform trends among the studied sites, with the low richness at the beginning of each site development and in the last 2000 years, and maximum values between 5000 to 2000 years ago (Appendix 2). Similarly to the richness trends, the EIVs based on woody taxa, showed relatively similar trends in all sites with N, R and K (continentality) exhibiting the largest variation (Appendix 2).

Table 3. *Results of linear mixed effects models with herbaceous taxon diversity and EIVs in relation to mire development phases. "Fen vs bog" was used as explanatory variable, Site as random variable and temporal autocorrelation structure was included in the model. Positive model estimates indicate that bog phase of mire development has higher values than fen phase, negative estimates indicate that fen phase has higher values than bog phase.*

Response variable	**Model estimate**	**T-value**	**P-value**
Richness	-1.47	-3.39	<0.0001
PD	-1.00	-8.61	<0.0001
PD angiosperms	-0.27	-3.91	0.0001
L	0.81	9.96	<0.0001
T	0.08	2.93	0.0038
R	-2.54	-18.77	<0.0001
N	-1.82	-17.53	<0.0001
F	-0.40	-6.69	<0.0001

Table 4. *Correlation matrix of herbaceous and woody taxa diversity measures and EIVs. Partial Pearson's correlation coefficients (with site accounted for) and Benjamini-Hochberg adjusted p-values.*

	Age		**L**		**T**		**R**		**N**		**F**	
	r	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p*-value	*r*	*p-value*
Herbaceous taxa												
Richness	0.01	0.8435	**-0.16**	0.0082	0.08	0.2156	**0.14**	0.0200	**0.19**	0.0016	0.02	0.8238
PD	**0.39**	0.0000	**-0.77**	0.0000	**-0.62**	0.0000	**0.36**	0.0000	**0.49**	0.0000	-0.01	0.8435
PD ang.	0.01	0.8435	-0.07	0.2467	**0.19**	0.0020	0.11	0.0829	**0.17**	0.0048	-0.02	0.8423
Woody taxa												
Richness	**-0.32**	0.0000	**-0.57**	0.0000	-0.02	0.8238	**0.53**	0.0000	**0.45**	0.0000	**-0.50**	0.0000
PD	0.05	0.5262	**0.55**	0.0000	**-0.30**	0.0000	**-0.42**	0.0000	**-0.50**	0.0000	**0.55**	0.0000
PD ang.	-0.10	0.1145	**-0.69**	0.0000	**0.44**	0.0000	**0.65**	0.0000	**0.72**	0.0000	**-0.77**	0.0000

Correlation analysis shows that richness of herbaceous taxa is significantly ($p<0.05$) positively correlated with R and N but negatively associated with L (Table 3). PD of all herbaceous taxa shows negative association with L and T but is positively correlated with R and N. PD for angiosperms shows significant positive associations with T and N (Table 4).

Richness of woody taxa is significantly ($p<0.05$) positively correlated with R and N but shows negative association with L and F (Table 4). PD of all woody taxa is significantly positively correlated with L and F but shows negative associations with T, R and N. PD of woody angiosperms shows opposite associations to PD of all taxa, and is positively correlated with T, R and N and negatively with L and F.

4. DISCUSSION

4.1. Modern pollen signal in open and forested fens and bogs

Pollen-based classification is widely used in palaeoecological studies to help to interpret historical changes in plant communities (e.g. Felde et al., 2014, Waller et al., 2017). Current results from modern pollen-plant samples and from different mire development trajectories add to the findings that have demonstrated the usefulness of pollen-based community classification for long-term ecological studies in wetland systems (e.g. Dehghani et al., 2017; Carvalho et al., 2019). Our results indicate that with some certainty, pollen data enable to differentiate between open fens, forested fens and bogs, allowing to study major changes in mire development with the help of sediment pollen assemblages, and could be especially usefull for data where plant macroremain analyses or other proxies are missing.

Already a visual interpretation of modern pollen assemblages suggests that bog samples have noticeably different herbaceous pollen composition compared to open fens and forested fens (Fig. 2), particularly with the high abundance of *Calluna vulgaris*, other Ericaceae pollen and *Sphagnum* spores. *Calluna* has been shown to be strongly associated with or even over-represented in bog pollen samples, especially when drier environmental conditions prevail (ref). Even though, *Calluna* cannot be considered exclusive for the bogs (Chambers et al., 2011), high abundance of *Calluna* coinciding with high abundance of *Sphagnum* spores that can be assumed to be of local origin (Blaauw and Mauquoy, 2012) suggests ombrotrophic conditions rather convincingly. In Estonia, hummocky type bogs that are overgrown by *Calluna* are relatively common (Sillasoo et al., 2007). *Sphagnum* species growing in minerotrophic conditions can also be associated with poor fens but then *Sphagnum* is accompanied by high abundances of Cyperaceae that is indicator of minerotrophic and wet conditions and high abundance of Ericaceae coinciding with *Sphagnum* would rather indicate bog habitat (O'Reilly et al., 2014; Väliranta et al., 2017).

Random forest classification indicated that identification of open and forested fens based on pollen data is more complicated than the fen-bog separation. However, IVM method revealed indicator pollen types for both open and forested fens. Cyperaceae is recognized as the main indicator of open fen habitats, it is present in all other samples, but clearly in lower abundances. Additionally, pollen taxa *Parnassia* and Primulaceae contribute as open fen indicators. Forested fens lack the dominant indicator and taxa such as *Oxalis*, *Succisa* and woody pollen of *Frangula*, *Prunus* and *Sorbus* are recognized to indicate this type of habitat. Our results are similar to the study from English fen system (Waller et al., 2017) where Cyperaceae were abundant in vegetation in both open and forested fens but in pollen signal, Cyperaceae was dominant only in open vegetation. In forested sites, Cyperaceae produce less pollen and the pollen signal is over-shaded by tree pollen (Waller et al., 2005). In addition to IVM, PCA ordination of herbaceous taxa shows that *Cladium mariscus* is associated with open fens, Polypodiaceae and *Filipendula* with forested fens (Fig. 3). However, these taxa were not highlighted by the IVM probably because of small number of samples (*Cladium mariscus*, n=4) or because of their overrepresentation in pollen signal of open habitats (Polypodiaceae and *Filipendula*). Polypodiaceae and *Prunus* have been shown to be associated with forested fen vegetation also in English fens (Waller et al., 2017).

Pollen of woody taxa did not separate different habitat types with any of the methods (Fig. 3, Appendix 1). Pollen signal of woody taxa is relatively uniform in all habitat types as the result of long-distance pollen dispersal where pollen of woody taxa reflects regional rather than local vegetation (Mazier et al., 2012; Wozniak and Steiner, 2017; Blaus et al., 2020).

Our results emphasize how important it is to include spores such as *Sphagnum* and Polypodiaceae in pollen analysis, especially when peatland development and vegetation is in focus. The usage of different methods for habitat classification is also important (Felde et al., 2014) since the results may differ to some extent and therefore may influence interpretation and decisions related to nature conservation and protection.

4.2 Mire succession in different study sites

Three major factors - postglacial isostatic uplift, autogenic succession and climate-induced changes - are usually discussed in connection with mire origin and succession in Northern Hemisphere (Weltzin et al., 2000; Hájková et al., 2012b; O'Reilly et al., 2014; Dendievel et al., 2020) and the mire development on Saaremaa Island is no exception. Among the studied sites, mire development has begun at different times and the beginning of peat accumulation is likely to be connected with the water level lowering (regression) of the Baltic Sea where the sediment began to accumulate right after the site emerged from the sea. The only exceptions are Viidumäe 1 and 2 which originated much later - about 3400 to 3000 years ago - and the start of peat accumulation is not connected with Baltic Sea water level. The highest site Surusoo, with mire surface at ca 43 m.a.s.l. (Veski, 1996), emerged at the beginning of Yoldia Sea and a small lake existed there during Ancylus Lake period. Jõhvika and Pitkasoo, located at lower altitudes on the West Saaremaa Upland, first appeared as Ancylus Lake lagoons (Veski, 1996; Königsson et al., 1998). Vedruka with the lowest elevation emerged as lagoon at the beginning of the Litorina sea. The comparison of Saaremaa mires is a good example of how the regression of the sea goes hand in hand with mire initiation and overall vegetation development on the island.

The timing of the beginning of peat accumulation varies between the sites. The earliest peat accumulation has been recorded in Pitkasoo mire around 9.8 ka, however the peat has been covered with thin layers of gyttja probably due to ingression or rise in water table (Königsson et al., 1998). Accumulation of organic material started at 9.2 ka in Surusoo and

Kanna, at 8.5 ka in Jõhvika and at 7 ka in Vedruka and Viidumäe 3 (Hansson et al., 1996; Poska and Saarse et al., 2002; Blaus et al., 2019), but much later (at ca 3 ka) in Viidumäe 1 and 2. While Surusoo developed as isolated lake and Pitkasoo and Vedruka as lagoons for approximately the first 1000 years, in other mires peat accumulation started right above the new mineral soil. Despite the fact, that some sites initially developed as lagoons or closed water bodies, this period is indistinguishable in visual interpretation and in cluster analysis of pollen assemblages, suggesting that probably the margins of the basins already had characteristic mire vegetation that played an important role in the pollen signal.

Despite the large number of studies related to postglacial rebound and shore displacement in the region (Tikkanen and Oksanen, 2002; Berglund, 2004; Hörnberg et al., 2005; Saarse et al., 2009), the impact of this process on mire development in the area is still unclear and would require extra attention beyond the scope of this paper. The fast land uplift during the earlier periods of the formation of Saaremaa Island (Rosentau et al., 2012) might have caused instabilities hindering bog formation and favoring fen development. The initiation of the fens on Saaremaa is most likely related to geological bedrock of the area with limestone providing discharge of calcium carbonate rich groundwater and thus preventing soil acidification (Grootjans et al., 2005). Nevertheless, ombrotrophic conditions have been recorded in the Kanna initial development phase (9.2-6 ka) that further developed into an open fen still present today (Blaus et al., 2019). Pitkasoo is particularly worth emphasizing since it has remained a fen throughout its entire development with only slightly changing composition characteristic to open or forested fens. In contrast, Surusoo site existed as fen for relatively short time period of 2000 years and shifted to bog around 7.2 ka - at the same time when Kanna began to “switch” towards fen-dominated vegetation. Around 7.6 ka Viidumäe 3 site originated coinciding with the origin of Apšuciems fen in the coast of Latvia – most probably as a result of Litorina Sea transgression (Gałka et al., 2016). Although Jõhvika is geographically close to Surusoo, the approximately 10 m difference in elevation has determined the later initiation of peat accumulation - around 8.5 ka as a result of groundwater level rise what Hansson et al. (1996) mistakenly connected with Ancylus transgression. According to Saarse et al. (2009), Litorina transgression started about 8.3 ka in Saaremaa and high sea level lasted until 7.7 ka. Succession to bog in Jõhvika began around 6 ka, with a period of forested fen vegetation from 4 to 3 ka, followed by open fen vegetation up to 2 ka (Fig. 6). The timing of these interruptions coincides with establishment of Viidumäe 1-2 fens and Vedruka changing to bog.

Continuous habitat openness has been emphasized as an important factor for the occurrence of relict species and high biodiversity in fens (Hájek et al., 2011). Our results showed that the fen phase vegetation of Jõhvika, Vedruka, Pitkasoo and Surusoo had varying proportions of both forested and open fen indicators indicating that the fens were encroached by forested vegetation to some extent. However, the forest periods in different sites are at different times and cannot be clearly associated with any climatic events in the region. The only site with consistently low proportions of forested fen indicators was Kanna spring fen.

Our results show that the initiation of mires in Saaremaa island is generally determined by the sea level changes. However, the mire initiation patterns in Saaremaa are in accordance with regional and global changes, where the majority of mires are known to initiate from 10 to 7 ka or during the last 4000 years as a result of climate change (Walker et al., 2012; Dendievel et al., 2020). Significant ombrotrophication during the 2-3 ka in Finnish mires has been connected to neoglacial cooling (Väliranta et al., 2017). However, the comparison of vegetation turnover patterns in our study indicates that the climatic changes are not uniformly reflected among the studied sites. In fact, some sites do not show clear response to climate change, highlighting that other factors like topography or hydrology have promoted their resilience. On the other hand, Blaauw and Mauquoy (2012) have emphasized that different factors related to mire micro topography, errors in 14C dating, differences in pollen influxes, biases in pollen counting and preservation can cause noise in mire development reconstructions even within a single mire. However, these possible sources of noise are likely to be more applicable in case of studies with much higher temporal resolution.

4.3 Diversity, environmental conditions and mire succession

Pollen richness and phylogenetic diversity are important biodiversity measures that are increasingly linked to different community processes and ecosystem functioning (Loreau et al., 2001; Tilman et al., 2006; Birks et al., 2016; Tredennick et al., 2017, Amador et al., 2019), and were used here to describe general diversity trends in relation to mire succession throughout the Holocene. It has also been emphasized that processes and functioning of the communities can be better explained by integrating environmental variables (Graham and Fine, 2008; Wiens, 2011, Duarte et al., 2018), plant-based indicator values such as EIVs offer that possibility (Diekmann, 2003) and thus it was another important aspect inspected in the present study.

4.3.1 Herbaceous taxa

We demonstrate that richness, phylogenetic diversity and certain environmental indicators of herbaceous taxa show relatively large variation within and between the sites. Palaeoclimate and human impact during the recent millennia have considerably changed the vegetation (O'Reilly et al., 2014, Whitlock et al., 2018). Differences in timing of the mire succession events between the sites make the diversity comparisons rather complicated.

Results of linear mixed-effects models comparing herbaceous taxon diversity and environmental variables in bog and fen phases showed that richness and PD are significantly higher in fen phases. The same was true for environmental indicators of R, N and F, but L and T were higher in bogs. These results are in accordance with the studies that previously have emphasized species richness and phylogenetic diversity in fens determined by environmental factors such as soil reaction, moisture, nutrient availability and light (Kotowski and van Diggelen, 2004; Horsáková et al., 2018; Blaus et al., 2020). However, when looking at individual sites (Fig. 7), the association of diversity and environmental factors with mire type is not that straightforward. Light availability has been shown to be a particularly important environmental filter in the fens where sedge-moss communities having the highest light availability and lowest productivity have the high number of species (Kotowski and van Diggelen, 2004). In correlation analysis (Table 4), light availability (L) was negatively correlated with richness and PD. As our analyses included samples from both fen and bog phases, the result reflects the fact that large raised bogs with high light availability such as present-day Vedruka and Surusoo, possess overall low diversity with high plant stress caused by limited nutrients and low soil reaction (Mauquoy and Yeloff, 2008; Laine et al., 2018).

The oldest sites that developed in the early Holocene around 10.5 ka - Surusoo and Pitkasoo - had the highest palynological richness in the beginning of the development. At that time, only the highest parts of West Saaremaa Upland were free from the water and various pioneer species were likely to occupy the free land and the coastal meadows (Poska and Saarse, 2002) creating complex communities and resulting in high phylogenetic diversity and palynological richness reflected in the initial phase of Surusoo and Pitkasoo development. General biodiversity trends in northern Europe during the early Holocene show similar high diversity values (Giesecke et al., 2012; Reitalu et al., 2015; Birks et al., 2016). Such surges of vascular plant diversity in newly emerged land are described also today (Magnúnsson et al., 2014). However, the high diversity in the earliest records might also be influenced by long-distance transport of extra regional pollen because the local pollen production was low (Reitalu et al., 2019). One would expect similar diversity patterns in sites that had relatively similar developmental pathways but Kanna, Vedruka and Jõhvika that originated one millennium later (9.5-8.5 ka) than Surusoo and Pitkasoo had the lowest palynological richness at the beginning of the site development. By that time, the landscape-scale vegetation succession had led to established woodlands and herbaceous pollen signal in mires surrounded by forest is likely to reflect mostly local vegetation (Blaus et al., 2020). Kanna, Vedruka and Jõhvika have the highest palynological richness during the mid-Holocene, where for Kanna and Jõhvika high richness coincides with transition from one type of mire to another. Similar diversity pattern with a gradual increase of richness from early succession towards fen–bog transition has been shown in the study of mire development pathways in Finland (Laine et al., 2018). The fen-bog transition stage has been described as locally extremely heterogeneous with the mire surface consisting of hummocks and pools (Laine et al., 2018; Blaus et al., 2019).

Significant phylogenetic divergence with coexisting species being phylogenetically more distant than expected by random characterizes the initial stage in Surusoo and the first 3 ka in Vedruka (Fig. 7). PD has been shown to be positively associated with long history of habitat continuity allowing for the “collection” of phylogenetically different species (Reitalu et al., 2014, Mienna et al., 2020). In addition, functional and phylogenetic diversity in fen systems, has been shown to be associated with management practices (Carvalho et al., 2020), which in our case is relevant only for the last millennia of mire development. In our results, the high phylogenetic diversity in the initial mire development stages agrees with the results from Reitalu et al. (2015) where PD was high in Late Glacial period and it was hypothesized to be related to environmental stress in early site development conditions.

Another interesting aspect of PD variation is connected to Jõhvika site, where a distinct increase in richness and PD occurred around 3 ka together with clear changes in environmental factors (Fig. 7). Habitat indicator species proportions suggest site overgrown by trees (Fig. 6), which is supported by the decrease in L indicator value. Pitkasoo shows signs of overgrowing around the same time with slight increase in PD of all taxa (Figs. 6 and 7). Similarly, to our results from Jõhvika and Pitkasoo, Locky and Bayley (2006) showed that the highest richness values were associated with moderately wooded fens when compared to the open fens.

Although pollen richness in the late Holocene is relatively high, PD of herbaceous angiosperms is low and PD of all herbaceous taxa at its lowest in most of the sites. Similarly, high palynological richness and low PD have been shown in the regional scale (Reitalu et al., 2015) and associated with human impact.

4.3.2 Woody taxa

As anticipated, diversity trends of woody taxa that can be expected to reflect the landscape and regional vegetation are relatively similar among the studied sites (Appendix 2). Woody plant richness patterns correspond to classical Holocene vegetation development scenario with the highest richness during the mid-Holocene (Poska and Saarse, 2002; Niinemets and Saarse, 2009, Veski et al., 2012; Reitalu et al., 2013; Blaus et al., 2020). We show how richness and PD closely follow vegetation turnovers and exhibit unimodal patterns having a strong association with environmental factors (Table 4). Highest richness in all the sites in mid-Holocene is correlated with high PD of angiosperms and corresponds to the highest values of R and N, but the lowest values of L and F. The association between species richness and soil reaction has been extensively investigated (eg. Chytrý et al., 2003; Nekola, 2004; Howie et al., 2016; Palpurina et al., 2016). For example, Locky and Bailey (2006) showed that plant species diversity is negatively associated with poor soils and low soil alkalinity. This relationship can be confirmed by the results showed by Pärtel (2002), who stressed the importance of soil reaction in evolutionary centers, showing that positive pH-richness associations are more probable at high latitudes and negative at low latitudes. In addition, nutrient availability is highlighted as an important factor influencing species richness (Wassen et al., 2005; Cleland and Harpole, 2010) as also affirmed by our results. After mid-Holocene, taxonomic richness of woody taxa decreased coinciding with increasing proportion of boreal taxa (*Pinus*, *Picea*, *Betula*), the change is well reflected in the decrease of PD of angiosperms. As documented in previous studies, high phylogenetic diversity is usually linked to mild temperatures and abundant water but tends to decrease with dryer conditions (Anacker and Harrisson et al., 2012; Li et al., 2019). In our results, PD of all taxa follows that trend, but PD of angiosperms shows opposite tendency. The landscape and regional changes in forests cover during the late Holocene show a tendency of shift towards a more homogeneous composition that has caused a reduction of taxonomic richness and reduction of PD of angiosperms. Biotic homogenization has been associated with the loss of biodiversity and ecosystem multifunctionality in different scales (Van der Plas et al., 2016). Current forest management systems are characterized by forests with single or few tree species and obscured natural regeneration that has led to an overlooked impact on biodiversity loss and divergence in ecosystem services (Duan et al., 2016). Although a great deal of responsibility comes down to human impact, studies on the regional vegetation have shown that both, climate and human impact have played a significant role in the dynamics of forest composition during the late Holocene (Reitalu et al., 2013; Kuosmanen et al., 2018).

4.4 Conclusions

Our results show that pollen data enable to differentiate between fens and bogs and give an indication of whether the site has been open during the fen phase of its development allowing to study major changes in mire development with the help of sediment pollen assemblages. While macrofossil data are better suited for studying within-mire changes giving better taxonomic resolution (Ronkainen et al., 2014; Gałka et al., 2016; Väliranta et al., 2017; Jabłońska et al., 2019), pollen data are more widely available for thousands of mire sites across the world (Williams et al., 2018) allowing for large-scale mire development studies with the help of pollen data.

The fen phases of the mire development showed varying levels of openness through time. Only Kanna spring fen had consistently low proportions of forested fen indicators. The timings of both fen-bog transitions and forest encroachment periods differed between the studied sites indicating that climate has not been the main driver of these changes. Current results suggest similarly to earlier studies (Väliranta et al., 2017, Jabłońska et al., 2019) that in addition to climate, different autogenic processes and allogenic disturbances are likely to be associated with changes in mire development trajectories. Mires are complex living ecosystems and not necessarily passive reflectors of climate conditions (Blaauw and Mauquoy, 2012). Additional studies involving more mires over larger region would help to better clarify the drivers behind mire development phases.

Historical fen and bog phases differed significantly in all diversity metrics and environmental indicators – a result that was expected because of the clear and well-known ecological differences between contemporary fens and bogs (c.f. Hájek et al., 2006). Our results show that the fen phases have significantly higher richness and phylogenetic diversity than bog phases of the same mires. Our results indicated tendency towards phylogenetic overdispersion in fen phases, that is likely related to the evolutionary age of the habitat (Lososová et al., 2015).

We conclude that pollen signal from mires is not always “noise” and adds valuable information to peatland development reconstructions allowing to separate between different mire types and to reconstruct past diversity and local environmental changes.

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Appendix 1. Results of random forest classification model confusion matrix used to assess site type based on pollen data from modern pollen samples in bogs, forested fens and open fens in Estonia.

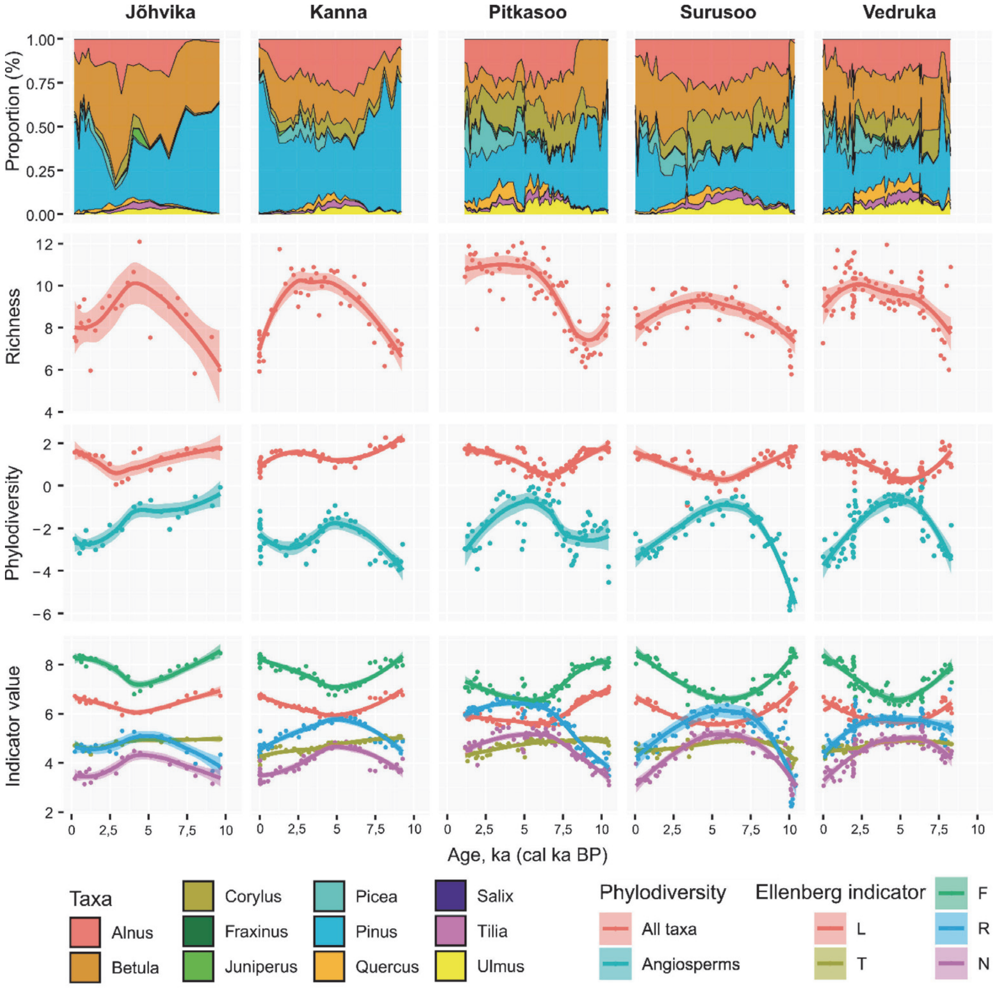
Herbaceous taxa. Model parameters: number of trees: 500, number of variables tried at each split: 20. Out of box (OOB) estimate of error rate: 25%.

	Bog	**Forested fen**	**Open fen**	**Classification error**
Bog	10	2	0	0.1666
Forested fen	1	11	3	0.2666
Open fen	0	5	12	0.2941

Woody taxa. Model parameters: number of trees: 500, number of variables tried at each split: 10. Out of box (OOB) estimate of error rate: 52.27%.

	Bog	**Forested fen**	**Open fen**	**Classification error**
Bog	8	2	2	0.3333
Forested fen	1	5	9	0.6666
Open fen	0	9	8	0.5294

Appendix 2. Dominant woody taxa, palynological richness, phylodiversity and Ellenberg Indicator value trends of woody taxa through the development of West Saaremaa mire sites. Ellenberg indicators are given as: L – light availability, T – temperature, F – moisture, R – reaction N - nutrient availability.



Publication IV

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Postglacial flooding and vegetation history on the Ob River terrace, central Western Siberia based on the palaeoecological record from Lake Svetlenkoye

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Abstract

The hemispheric-scale climatic fluctuations during the Holocene have probably influenced the large Siberian rivers. However, detailed studies of the West Siberian Plain postglacial environmental change are scarce and the records of millennial-scale palaeohydrology are nearly absent. This paper presents the Holocene palaeoecological reconstruction based on the sedimentary record of Lake Svetlenkoye, located near the confluence of major Siberian rivers Ob and Irtysh. Postglacial history of flooding, dynamics of regional and local vegetation, sedimentation regime, geochemical changes and lake water pH were reconstructed based on multi-proxy studies. We used palaeobotanical (plant macrofossils, pollen, diatoms), geochemical (organic matter, total organic carbon and nitrogen content, carbon/nitrogen ratio) and chronological (^{14}C dates, spheroidal fly-ash particle counts) methods. The studied sediment section started to accumulate ~11,400 cal. yr BP. The initial shallow water body was flooded by Ob River waters ~8100–8000 cal. yr BP as confirmed by a remarkable increase in the sedimentation rate and the accumulation rate of the aquatic vegetation proxies. The period of flooding coincides with the high humidity periods reconstructed from regional palaeobotanical records. About 6800–6700 cal. yr BP, the study site became isolated from the Ob River floodplain and remained a small lake until present. The diatom-based lake water pH estimates suggest fluctuations in the pH values during the Holocene, the recent decrease since 1960s being the most notable. The vegetation record revealed constant postglacial presence of tree taxa – *Betula, Pinus* and *Picea* – although in different pollen ratios and accumulation rates through time. The paludification of the surroundings occurred since ca. 8500 cal. yr BP.

Keywords

C/N ratio, diatoms, fly-ash particles, Holocene, Ob River, palaeolimnology, plant macrofossils, pollen, Siberia

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Introduction

The West Siberian Plain covers thousands of square kilometres and is the world's largest mid/high-latitude wetland (Kremenetski et al., 2003) crossed by prominent rivers Ob and Yenisei. The Ob River is one of the largest rivers in the West Siberian Plain flowing into the Kara Sea of the Arctic Ocean. The Ob River contributes about 404 km^3 freshwater per year (Peterson et al., 2002) and is the third largest Eurasian river by runoff, supplying heat and freshwater to the Arctic Ocean (Agafonov et al., 2016). Correlation between the dynamics of the discharge of the Northern Eurasian rivers, North Atlantic Oscillation and global mean surface air temperature suggests that the rivers are responding to hemispheric-scale climatic patterns (Peterson et al., 2002).

The pollen-based postglacial long-term climate reconstructions for Western Siberia (Blyakharchuk, 2009; Groisman et al., 2013) distinguish drier and wetter time periods. The increased precipitation or decreased runoff probably influenced the rivers; however, there is only limited knowledge on the postglacial palaeoecology, including the flooding history from the Ob region. There are only few remarks that the peat deposited in the wetlands next to the Ob River contains occasional clay and silt layers as a probable result of past river flooding (Mironycheva-Tokareva et al., 2014; Schipper et al., 2007) and one centennial-scale reconstruction from tree-ring record focusing on floodplain hydroclimate and past river discharge estimations (Agafonov et al., 2016).

The changes in climate and hydrological regime have a profound effect on the vegetation dynamics. Peat and lake sediments are well-known continental archives that contain records of past climate, environmental and vegetation changes. The easily retrievable peat archives have been mostly used as a source for palaeobotanical (Akhteryakova and Leshchinskiy, 2014; Blyakharchuk, 2003; Blyakharchuk and Sulerzhitsky, 1999; Peregon et al., 2007; Pitkänen et al., 2002) and carbon cycle (e.g. Beilman et al., 2009; Borren et al., 2004; Sheng et al., 2004; Turunen et al., 2001) studies in West Siberian Plain.

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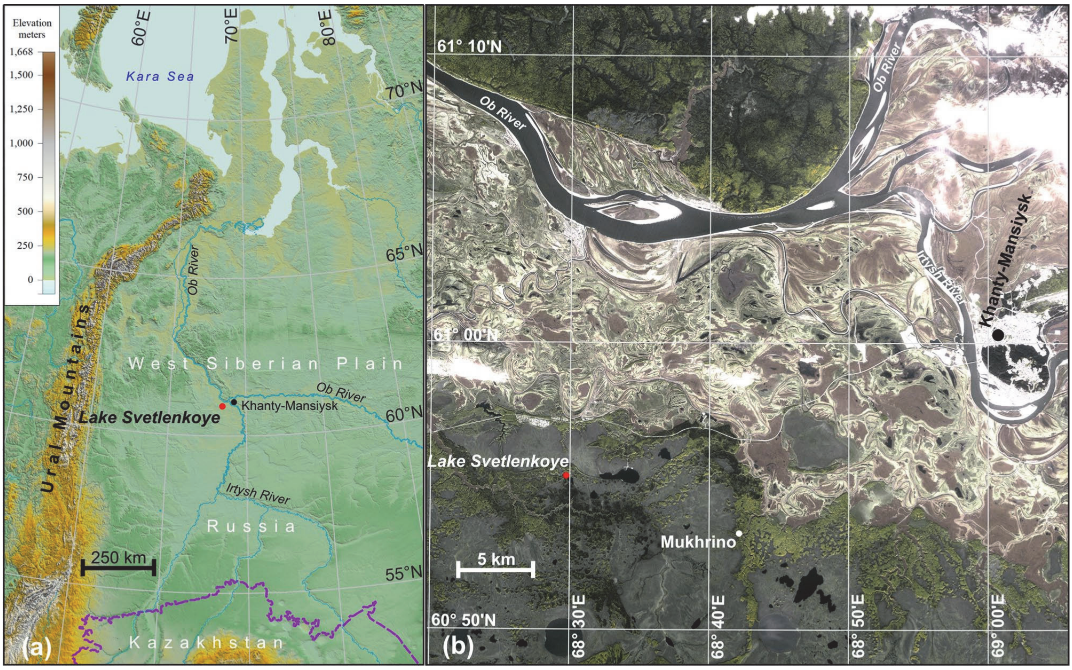

Figure 1. The overview map of (a) West Siberian Plain and (b) detailed location of the study site.

The present study focuses on the Holocene environmental changes as recorded by lake sediments that reflect the development of the studied sedimentary basin – Lake Svetlenkoye. The main topics are the flooding history of one of the major Siberian river Ob and the postglacial dynamics of the local and regional flora in the heart of Western Siberia. How did Holocene moisture changes affect the Ob River around its confluence with Irtysh River and what effect did it pose on the vegetation dynamics? Nowadays, there is notable human management on the Siberian rivers (Yang et al., 2004), but palaeoenvironmental data on how past climatic/hydrological changes affected the local environmental conditions could provide information for estimating reactions to the present and future global climate change.

Study area

Lake Svetlenkoye (60°55′N, 68°30′E, length 900 m, width 300 m, water depth 250 cm, elevation 32 m a.s.l.) is located on a terrain 4 km south of the contemporary floodplain of Ob River (Figure 1). The confluence of the Irtysh and Ob rivers is located approximately 25 km northeast and the nearest city, Khanty-Mansiysk about 30 km east of the study site. The generally flat topography of Western Siberia is in this area characterized by modern river floodplain and river terraces formed during the Pleistocene and Holocene. The region is rich in wetlands and mires. In Ob region, over 6% of river drainage basin is covered with wetlands (Serreze et al., 2003) reaching locally up to 40% in the taiga zone (Mironycheva-Tokareva et al., 2014). The mire development of the area is tied to the hydrology of the rivers, as the riverbeds are shallow and meander strongly, thus obstructing the flow of water (Turunen et al., 2001). Phytogeographically, the region is located in the middle taiga zone characterized by the dominance of dark-coniferous (*Picea obovata, Abies sibirica, Pinus sibirica*) and *Pinus sylvestris* forests. *Picea obovata–Pinus sylvestris* forests, occasionally in association with *Larix sibirica*, typify the interfluvial regions between the large Western Siberian rivers (Laukhin, 2011). There is no present permafrost in the region (Bleuten and Filippov, 2008). The climate is continental (Kremenetski et al., 2003). The mean annual precipitation (for period 1961–1990) is 544 mm. The mean January temperature is −25°C (night)/−16.4°C (day) and the mean July temperature is +13.7°C (night)/+23°C (day) (Hydrometeorological Research Centre of Russian Federation, Khanty-Mansiysk meteorological station, https://meteoinfo.ru/?option=com_content&view=article&id=1750).

The knowledge of the late Quaternary geology of the region has been revised during the last decade (Astakhov, 2011, 2013, 2014) concluding that the study region was not directly affected by the ice masses of the last glaciation but by previous Quaternary glaciers. Previous postglacial/Holocene palaeoecological studies in the region have shed light to past regional vegetation dynamics (Akhteryakova and Leshchinskiy, 2014; Pitkänen et al., 2002) but also mire hydrology and fire history (Lamentowicz et al., 2015).

Material and methods

The sediment was cored from lake ice in March 2014 from the deepest part of the lake, where water depth was 250 cm (60°55.31′N, 68°29.92′E). The sediment depth reached 325 cm. Sediment was cored using a Russian-type corer and the uppermost 54 cm was collected by a Willner type sampler. The sediment cores were described in the field, later cut to 1-cm thick subsamples and transported to the laboratory for further analyses.

Chronology

The chronology of the Lake Svetlenkoye sediment sequences was modelled by OxCal 4.2.4 depositional model (Bronk Ramsey, 2008, 2009) using IntCal13 calibration curve (Reimer et al., 2013), lithological boundaries, radiocarbon dates and spheroidal fly-ash particle (SFAP)-derived ages. Seven horizons were accelerated mass spectrometry (AMS) radiocarbon dated. Two samples containing wooden material were selected and packed separately directly in the field, while additional dating material (bulk gyttja samples) was selected later in the laboratory and were sent to Poznan Radiocarbon Laboratory, Poland.

SFAP analysis was used as an indirect dating method of surface sediments (Alliksaar et al., 1998; Renberg and Wik, 1985; Rose et al., 1995). SFAPs are high-temperature combustion products of fossil fuels, characteristic globally for all accumulative environments of the last 100–150 years (Swindles et al., 2015) and their distribution profile in sediments follows fuel consumption history of the study area. For SFAP analysis, subsamples from the uppermost 20-cm sediment layer followed sequential chemical treatment with 30% H_2O_2, 2.7M HCl and 0.3M NaOH to remove organic, calcareous and biogenic siliceous material, respectively, and thereafter *Lycopodium* spores were added to calculate particle concentration (Stockmarr, 1971). Particles together with *Lycopodium* spores were counted at 250× magnification under a light microscope. Counted SFAPs included both spheroidal carbonaceous particles (SCPs) and inorganic ash spheres (IASs) (Rose, 1990a, 1990b) and are expressed as number in gram dry sediment weight (g^{-1} DW).

Palaeobotanical analyses

Macrofossils. Plant macrofossil analysis was performed contiguously along the sediment core. The sample thickness varied between 3 and 10 cm between the depths of 322 and 284 cm, was uniformly 5 cm between the depths of 284 and 149 cm, and 10 cm between the depths of 149 and 24 cm. The sample volumes varied from 10 to 70 cm^3. In total, 47 sediment samples were searched for plant macrofossil content. The preparation for plant macrofossil analysis followed conventional procedures (Birks, 2001). Samples were wet-sieved through the mesh of 0.125 mm. Plant macrofossils and other remaining materials were examined using a stereo and light microscope. Relevant literature, atlases (Cappers et al., 2006; Katz et al., 1977) and reference collection were used for plant macrofossil identification. The results are expressed as a number of plant macrofossils per 100 cm^3 of sediment (concentration) and as plant macrofossil accumulation rate (AR). The plant macrofossil diagram was divided into statistically significant zones defined based on constrained hierarchical clustering of a Bray–Curtis distance matrix and broken stick method for determining the zones using programme package rioja for R (Juggins, 2017).

Pollen. Pollen sample preparation followed a standard acetolysis method (Berglund and Ralska-Jasiewiczowa, 1986) combined with hot concentrated 40% and 70% hydrofluoric acid (HF) treatment to remove inorganic matter (Bennett and Willis, 2001). *Lycopodium* spores were added to calculate pollen concentration and, subsequently, the pollen AR values (Stockmarr, 1971). In total, 88 sediment samples were analysed for pollen content. A pollen sum of at least 500 grains was aimed. Pollen data were expressed as percentages of the total terrestrial pollen sum, and pollen AR values were expressed as pollen grains cm^{-2} yr^{-1}. Counts of spores, microscopic green algae, charcoal and other microfossils were calculated as percentages of the total sum of terrestrial pollen. Corroded and degraded grains of *Betula* were counted separately during routine pollen analysis and used as a measure of redeposition or inwash from older sediments. The pollen data were clustered based on constrained hierarchical clustering of Bray–Curtis vegetation distance matrix and divided into statistically significant subzones with the help of broken stick method using programme package rioja for R (Juggins, 2017). Pollen sample richness was calculated using the rarefaction method (Birks and Line, 1992).

Diatoms. For diatom analysis, subsamples of known volume (0.1–0.3 cm^3) were taken and those were digested in 30% H_2O_2 until the organic material was oxidized. Divinylbenzene microscopic markers were added to determine diatom concentration. A few drops of the cleaned subsample were dried onto the cover glass and mounted on slides using Naphrax medium and analysed for microfossils under an Axio Imager light microscope at 1000× magnification, using oil immersion and differential interference contrast optics. A total of 39 sediment samples were screened for diatoms; 23 were void of diatoms. Diatoms were identified using standard floras (e.g. Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b) and were grouped according to their habitat into planktonic and periphytic taxa, the latter including epipelic, epipsammic and epiphytic life forms. Diatom-inferred lake surface water pH was reconstructed using weighted averaging regression model (Juggins, 2001) and the combined pH training set of the European Diatom Database calibration dataset (Battarbee et al., 2000). The modelling was performed online (http://craticula.ncl.ac.uk/Eddi/jsp/).

Geochemical analyses

The organic matter (OM) content of the sediment was determined by loss on ignition at 550°C for 4 h (Heiri et al., 2001). In total, 66 samples were analysed for total organic carbon (TOC) and total nitrogen (TN) content by combusting in the FLASH 2000 Organic Elemental Analyzer. Approximately 8 mg of freeze-dried powdered sediment was placed into special silver containers. In order to remove carbonates, the samples were initially pre-treated with 4M HCl and dried on a hotplate at 80°C for 4 h. Before analysis, silver containers were packed into tin containers for more efficient burning. For the measurements, BBOT ($C_{26}H_{26}N_2O_2S$) was used as a standard (ThermoFisher Scientific) and the algae *Spirulina* was used as reference material (IVA Analysentechnik e. K). Analyses were performed in triplicate. TOC and TN were expressed in percentages and their TOC/TN ratio (C/N) values as atomic ratios (Meyers and Teranes, 2001).

Results

Lithology

The basal part of the core (325–308 cm) consists of bluish grey silt with a darker interlayer at depth of 316–314 cm (Figure 2). The OM content of silt is low, reaching up to 2.7% (Figure 3). The next sediment unit described is solid dark brown gyttja with plant detritus and wood remains (308–280 cm). The OM content rises notably and is higher in the lower part of the sediment unit (50% at the depth 300–299 cm). The brown gyttja consists of less visible plant detritus between the depths of 280 and 264 cm. The OM content varies between 25% and 30% and the calculated sedimentation rate is the same as for previous units, 0.02 cm yr^{-1}. The shift in sedimentation rate from 0.02 to 0.07–0.08 cm yr^{-1} and slightly lower OM content characterize the greenish brown homogeneous gyttja unit (264–157 cm). The upper portion of the sediment core consists of unconsolidated dark brown gyttja (157–0 cm). The sedimentation rate decreases (from 0.08 to 0.02–0.04 cm yr^{-1}) and increases again in the subsurface portion of gyttja (12–0 cm). The OM content increases rapidly reaching 78% (at depth of 115 cm). The carbonate content in this section reaches the highest value of the entire core, 5.2%.

Chronology

The chronology is based on seven radiocarbon dates (Table 1) and the upper part is corrected according to the SFAP distribution curve in the sediments. In the following text, we use calibrated ages before present where 0 corresponds to AD 1950. The formation of the studied sediment section in Lake Svetlenkoye started about 11,400 cal. yr BP.

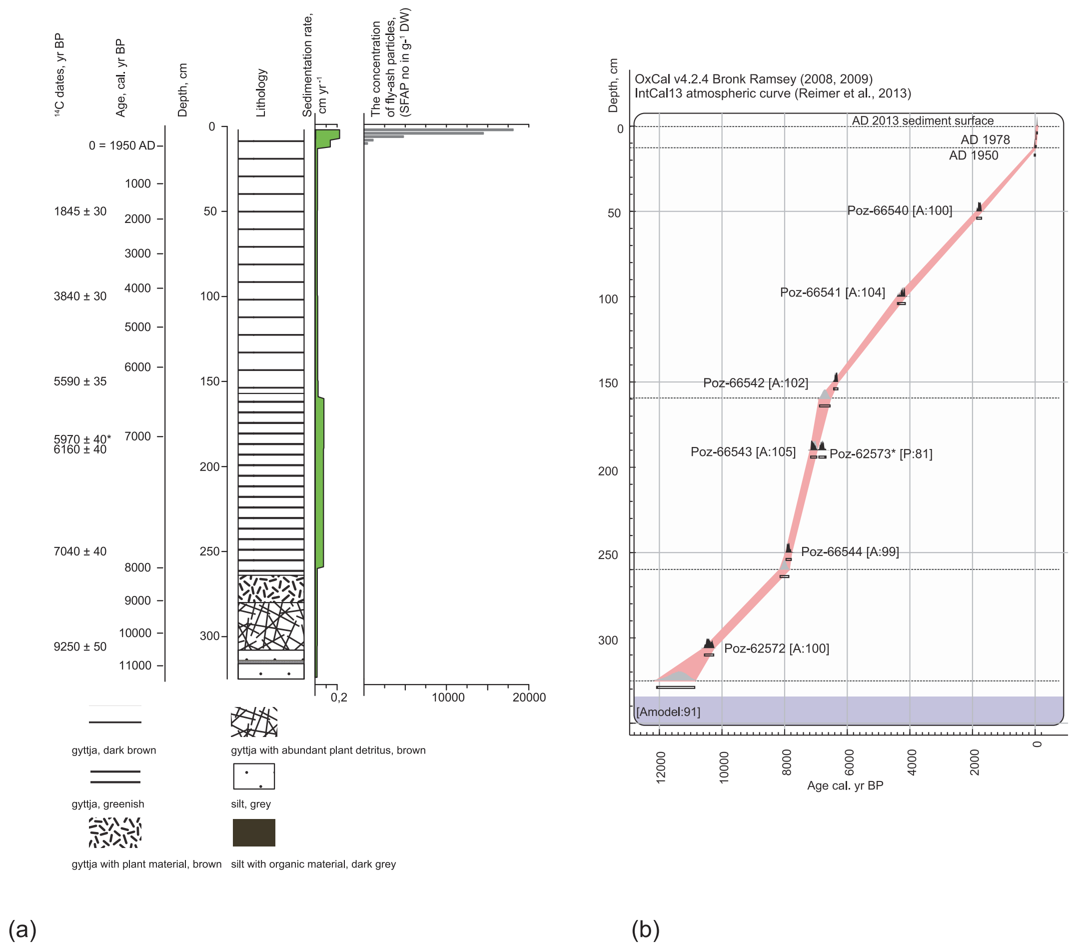

Figure 2. (a) The lithology, sedimentation rate, placement of radiocarbon dates and the concentration of the spheroidal fly-ash particles on the sediment core of Lake Svetlenkoye. *marks the result not included in the age modelling. (b) Lake Svetlenkoye age-depth model at 95.4% probability range. The graphs on the age-depth curve show the likelihood (grey) and posterior (black) probability distribution of the calibrated radiocarbon dates. Dashed lines mark the lithological boundaries and agreement indexes for radiocarbon dates are shown in the brackets.

The first signs of SFAP are recorded at the core depth of 12 cm. The onset with very low concentration of SFAP (<400 in g^{-1} DW) and small particle size quickly turns to much larger particle size (~40 µm) at the depth of 8 cm. At the depth 6 cm, the concentration of SFAP increases sharply and proceeds to increase up to the surface sediment layer where particle concentration exceeds 18,000 g^{-1} DW. In the uppermost sediment layers (6–0 cm), SCPs up to 65 µm in size and IASs in size 25 µm are recorded. This large size of SFAP is an indicator of local high-temperature combustion of fossil fuels and marks industrialization within the region, increase in fuel burning and emissions. In the well-dated peat core of Mukhrino mire, just about 10 km southeast from Lake Svetlenkoye (Figure 1), Lamentowicz et al. (2015) registered sharp increase in the SFAP AR around AD 1978. Accordingly, we also estimate the rise in SFAP distribution in our core as AD 1978.

Palaeobotany

The plant macrofossil zonation indicates four significant zones: LSM1 (307–289 cm, corresponds to ca. 10,500–9500 cal. yr BP), LSM2 (289–244 cm; ca. 9500–7800 cal. yr BP), LSM3 (244–149 cm; ca. 7800–6300 cal. yr BP) and LSM4 (149–24 cm; ca. 6300–500 cal. yr BP) (Figure 4). The lowermost part of the studied sediment (325–307 cm) is void of plant macrofossils but contains macroscopic charcoal pieces. LSM1 (ca. 10,500–9500 cal. yr BP) is the only zone that displays the remains of aquatic plants (*Potamogeton* spp., *Hippuris vulgaris*), suggesting that the locality was under water or at least flooded. Most of the plant remains belong to shoreline taxa (*Schoenoplectus lacustris, Carex* spp., *Typha latifolia*). However, the tree macrofossils are also present (tree-birch, spruce). The understory layer consisted of *Cotoneaster*, blackberry (*Rubus fruticosus*), goosefoots (*Chenopodium*) and grasses. The next zone, LSM2 (ca. 9500–7800 cal. yr BP), is dominated by tree remains (tree-birch seeds and catkin scales, pine and spruce needles). The presence of *Typha* and *Salix* seeds suggests humid conditions and the remains of *Juncus, Eriophorum, Andromeda polifolia* and *Comarum palustre* indicate wet mire surroundings of the sedimentary basin. In the LSM3 zone (ca. 7800–6300 cal. yr BP), the number of plant macroremains decreases notably. The birch and spruce macrofossils are present but in much smaller numbers than in previous zones. The seeds of *Typha latifolia, Eriophorum* and *Juncus* suggest wet conditions around the sedimentary basin while the seeds of bilberry (*Vaccinium myrtillus*) and grasses belong to the non-telmatic terrestrial vegetation. The upper zone LSM4 (ca. 6300–500 cal. yr BP) is nearly barren of terrestrial plant macroremains, except for the scarce conifer bud scales and few *Vaccinium* spp. seeds. The oospores of *Nitella* and remains of *Daphnia* (Cladocera) illustrate the aquatic environment.

Five pollen assemblages are differentiated based on hierarchical clustering and the broken stick method: LSP1 (325–315 cm; ca. 11,400–10,900 cal. yr BP), LSP2 (315–273 cm; ca. 10,900–8000 cal. yr BP), LSP3 (273–170 cm; ca. 8000–6800 cal. yr BP), LSP4 (170–105 cm; ca. 6800–4400 cal. yr BP) and LSP5 (105–2 cm; ca. 4400 cal. yr BP to ~ AD 2003) (Figure 5).

The earliest pollen zone is characterized by *Pinus* dominance, up to 44%, and the minimum values of *Betula*. In addition, the zone is composed of *Alnus* maximum values and relatively high values of *Picea* (22%). Poaceae and Cyperaceae show high values of their occurrence, with no presence of other terrestrial herbs. Among the spores, *Sphagnum* and ferns (*Thelypteris palustris* type) are present. Ferns show constant, relatively low values, but *Sphagnum* has its peak value compared with the other zones.

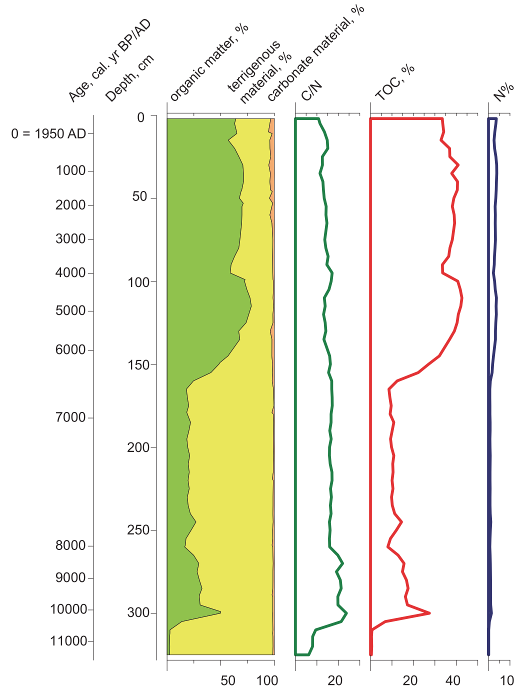

Figure 3. The geochemical proxies analysed from the sediment of Lake Svetlenkoye.
C/N: carbon and nitrogen atomic ratio; TOC: total organic carbon content; N: nitrogen content.

The pollen zone LSP2 (10,900–8000 cal. yr BP) is characterized by a rapid decline of *Pinus* and *Picea* pollen and an abrupt increase of *Betula* pollen up to 70%. The general composition of arboreal pollen (AP) has become more diverse with *Juniperus, Salix, Ulmus* and *Populus*, although in low quantities. In contrast to the previous zone, *Alnus* pollen is nearly absent. While non-arboreal pollen (NAP) *Artemisia* and other terrestrial herbs such as Chenopodiaceae, *Calluna, Urtica, Filipendula*, Caryophyllaceae, *Thalictrum, Ledum* appear in the pollen record, the values of Poaceae and Cyperaceae are slightly decreasing. Nevertheless, the main feature of this pollen zone is the high abundance of aquatic plants – *Typha/Sparganium, Myriophyllum spicatum, Nuphar, Nymphaea, Ceratophyllum*, which occur in ponds, lakes and slow-moving rivers. *Sphagnum* and fern spores with its highest values are present throughout the zone and are complemented by the occurrence of *Equisetum*.

The pollen zone LSP3 is differentiated by the maximum values of *Picea* up to 29% and the drop of *Betula* pollen from 70% to 40%. A slight decrease of Poaceae, Cyperaceae and *Artemisia* can be seen towards the present day. Some other herbaceous plants such as Caryophyllaceae, Umbelliferae, *Ledum* and most aquatic plants have definitive decline compared with previous pollen zone. The same declining trend is also apparent among the sporophytes. The percentages of green algae from genus *Pediastrum, Tetraedron* and *Scenedesmus* increase significantly. Pollen AR (PAR) is twice as high in comparison with other zones (Supplemental Appendix, available online). The following pollen zone LSP4 is strongly characterized by the lowest values of *Pinus* only 6–18%, a decline of *Picea* and the highest values of *Betula* with some of its peaks exceeding 80%. The pollen assemblage in the zone is also characterized by an increase of *Alnus, Quercus* and *Ulmus* pollen. The terrestrial herbs Poaceae, Cyperaceae, *Artemisia*, Chenopodiaceae retain constant values, and *Filipendula, Aster* type and Apiaceae are irregularly present throughout the period. Sporophytes and green algae have declined significantly and are nearly absent. Levels of corroded *Betula* pollen start to increase within this zone.

The most recent pollen zone LSP5 spans the longest time period from 4400 cal. yr BP to the present. Relatively low *Picea* values vary from 2% to 11% of total the pollen sum. The dominant tree pollen is from *Betula* with the values from 50% to 70%, followed by *Pinus* with 10–30%. *Salix, Alnus* and *Ulmus* are enriching the AP throughout all pollen zone, with low values of *Larix, Quercus* and *Juniperus* pollen. Poaceae, Cyperaceae, *Artemisia* and Chenopodiaceae are still dominant in NAP. *Artemisia* pollen quantities have a slight trend to increase towards the recent period. Several NAP (*Calluna, Filipendula, Aster*, Umbelliferae, *Ledum*) which were already present in the previous

Table 1. Results of radiocarbon dating from the Lake Svetlenkoye profile.

Depth of the sample, cm	Laboratory code	Date, ^{14}C years before present	Calibrated/modelled ages at 95.4% probability	Dated material
50	Poz-66540	1845 ± 30 BP	1860–1710 cal. yr BP	gyttja
100	Poz-66541	3840 ± 30 BP	4400–4150 cal. yr BP	gyttja
150	Poz-66542	5590 ± 35 BP	6430–6300 cal. yr BP	gyttja
190	Poz-62573	5970 ± 40 BP	6900–6680 cal. yr BP[a]	wood twigs
190	Poz-66543	6160 ± 40 BP	7170–6970 cal. yr BP	gyttja
250	Poz-66544	7040 ± 40 BP	7950–7790 cal. yr BP	gyttja
306	Poz-62572	9250 ± 50 BP	10,560–10,270 cal. yr BP	wood twigs

Poz: laboratory code of the Poznań Radiocarbon Laboratory (Poland).
[a] Not used for Oxcal modelling.

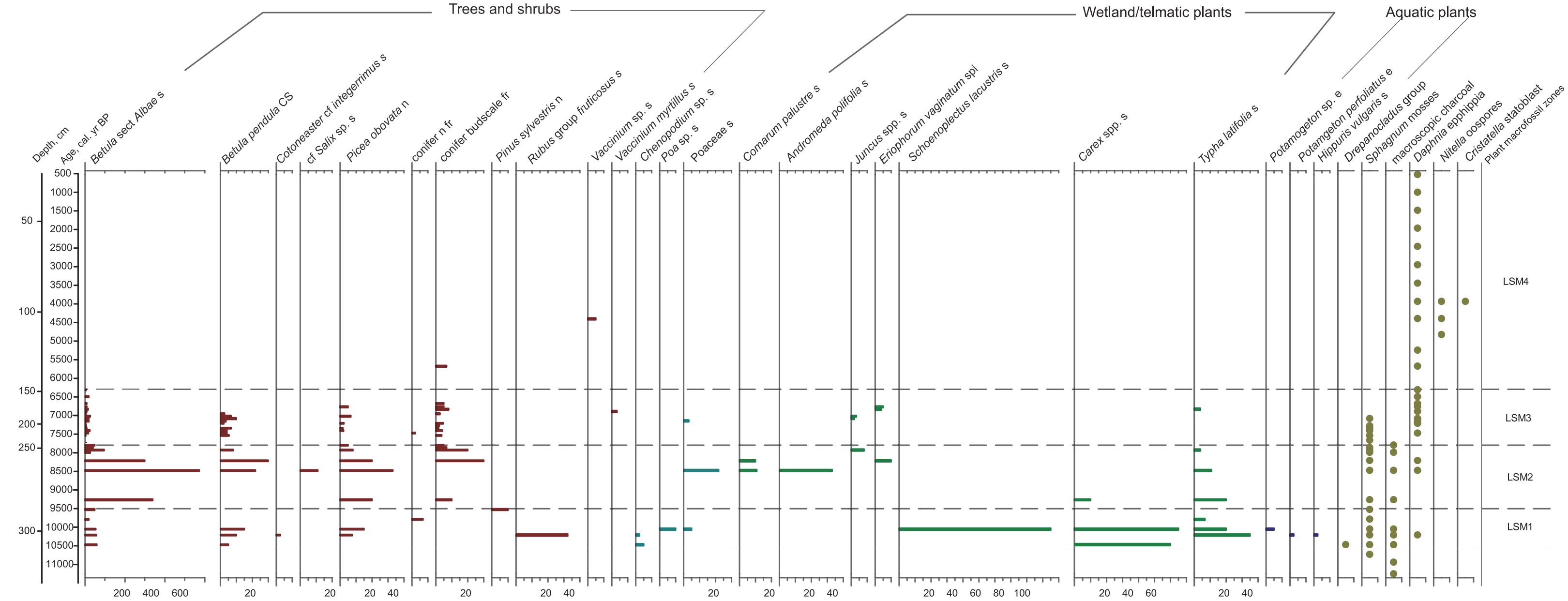

Figure 4. The concentration of plant macrofossils and zoological macroremains (number of macroremains in 100 cm³ of sediment) of Lake Svetlenkoye.
s: seed; CS: catkin scale; n: needle; fr: fragment; spi: spindle; e: endocarp.

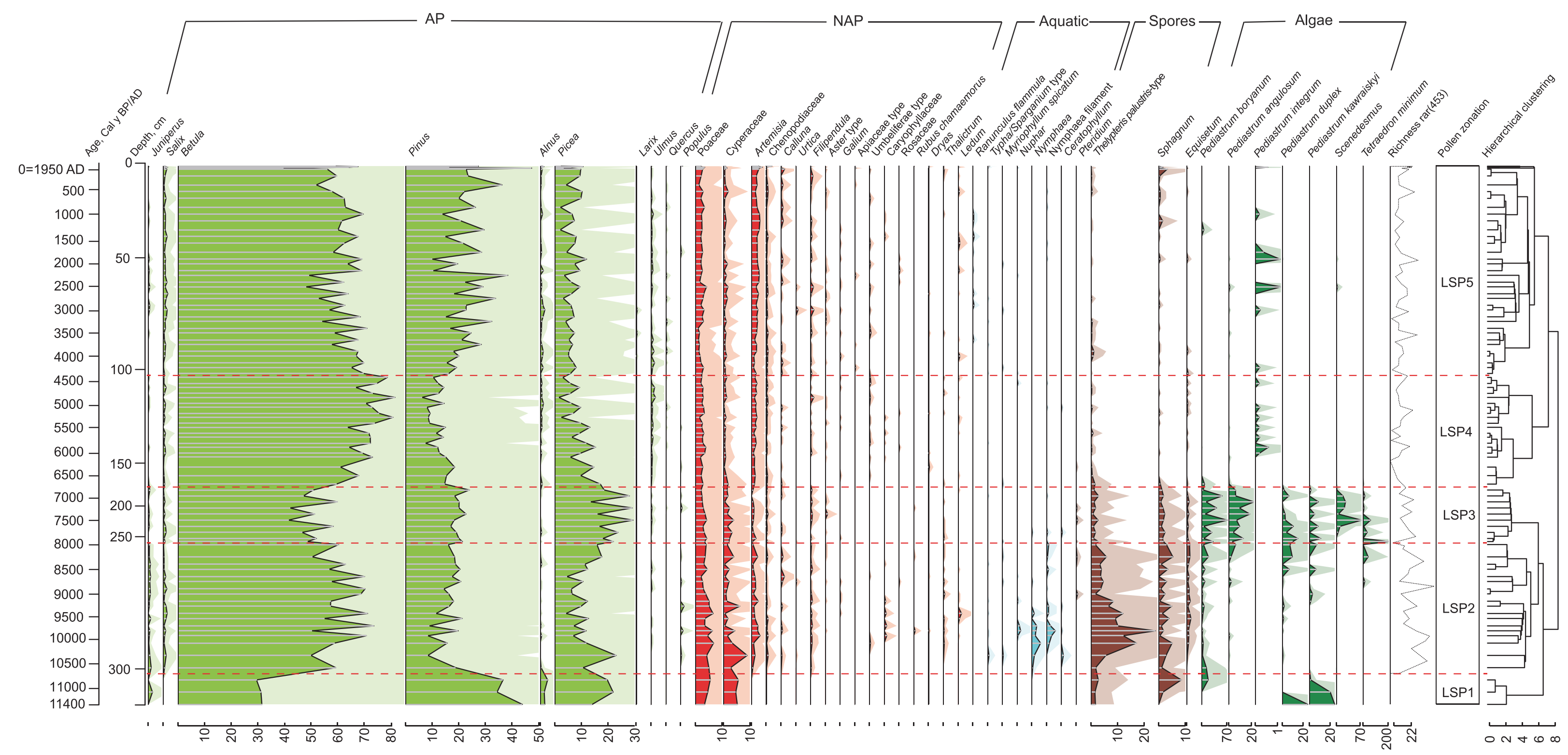

Figure 5. Pollen diagram of selected species of Lake Svetlenkoye displaying postglacial changes of pollen richness (rarefaction-estimated number of taxa). The full pollen record, percentages, corrosion and accumulation rates are presented in Supplemental Appendix (available online).

zones, and newly emerged *Ranunculus flammula* pollen appear irregularly in low amounts. Among the spores, ferns show low quantities at the beginning of the zone and *Sphagnum* increases in the top samples.

Pollen richness does not show any major trends throughout the study period. It was not possible to calculate pollen richness for LSP1 because of the scarcity of the pollen record. LSP2 has slightly higher pollen richness values with average of 16 pollen types per sample (max. 22) compared with the other zones which had on average 13–14 pollen types.

Diatoms were not present throughout the entire sediment record of Lake Svetlenkoye (Figure 6a); the base of the core (320–265 cm; ca. 11,200–8300 cal. yr BP) and the middle part of the core (160–100 cm; ca. 6700–4200 cal. yr BP) contain none or very few diatoms and preserved diatoms bear signs of significant valve damage and dissolution. The peak of diatom concentration (up to 630 × 10^4 valves cm^{-1} sediment) occurs at 250–190 cm (ca. 7900–7100 cal. yr BP) and is dominated by planktonic diatom *Aulacoseira ambigua*. Diatom-inferred lake water pH value for that time is neutral (Figure 6b).

Even if the diatom abundance shows significant valve damage, there is a change in diatom composition in the depth of 160 cm (6700 cal. yr BP). Planktonic diatom *Aulacoseira ambigua* disappears and is replaced by another centric diatom taxa *Aulacoseira perglabra* var. *florinae* and periphytic diatoms such as *Neidium ampliatum, Stauroneis anceps* and *Pinnularia* spp. Above the depth of 90 cm (ca. 3700 cal. yr BP), diatom preservation is relatively good and allows to calculate relative abundance of the taxa. Planktonic diatom *Aulacoseira lirata* predominates, and diatom-inferred lake water pH is 6.4 (Figure 6b). Further onwards, planktonic diatoms show declining trend and periphytic diatoms, such as *Fragilaria construens* var. *venter*, become more important, whereas diatom-inferred lake water pH slightly increases.

In the top of the core (in ca. 1960s), a prominent change in diatom composition occurs. The abundance of acidophilus diatoms, particularly *Eunotia* and *Pinnularia* taxa, increase; meroplanktonic diatoms are less common; diatom concentration reaches 700 × 10^4 valves cm^{-1} sediment; diatom-inferred lake water pH drops one unit from 6.9 to 5.9. In the surface sample, notable increase of *Navicula schassmannii, Navicula submuralis* and *Pleurotoma mediocris* is registered, and diatom concentration increases to 3800 × 10^4 valves cm^{-1} sediment; however, the diatom-inferred lake water pH remains low (Figure 6b).

The whole sediment record, except the intervals where diatom concentration is high, contains some diatom valves that suggest high salinity conditions, for example, *Paralia sulcata*, or pieces of unidentified marine diatoms. These diatoms with marine and brackish-marine affinity have derived from non-freshwater environments and should thus be interpreted as redeposited from older, for example, Paleogene deposits, when West Siberian Plain was captured by marine transgressions (Volkova, 2014).

Geochemistry

TOC and TN values vary from 0.38% to 42.6% and from 0.07% to 3.9%, respectively, and show similar trends over the studied time period (Figure 3). The minimum values of the whole core are registered at the depth of 325–310 cm (ca. 11,400–10,600 cal. yr BP). Thereafter, TOC and TN concentrations increase. Despite the quite abrupt increase of TOC at 300 cm, both TOC and TN stay relatively stable and low between 295 and 160 cm (ca. 9800–6700 cal. yr BP). Most prominent increase in the TOC and TN starts at the depth of 155 cm (ca. 6500 cal. yr BP). From 115 cm (ca. 4900 cal. yr BP) up to the surface of the core, values stay high.

Calculated atomic C/N ratio varies up to 18 units in the studied sediment profile (Figure 3). At the depth of 325–310 cm (ca. 11,400–10,600 cal. yr BP) C/N ratio is low and stays between 6 and 9. Thereafter, it increases abruptly to a maximum value of 24 at the depth of 300 cm (ca. 10,200 cal. yr BP) and stays high until 265 cm (ca. 8300 cal. yr BP). After this, C/N ratio gradually decreases towards the topmost part of the studied sediment sequence where it reaches the value of 10.

Discussion

The (hydro)climate of the Western Siberia during the Holocene has been changeable. The past climate reconstructions are based on indirect proxies – palaeobotanical record as the vegetation proxy is considered to react to climate changes (Blyakharchuk, 2009; Groisman et al., 2013). Western Siberia is a large and diverse region, and thus one of the issues regarding the palaeoecological reconstructions is the scattered palaeobotanical record and differences in local conditions (topography, permafrost, etc). It has been hypothesized that Ob River can influence the local climate characterized by air temperature anomalies related to water level (Agafonov et al., 2016). The main palaeoclimatic trend for the whole region shows the gradual warming in the first part of Holocene and gradual cooling later (Blyakharchuk, 2009) and suggests wet phases in Boreal and Atlantic periods (Groisman et al., 2013). The documentation of the past water level changes via the instrumental measurements of Ob River started at the 1930s (Yang et al., 2004). Presently, approximately 70% of the Ob River annual discharge occurs during the ice-free period from May to October; 80% of the annual runoff originates from south of the 61° north latitude. The hydrological regime of the Ob River is dominated by snowmelt, with peak flows in June to July (Agafonov et al., 2016).

The present study site is located near the confluence of the large rivers Ob and Irtysh and thus could be sensitive to the changes in the hydroclimate. The postglacial sedimentation in the Lake Svetlenkoye basin started approximately 11,400 cal. yr BP. The silty sediment indicates aquatic conditions within the sedimentary basin. Low C/N ratios, between 6 and 9 (Figure 3), reflect algal origin of OM (Meyers and Ishiwatari, 1993) and confirm that lacustrine environment existed. The humidity reconstructions suggest dry conditions at this time (Blyakharchuk, 2009). There is no plant macrofossil record from this layer, but the pollen spectrum reveals the regional dominance of pine, birch and spruce pollen with the addition of sedge and grass (Figure 5). The study from Salym Yugan mire (about 100 km SE from the present study site), contrarily, displays virtually no pine pollen record in the basal sediment section and proposes the treeless situation until 9900 cal. yr BP. However, the authors admit that the basal ages may be affected by the downwards transportation of younger carbon by roots or water (Pitkänen et al., 2002). The palaeo-record from Torfyanoy Yar (about 100 km south from the present study site) contains the pollen grains of trees (mixed forest), sedges and grasses since 11,500 cal. yr BP (Akhteryakova and Leshchinskiy, 2014). The pollen could be transported over the long distances while the plant macrofossils reflect the local dominant vegetation components. In the present study site, the tree-birch and spruce remains confirm the local presence of trees since at least 10,500 cal. yr BP.

A notable shift is recorded in most studied proxies from Lake Svetlenkoye approximately *10,500 cal. yr BP*. The sediment type changes from minerogenic silt to gyttja with visible plant detritus. C/N ratio doubles and reaches to its maximum of the whole sediment core (20–24), suggesting that the OM input was dominantly catchment-originated (Meyers, 1994; Meyers and Ishiwatari, 1993). Both TOC and TN content of the sediment increase (Figure 3). Numerous plant macrofossils could be found in the sediment afterwards (Figure 4). Our results most probably indicate the change in the size, depth and surroundings of the sedimentary basin. At first (10,500–9400 cal. yr BP), the plant macrofossil

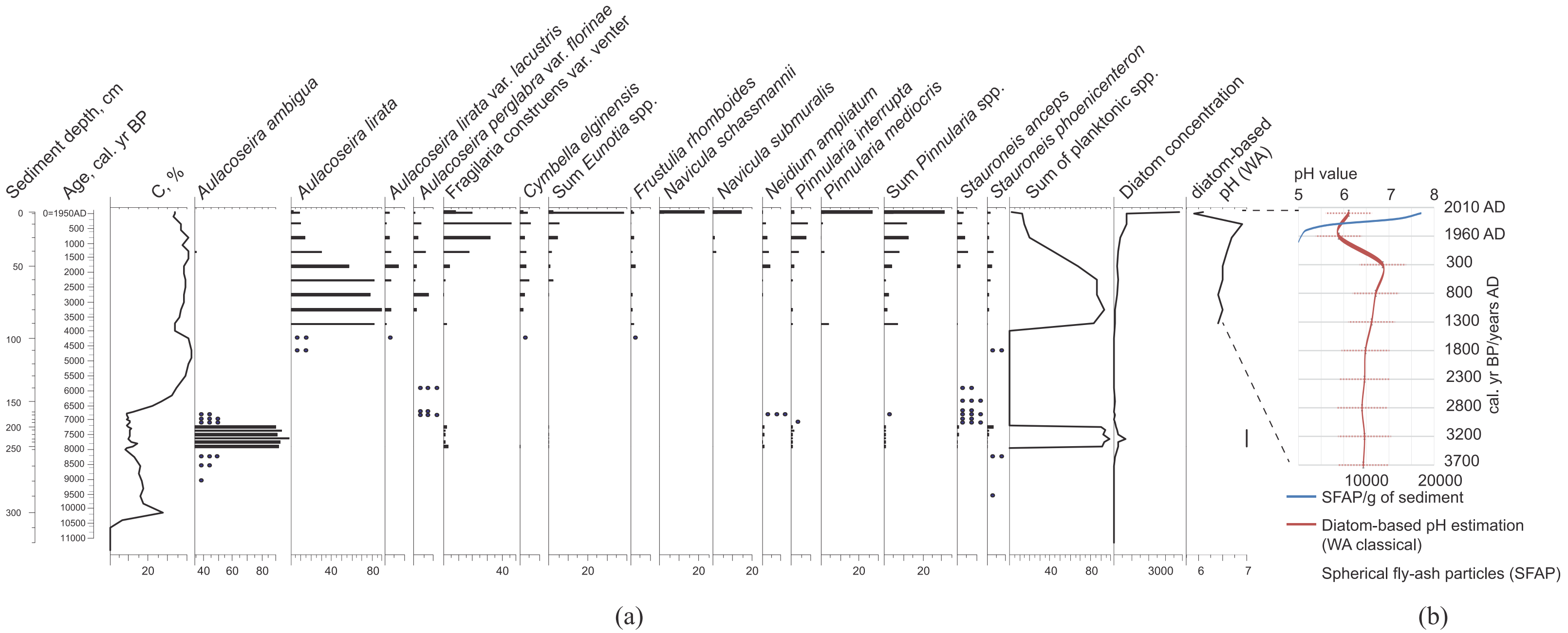

Figure 6. (a) Diatom record of Lake Svetlenkoye, carbon content of the sediment (C%) and diatom-based pH dynamics; (b) the fluctuation in the diatom-inferred lake water pH value in the upper 3700 cal. years of sediment plotted against the concentration of the spheroidal fly-ash particles (SFAPs). The dashed lines mark the calculated error margins of the diatom-based lake water pH values.

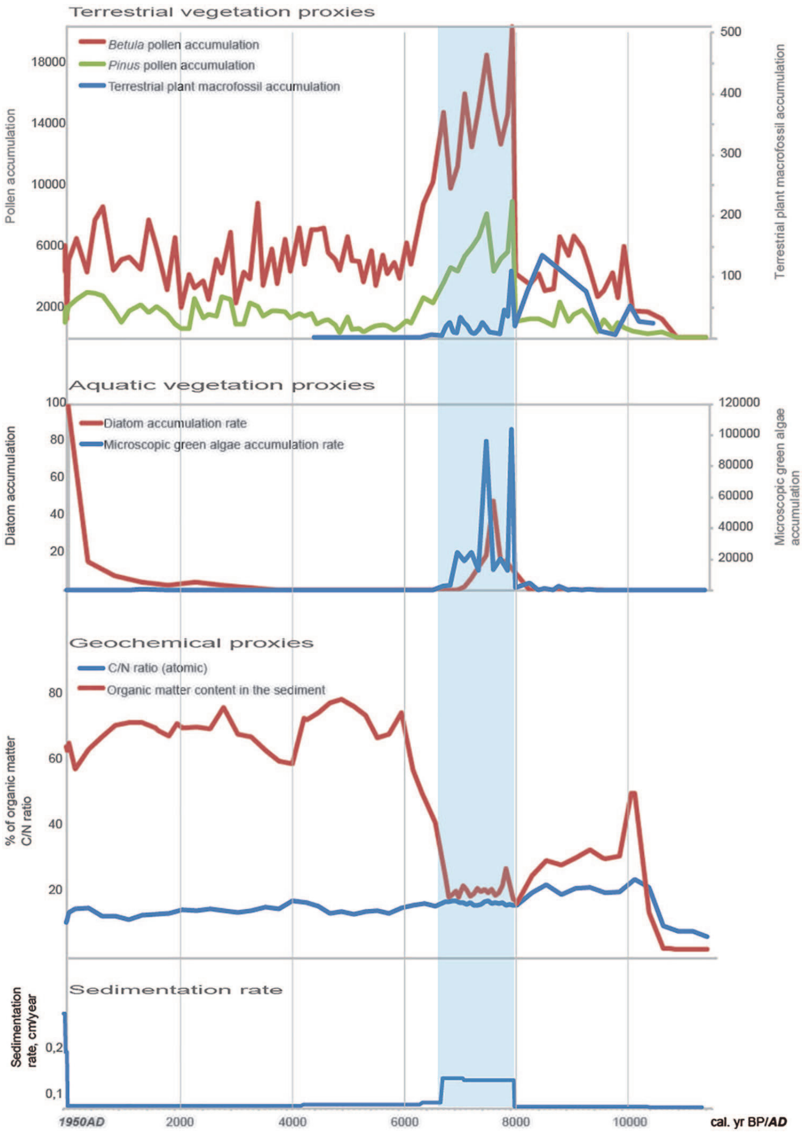

Figure 7. The compilation of sedimentation rate, various floral and geochemical data of Lake Svetlenkoye. The data are plotted against the chronology. Terrestrial vegetation proxies: birch and pine pollen, terrestrial plant macrofossil record. Aquatic vegetation proxies: microscopic green algae (*Pediastrum, Scenedesmus, Tetraedron*), diatoms. The unit of accumulation: number/cm^2/year. Geochemical proxies: organic matter content (as recorded by loss-on-ignition), C/N ratio. The shaded area depicts the period of flooding the study site by Ob River.

composition suggests that the vicinity of the coring point was under water or flooded but close to the palaeo-shore. On the shores of the study site grew mixed forest (birch, spruce, pine). The understory consisted of shrubs (cotoneaster, blackberry), grasses and ferns but also *Sphagnum* remains are recorded. Later, the surroundings of shallow Lake Svetlenkoye started to paludify. It is suggested by the shift in the plant macrofossil composition from species that prefer to grow near or in the water (e.g. *Potamogeton, Hippuris, Schoenoplectus*) to wetland/mire species (e.g. *Andromeda, Comarum*). The occurrence of mire/bog species (*Comarum, Andomeda, Eriophorum*) suggests that the notable paludification of the shore took place ~8500 cal. yr BP. The wetland was still surrounded by mixed forest.

The rich local flora relates to past warming. In the second half of the Preboreal period (Figure 7; 10,300–9100 ^{14}C yr BP) (Groisman et al., 2013), the warmer climate promoted the migration of *Abies* in the taiga zone and more drier conditions facilitated the spread of the birch-steppe in the forest zone of Western Siberia. The summary of the next palaeoclimatic epoch, Boreal, reveals the warmer winter and cooler summer temperatures than today. The decreased glaciation of the Arctic Sea influenced warm sea currents and formation of intensive northwestern transfer of wet air masses from the north of Fennoscandia increasing the precipitation over Siberia. The total annual precipitation rate was approximately 25 mm higher than today (Groisman et al., 2013). One of the available humidity reconstructions shows the maximum level of wetness of the Holocene during the Boreal period (Blyakharchuk, 2009). The observed shift from the lake-shore community to the mire community that marks the exceeding of the wetland is in good agreement with the study from Salym

Yugan where large-scale paludification is suggested between 10,000 and 7000 cal. yr BP (Turunen et al., 2001). In our study, the change took place 9400–8500 cal. yr BP, that is, during the second part of Boreal and the first part of Atlantic period.

The next major palaeoenvironmental shift in Lake Svetlenkoye occurs approximately *8100–8000 cal. yr BP* (Figure 7). The sediment type changes from plant-rich detrital gyttja to homogeneous gyttja; the AR increases more than four times. Both TOC and TN content have a small rise around 8100 cal. yr BP that is followed by generally low values (Figure 3). C/N ratio starts to gradually decline, indicating that OM of terrestrial origin was slowly replaced by the OM from lacustrine sources. The number of plant macrofossils in the sediment decreases except for one peak in plant macrofossil AR around 8100 cal. yr BP. The AR of birch and pine pollen as well total PAR increases (Figure 7). The rise in the AR of terrestrial proxies is presumably tied to the change in sedimentation rate. The occurrence of planktonic diatoms is symptomatic to lotic ecosystem (Figure 6) and the microscopic green algae appear in notable quantities in the pollen spectrum (Figure 5).

Even if the diatom-based palaeohydrological reconstruction is impossible because of the dissolution of diatoms in the lowermost sediment sequence, diatom composition in the time interval from 7900 to 7100 cal. yr BP mostly includes heavily silicified planktonic *Aulacoseira* taxa, including *Aulacoseira ambigua.* Freshwater riverine planktonic species of the genus *Aulacoseira* (e.g. *Aulacoseira granulata, Aulacoseira ambigua, Aulacoseira subarctica*) are common in large Siberian rivers (e.g. Bauch and Polyakova, 2003; Genkal and Romanov, 2012; Sukhanova et al., 2015). Based on that evidence, one could presume that the studied basin of that time resembled fluvial-erosional lakes on modern floodplain of the large rivers that are remnants of former river channels or meanders (Pestryakova et al., 2012). In addition, constantly low TOC values and high sediment AR also point to periodical and enhanced Ob River water supply.

All the mentioned changes suggest the increase in the water level – the basin of Lake Svetlenkoye was connected or flooded by Ob River waters. This period of flooding (8000–6700 cal. yr BP) could be tied to the palaeoclimatic situation: during the Atlantic period, the climate was warmer and wetter than today (Blyakharchuk, 2009; Groisman et al., 2013). In the Atlantic period, the final retreat of Scandinavian Ice Sheet and weakening of the associated European High led to the formation of direct transfer of air masses eastwards from the Atlantic (Groisman et al., 2013). The flat relief of the vicinity of Ob River contributes to the poor drainage and induces the local floodings (Kremenetski et al., 2003). The extra input of precipitation/water to the Ob River and maybe limited infiltration may have caused the flooding in the study site area. The humidity reconstructions display the notably wet period in Western Siberian forest zone (Blyakharchuk, 2009). It is difficult to evaluate past reaction time of Ob River water amount to the increased precipitation regime. One reconstruction indicates the wettest period during the Boreal, that is, earlier than the flooding period in the present study site although the flooding period is reconstructed as wet one, too (Blyakharchuk, 2009). Another reconstruction from the central part of Western Siberian forest zone (Blyakharchuk, 2009) corresponds better with our results showing the Holocene maximum wet period at the time of flooding of Lake Svetlenkoye. Another question that stays unanswered in this paper is whether the flooding was a local event or did it also cause higher water discharge rates to the Arctic ocean, thereby indirectly affecting the hydrology of the Arctic Sea, Atlantic meridional overturning circulation, and so on.

The elevated temperature (up to 1.5°C higher than today) and precipitation during the Atlantic period promoted the spread of mixed forest and the vegetation zones shifted 200–300 km northwards (Groisman et al., 2013). The pollen analysis of the present study site found the maximum postglacial percentage of spruce pollen grains in the spectrum between 8000 and 6400 cal. yr BP (Figure 5). The sediments from this period contained macroremains of both spruce (*Picea obovata*) and tree-birch (*Betula pendula*). However, the flooding might also have brought additional palaeobotanical material. The pollen record of Torfyanoy Yar from about 8000 cal. yr BP reveals the dominance of birch pollen with pine and spruce, but also flourishing of Rosaceae and sedges (Akhteryakova and Leshchinskiy, 2014).

Another shift in most proxies of Lake Svetlenkoye occurs approximately *6800–6700 cal. yr BP* (Figure 7). The microscopic green algae disappear, but since ~6500 cal. yr BP, the sediment includes large quantities of chironomid head capsules. The sediment AR starts to decrease since 6700 cal. yr BP. Simultaneously, TN and TOC contents increase distinctly since ~6600 cal. yr BP (Figure 3); combined with lower C/N ratios, it could be interpreted as a signal of enhanced limnic phytoplankton (N-rich) productivity (Meyers, 1994). In addition, aforementioned observations are coincident with disappearance of riverine planktonic *Aulacoseira* taxa, and appearance of another centric diatom *Aulacoseira perglabra* var. *florinae* and periphytic diatoms such as *Neidium ampliatum, Stauroneis anceps* and *Pinnularia* spp., taxa common in the nutrient poor freshwater clear water small lakes.

The set of changes in proxies leads to a hypothesis that at this period, Lake Svetlenkoye became isolated from the Ob River. The isolation may have been because of different factors. The humidity reconstructions display a decrease suggesting drier conditions in West Siberian forest zone (Blyakharchuk, 2009). On the contrary, the previous vegetation growth and peat accumulation might have reached a level when it slowly started to build the barriers in the flat landscape.

Lakes are intimately linked to their watershed. The vegetation around Lake Svetlenkoye after the isolation event can be described only based on pollen record as there are almost no plant macrofossils in the sediment. No major changes are visible in the pollen composition indicating that lake catchment terrestrial soils and vegetation remained stable over a long period of time. European pollen studies usually show an increase of palynological richness during the last millennia of the Holocene which is associated with human impact (Berglund et al., 2008; Reitalu et al., 2015). In Lake Svetlenkoye pollen record, there is no clear temporal trend in the richness values towards the present day indicating none or very low human impact on the vegetation.

Sediments accumulated in between time frame of 7000 and 4000 cal. yr BP are characterized by poor diatom preservation, few taxa and low diatom concentration. Paull et al. (2017) suggest that poor diatom preservation in lake sediments records from Canadian Arctic may be associated with warmer climate conditions. Around 3700 cal. yr BP, diatom record shows much better preservation than before. *Aulacoseira lirata, Aulacoseira lirata* var. *lacustris* and *Aulacoseira perglabra* var. *florinae* dominate until 1800 cal. yr BP. These diatoms are regarded as meroplanktonic diatoms (Anderson et al., 1996) that spend at least part of the life span in the open water and part on the bottom substrate. These species can be components of chemically dilute, arctic tundra and forest-tundra open water lakes as these heavily silicified centric taxa prefer windy turbulent lake conditions to maintain their position in the photic zone (e.g. Rühland and Smol, 2002). The diatom-inferred pH (6.4) suggests slightly acidic lake water. After 1300 cal. yr BP, small benthic *Fragilaria* taxon increases, and proportion of meroplanktonic taxa decreases, whereas inferred lake water pH remains stable. Climate change influences the timing of lake ice melt, ice duration, and lake thermal dynamics in cold regions (Weckström et al., 2014). Small-sized fragilarioid diatoms are often associated with colder and longer winters, and are more competitive in lakes with an extensive and long-lasting ice cover (Smol et al., 2005). However, the concurrent climate cooling in the late-Holocene is not revealed by independent terrestrial floristic proxies.

The considerable short-term shift in the diatom composition and diatom-inferred lake water pH reconstruction suggests recent acidification of 1.0 pH units during the last 50 years (Figure 6b). There is a clear temporal overlap between the increase of acidophilus diatoms and fossil fuel burning–derived SFAP concentration. Atmospheric emissions associated with increased anthropogenic activity, such as burning of fossil fuels, resource extraction, accelerating industry, and so on, have led to distinct pH drop and the acidification of aquatic freshwater systems since second half of 20th century in many parts of Europe (e.g. Renberg and Hellberg, 1982) and North America (e.g. Kingston et al., 1990). Studies on the possible anthropogenic airborne forcing influence on lake ecosystems are still limited in Western Siberia. Mining and smelting activities have resulted in tremendous emissions of sulphur acidic compounds at Norilsk area, central-northern Siberia; however, the lakes' diatom composition has experienced relatively little change since pre-industrial times because of lakes' strong buffering capacities as a result of the surrounding carbonate bedrock and overlying calcareous glacial deposits (Michelutti et al., 2001). Fedotov et al. (2016) recognized example of lake water acidification and declined pH values within the recent decades (past ~50 years) in mountain Lake Oron, East Siberia. However, they assumed that recent acidification presumably follows natural factors, such as climate warming and inflow of ultrafresh waters from the thawing glaciers, in addition to accelerated emissions of endogenous methane, rather than human-induced long-range acid emissions.

In addition, to drop in diatom-derived lake water pH, Lake Svetlenkoye recent sediment diatom assemblage indicates loss in the meroplanktonic diatoms that are commonly less encountered in acidic dilute lakes. Moreover, epiphytic bryophilous *Eunotia* spp. taxa and *Navicula schmassmannii* are common in oligotrophic Arctic environments and have been reported to be aerophilic moss-dwelling species (Paul et al., 2010). Current paleolimnological study has performed at relatively coarse sampling intervals, also field measurements of pH in Lake Svetlenkoye are not available. Therefore, our study does not allow to make final conclusion that the drop in lake water pH during the final decades of the 20th century can be either related to long-range airborne anthropogenic acidification or associated with recent climate warming. Finkelstein et al. (2014) suggest that lake water pH changes in Arctic lakes can be the complex relationships between geology, catchment and lake processes, including paludification and vegetation succession, and climate forcing.

Conclusion

- Our results illustrate the effect of changing wetness on the local hydrology and vegetation based on the sediment record from a small lake near the confluence of two large Siberian rivers, Ob and Irtysh. The palaeoecological proxies suggest that during the Holocene, the humidity levels in the Western Siberia fluctuated and probably had a feedback on the large Siberian rivers. The wetter palaeoclimatic periods resulted in larger amount of water to the rivers. This possibly caused flooding on the flat surroundings or change in streams/riverbed size and shape.
- Three stages in the development of Lake Svetlenkoye were detected. First (ca. 11,400 until 8100 cal. yr BP), a relatively shallow water body existed as suggested by large amounts of plant macrofossils and high C/N ratio. Second, from 8100–8000 until ca. 6800–6700 cal. yr BP, the Ob River waters flooded the location as confirmed by remarkable increase in the accumulation of the aquatic vegetation proxies and the sedimentation rate as well by the specific diatom record. This period coincides with the wet or even Holocene maximum level of humidity suggested by the palaeo-humidity reconstructions (Blyakharchuk, 2009) for the central Western Siberian forest zone. Third, ~6700–6800 cal. yr BP, the study site became isolated from the Ob River and stayed as a small lake until present.
- The diatom-based lake water pH estimations suggest the fluctuations in the pH values, the recent decrease being the most notable. The drop in the pH value coincides with the rise in the number of anthropogenic fossil fuel combustion recorded by SFAPs and dates the onset of the industrialization process to the 1960s. However, our study does not allow to make conclusion that the cause of lake water acidification during the final decades of the 20th century can be either related to long-range airborne anthropogenic emissions or associated with natural processes like recent climate warming.
- The climate and humidity changes are reflected by the vegetation development. The findings confirm the presence of local mixed forest around the sedimentary basin since 10,500 cal. yr BP while the lake shores were covered by *Schoenoplectus, Carex* and *Typha*. Later (~8500 cal. yr BP), the species more typical to mires and bogs were found in sediment (*Andromeda, Comarum, Eriophorum*) suggesting the formation of wetland on the surroundings of the study site. Until 6400 cal. yr BP, a mixed forest surrounded the mire. Afterwards, the significance of *Betula* pollen proportion increased, contrary to the decrease of *Pinus* and *Picea* pollen. At the same time, occurrence of broad-leaved taxa (*Ulmus, Alnus*), decrease of Cyperaceae and increase in variety of different herbaceous pollen types such as *Artemisia*, Chenopodiaceae and Apiaceae indicate climate shift to warmer and drier conditions associated with Atlantic period.

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Supplemental material

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RESEARCH ARTICLE

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Patterns of modern pollen and plant richness across northern Europe

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Abstract

1. Sedimentary pollen offers excellent opportunities to reconstruct vegetation changes over past millennia. Number of different pollen taxa or pollen richness is used to characterise past plant richness. To improve the interpretation of sedimentary pollen richness, it is essential to understand the relationship between pollen and plant richness in contemporary landscapes. This study presents a regional-scale comparison of pollen and plant richness from northern Europe and evaluates the importance of environmental variables on pollen and plant richness.
2. We use a pollen dataset of 511 lake-surface pollen samples ranging through temperate, boreal and tundra biomes. To characterise plant diversity, we use a dataset formulated from the two largest plant atlases available in Europe. We compare pollen and plant richness estimates in different groups of taxa (wind-pollinated vs. non-wind-pollinated, trees and shrubs vs. herbs and grasses) and test their relationships with climate and landscape variables.
3. Pollen richness is significantly positively correlated with plant richness ($r = 0.53$). The pollen plant richness correlation improves ($r = 0.63$) when high pollen producers are downweighted prior to estimating richness minimising the influence of pollen production on the pollen richness estimate. This suggests that methods accommodating pollen-production differences in richness estimates deserve further attention and should become more widely used in Quaternary pollen diversity studies.
4. The highest correlations are found between pollen and plant richness of trees and shrubs ($r = 0.83$) and of wind-pollinated taxa ($r = 0.75$) suggesting that these are the best measures of broad-scale plant richness over several thousands of square kilometres.

5. Mean annual temperature is the strongest predictor of both pollen and plant richness. Landscape openness is positively associated with pollen richness but not with plant richness. Pollen richness values from extremely open and/or cold areas where pollen production is low should be interpreted with caution because low local pollen production increases the proportion of extra-regional pollen.
6. *Synthesis*. Our results confirm that pollen data can provide insights into past plant richness changes in northern Europe, and with careful consideration of pollen-production differences and spatial scale represented, pollen data make it possible to investigate vegetation diversity trends over long time-scales and under changing climatic and habitat conditions.

KEYWORDS
climate, diversity, Holocene, landscape, palynological diversity, pollen–plant relationship, Quaternary

1 | INTRODUCTION

The regional and global gradients of species diversity—with richness in most taxon groups decreasing from lower to higher latitudes—are well known and the mechanisms behind this pattern are widely discussed (e.g. Gaston, 2000; Hawkins et al., 2003; Ronk, Szava-Kovats, & Pärtel, 2015; Whittaker, Nogués-Bravo, & Araújo, 2007; Worm & Tittensor, 2018). Contemporary climate regulates the availability of water and energy and is strongly associated with broad-scale richness patterns (Hawkins et al., 2003). However, historical factors—both evolutionary history and migration during periods of rapid climate change—have undoubtedly also influenced the patterns of present-day diversity (e.g. Flenley, 2005; Gaston, 2000; Kreft & Jetz, 2007). For example, the contemporary relationships of plant diversity with pH and productivity depend on the environmental conditions in evolutionary centres and the consequent size of regional species pools (Hájek et al., 2007; Harrison & Grace, 2007; Pärtel, 2002). The spread of species and the development of vegetation patterns during the Pleistocene–Holocene transition about 14,000–11,000 years ago offers the closest analogue to the ongoing climate change and helps to improve the projections of biodiversity responses to changing climate (Stivrins et al., 2016). Insights into past long-term changes in vegetation diversity are therefore extremely valuable for evaluating the current and future biodiversity changes.

Palaeoecological material, for example remains of organisms preserved in lake and mire deposits and caves, provides a means to study the historical development of vegetation types and landscapes over the last millennia. In fact, most of our knowledge about regional-scale vegetation history in the late Quaternary comes from sedimentary pollen data (e.g. Smol, Birks, & Last, 2001). Plant macrofossils (e.g. Amon, Veski, & Vassiljev, 2014; Birks, 2003) and, during the last decade, ancient DNA (e.g. Jørgensen et al., 2012; Parducci et al., 2013) can complement the picture by providing a more local-scale signal. In addition to reconstructing land-cover changes and species-spreading patterns, pollen data can be used to derive information about past vegetation diversity (e.g. Birks, Felde, & Seddon, 2016; Giesecke, Wolters, Jahns, & Brande, 2012; Reitalu et al., 2015; Weng, Hooghiemstra, & Duivenvoorden, 2007). Pollen richness is often used in addition to traditional pollen diagrams to characterise changes in plant richness. To improve the interpretation of the sedimentary pollen diversity, it is essential to understand the relationships between pollen and plant data in contemporary landscapes. There are several studies that have investigated modern pollen–plant diversity relationships (e.g. Felde, Peglar, Bjune, Grytnes, & Birks, 2016; Matthias, Semmler, & Giesecke, 2015; Meltsov, Poska, Odgaard, Sammul, & Kull, 2011; Meltsov, Poska, Reitalu, Sammul, & Kull, 2013) and the results usually show a positive relationship between modern pollen and plant diversity estimates (but see Goring, Lacourse, Pellatt, & Mathewes, 2013; Gosling et al., 2018). Most of these modern-day pollen–plant studies are done at relatively local scales where climate variation is small and the diversity relationships mainly depend on landscape factors (e.g. Matthias et al., 2015; Meltsov et al., 2013) within the relevant source area of pollen (RSAP). RSAP is defined by Sugita (1994) as the area beyond which the strength of the pollen–vegetation relationship does not improve. However, when using pollen richness in stratigraphic studies that cover the entire postglacial, the climate gradient is relatively large and it is not clear how the pollen–plant diversity relationship behaves along such a gradient and whether climate and/or landscape variables interact with the pollen–plant diversity relationship. In the present study, we test the relationships between pollen and plant richness across northern Europe covering a mean annual temperature range from −6.8°C to 9.2°C. We take advantage of existing European-scale modern pollen and plant datasets allowing us to consider both pollen and plant richness estimates.

The relationship between pollen and plant richness is influenced by interspecific differences in pollen production and dispersal causing over-representation of some taxa and under-representation or absence of other taxa in pollen assemblages (Birks, Felde, Bjune et al., 2016; Odgaard, 1999; Weng, Hooghiemstra, & Duivenvoorden, 2006). One proposed solution is to use representation factors that downweight the influence of numerically dominant pollen taxa (Andersen, 1970; Felde et al., 2016) or to look separately at groups of taxa with different pollination types, for example wind-pollination versus insect-pollination (Weng et al., 2006).

When using pollen richness as a proxy for plant richness, it is assumed that the relationship remains constant in different climatic and landscape conditions and that environmental variables influence pollen richness via their influence on plant richness. However, it is unclear how much of the variation in pollen richness is a reflection of plant richness and how much the variation in pollen richness is influenced directly by environmental variables. For example, it is well known that plant richness in Europe follows the major temperature gradient (Whittaker et al., 2007) but pollen richness can be influenced by temperature both indirectly through plant richness and directly through the influence of temperature on pollen production. Landscape diversity and openness are known to influence plant diversity (Reitalu et al., 2014; Ronk et al., 2015) but both factors can also directly influence pollen dispersal patterns (Odgaard, 1999; Sugita, Gaillard, & Broström, 1999). For example, it is known that the pollen-source area is larger in open areas and richness estimates tend to be higher because of a larger "sampling" area (Odgaard, 1999; Sugita et al., 1999). In mountainous areas at high elevations, pollen has been shown to be transported from the lowlands (Bajpai & Kar, 2018; Bell & Fletcher, 2016) and might thereby influence the pollen–plant richness relationship. Landscape openness in the present-day world is closely associated with human impact with agriculture greatly increasing the extent of open area. Over broad spatial scales, human population size has been shown to correlate positively with species richness in different taxonomic groups (Pautasso, 2007) suggesting that people have preferred to settle in areas of high biodiversity. Moderate human impact increasing landscape diversity and providing habitats for synanthropic species is known to increase both species and pollen richness (Colombaroli, Beckmann, Knaap, Curdy, & Tinner, 2013; Felde, Grytnes, Bjune, Peglar, & Birks, 2018; Reitalu et al., 2015, 2014), while too intensive human impact can cause local or even total extinction of species (Ceballos et al., 2015).

In the present study, we look in detail into the relationships of plant and pollen richness with a range of environmental factors that characterise both climate and landscape structure. Linear mixed effects (LME) modelling and variation partitioning are used to examine the differences and similarities between pollen and plant richness in relation to environmental factors.

The main aim of this study was to compare patterns of pollen and plant richness across northern Europe in relation to a range of climate and landscape factors. More specifically, we address the following questions:

1. Does pollen richness reflect plant richness?
2. Are pollen–plant richness relationships different within groups of taxa (wind-pollinated vs. not wind-pollinated, trees and shrubs vs. herbs and grasses)?
3. Are plant and pollen richness influenced by climate and landscape factors?

2 | MATERIALS AND METHODS

2.1 | Pollen data

The modern pollen dataset of lake-surface samples was compiled from Salonen, Seppä, Luoto, Bjune, and Birks (2012) and Matthias et al. (2015) and comes from small- to medium-sized lakes (median lake size 9 ha). These samples were collected and prepared in the laboratory using harmonised methodology (Seppä, Birks, Odland, Poska, & Veski, 2004) but counted by a number of different pollen analysts. Geographically, the dataset covers Scandinavia (including Svalbard), Finland, the Baltic countries, the western and northwestern parts of Russia (Salonen et al., 2012) and northern Germany (Matthias et al., 2015) (Figure 1), ranging through temperate, boreal and tundra biomes. In total, the dataset includes 633 pollen lake-surface samples. Spores from sporophytes were excluded from the dataset and the richness estimates only include seed plants. Aquatic plants are included in the richness estimation. After taxonomic harmonisation, there are 173 pollen types (Appendix S1).

The combined dataset includes pollen data from different subregions and different analysts resulting in some variation in the number of pollen grains counted from each pollen sample (the pollen sum) ranging from below 200 in the northernmost sites to over 1,000 in the southern sites. For pollen richness, rarefaction analysis where the richness is estimated for a fixed pollen sum is usually recommended (Birks & Line, 1992). In the present study, we use a pollen sum of 500 terrestrial pollen grains. There were 143 samples with a pollen sum below 500. In areas where several sites with low pollen sums are spatially close (less than 50 km), the samples were pooled to achieve the >500 pollen sum. The samples with pollen sums below 500 which could not be grouped together were excluded from the analyses. As a result, we used data from 511 samples: 21 combined samples (from Svalbard, northern Norway and Russia) and 490 samples where the pollen sum was already >500.

2.2 | Plant data

To characterise plant richness, we merged the two largest plant atlases available in Europe, Atlas Florae Europaeae (Jalas & Suominen, 1972; Jalas, Suominen, & Lampinen, 1996; Jalas, Suominen, Lampinen, & Kurtto, 1999; Kurtto, Lampinen, & Junikka, 2004) and Atlas of North European Vascular Plants (Hultén & Fries, 1986) as described in Kalwij, Robertson, Ronk, Zobel, and Pärtel (2014). The resulting dataset is the most comprehensive broad-scale plant distribution data to date, with distribution information for 5,221 European plant taxa (species and subspecies), i.e. approximately half the estimated number of flowering plant taxa in Europe (Mutke, Kreft, Kier, & Barthlott, 2010; Tutin, 1980).

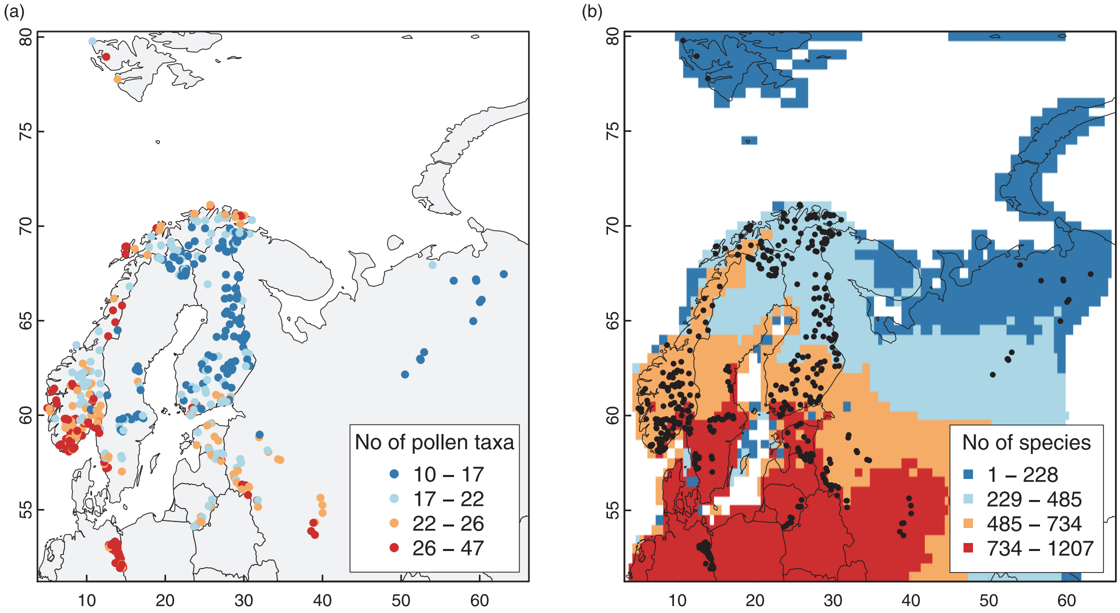

FIGURE 1 Map of northern Europe with (a) pollen richness (per 500 pollen grains) in lake-surface samples and (b) locations of surface-sample lakes on the plant richness map

The resolution of the plant dataset is 50 × 50 km. We first calculated plant richness for the grid cells where the pollen-sample lakes are situated. Second, we calculated the cumulative richness of three grid cells with centroids closest to each of the lakes. A preliminary correlation test indicates that the relationship between pollen and plant data is stronger with plant richness from the larger area ($r = 0.47$ for one 50 × 50 km quadrat and $r = 0.53$ for three 50 × 50 km quadrats). The richness data from one grid cell are likely to include a larger random component compared to larger areas. The sampled lakes are not necessarily in the middle of the grid cells and the richness of the larger area therefore gives a more stable result. We thus use the plant richness data from three grid cells in all subsequent analyses and all plant richness estimates were calculated at that scale of 3 × 50 × 50 km (=7,500 km^2). In case of the 21 pooled pollen samples with pollen data from several lakes, all lakes are situated within the same three plant grid cells and plant richness is calculated similarly to other samples based on cumulative number of species in the three cells. The plant dataset includes 1982 species in total. In the pollen analysis, only a few plant species are separable to species level. To test the effect of this taxonomic bias, the plant data were translated into pollen types according to Felde, Birks, Peglar, Grytnes, and Bjune (2017), which resulted in 388 pollen types or pollen equivalents (Birks, Felde, Bjune et al., 2016).

2.3 | Richness calculations

To equalise sampling effort in the richness estimations using 500 pollen grains, we randomly resampled 500 pollen grains from each pollen sample without replacement and repeated the randomisation 1,000 times—a procedure analogous to rarefaction analysis (Birks, Felde, Bjune et al., 2016; Felde et al., 2016). All the subsequent calculations of different pollen richness measures are based on each of the 1,000 randomisation draws and the average of the 1,000 is used as the richness estimate.

Pollen richness (number of all pollen taxa among 500 grains) and plant richness (number of all plant species) (Figure 1) are used as the main descriptors of pollen and plant diversity and for testing the relationships with environmental variables. To test whether pollen richness is a better predictor of plant richness in some taxon groups, we calculate both pollen and plant richness separately for wind-pollinated taxa and for non-wind-pollinated taxa, for trees and shrubs, and for herbs and grasses. Information about pollination modes was obtained from the plant trait database BiolFlor (Kühn, Durka, & Klotz, 2004). The pollination mode of pollen taxa is determined based on the prevailing pollination mode of the species within the taxon. The division of pollen taxa into these different taxon groups is given in Appendix S1. To estimate how the differences in taxonomic resolution in the pollen and plant data affect the possibilities of inferring plant diversity from pollen diversity, plant richness is expressed as richness of pollen types and both plant and pollen richness are expressed as richness of families.

To test for the effect of pollen-representation bias on pollen diversity estimates, we use Andersen-transformed pollen values (cf. Felde et al., 2016). Pollen counts of common tree and shrub taxa were multiplied by Andersen's (1970) general pollen-representation values and the new minimum pollen sum (149 pollen grains) used for rarefaction analysis with 1,000 randomisations.

In summary, pollen diversity is characterised as: total pollen richness (R_{po}), Andersen-transformed R_{po}, R_{po} of families, R_{po} of herbs and grasses, R_{po} of trees and shrubs, R_{po} of wind-pollinated taxa and R_{po} of non-wind-pollinated taxa. Plant diversity is characterised as: total richness (R_{pl}), R_{pl} of pollen types, R_{pl} of families, R_{pl} of herbs and grasses, R_{pl} of trees and shrubs, R_{pl} of wind-pollinated species and R_{pl} of non-wind-pollinated species.

2.4 | Environmental data

We use climate data from the WorldClim database (www.worldclim.org) (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) and the 10-arc-minute "bioclim" dataset which includes 19 bioclimatic variables that are calculated from monthly temperatures and rainfall data for 1961–1990 (O'Donnell & Ignizio, 2012). In addition to these bioclimatic data, we use windspeed data from the ERA-Interim analysis (Dee et al., 2011). Because the bioclimatic variables are highly intercorrelated, we used principal components analysis (PCA) to choose a subset of climate variables. The first six PCA axes explain 98% of the variation in the climate dataset (PC1 explains 54% of the variation, PC2 22%, PC3 9%, PC4 6%, PC5 4%, PC6 3% and all the other principal components less than 1%). Six climate variables are chosen for subsequent analyses based on their correlations with the first six PCA axes (Appendix S2 Table S2.1) and intercorrelations with other climate variables (Appendix S2 Table S2.2). For example, the first PCA axis was clearly associated with precipitation—precipitation of driest quarter, precipitation of coldest quarter, precipitation of driest month and annual precipitation have the highest loadings along PC1. Because all four precipitation variables are highly intercorrelated ($r > 0.98$), we choose annual precipitation as the most widely known precipitation variable in our analysis.

1. **Annual precipitation**—total annual precipitation (mm/year);
2. **Mean annual temperature**—mean annual temperature (°C);
3. **Precipitation seasonality**—coefficient of variation in monthly precipitation totals;
4. **Temperature seasonality**—standard deviation of monthly temperature averages;
5. **Isothermality**—size of day-to-night temperature oscillation in relation to annual oscillations, mean diurnal range divided by the annual temperature range;
6. **Windspeed**—average windspeed (m/s) for spring and summer (April–August) 10 m above the ground (averaged for 1979–1998).

Six landscape variables known from previous studies (overview in Birks, Felde, Bjune et al., 2016) to influence plant and/or pollen richness are used to characterise the landscape:

1. **Lake area**—the surface area of the pollen-sample lake (in ha), estimated from Google Maps (Google, 2016);
2. **Elevation**—elevation of each pollen-sample site (m above sea level), extracted from ETOPO1 1 Arc-Minute Global Relief Model (Amante & Eakins, 2009);
3. **Elevation variation**—characterises the variation in topography in a 50 km radius around each pollen-sample site, standard deviation of the elevation of ETOPO1 model (Amante & Eakins, 2009);
4. **Openness**—landscape openness calculated from a global forest-cover dataset (Hansen et al., 2013): the original 30-m-resolution dataset was resampled to a 900-m-resolution and average openness in a 50-m radius around the pollen-sample sites is calculated as 100 minus the forest cover;
5. **Landscape diversity**—Simpson diversity estimate for a 50 km radius around each pollen-sample site, based on the land-cover types in the Global Land Cover 2000 database at 1 km resolution (Hartley et al., 2006);
6. **Human population**—human population density (persons/km^2), extracted from the Gridded Population of the World (GPW) database (Center for International Earth Science Information Network, 2016). We use the average population density of the 50 km radius area around each pollen-sample site calculated from the 0.5 arc-minute resolution map.

In case of the 21 pooled pollen samples with pollen data from several lakes, environmental variables are calculated as averages of the lakes included in the pooling with the exception of lake area that is calculated as the sum of lake areas. The correlations among the landscape variables do not exceed 0.6 and all variables are retained in the subsequent analyses (Appendix S2 Table S2.2).

2.5 | Statistical analyses

Correlations between the pollen and plant variables and among the environmental variables are quantified by Pearson's product moment correlation coefficients.

To identify environmental and climate variables associated with plant and pollen richness, we use LME models (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To account for the pollen data from different regions being analysed by different scientists and to account for the regional differences in the plant and pollen data, we use "Region" as a random variable in the LME model. Nine regions were used: Estonia, Finland, Germany, Lithuania, Norway (including Svalbard), Sweden1 (analysed in Bergen), Sweden2 (analysed in Helsinki), Russia1 (Komi region) and Russia2 (western Russia). Pollen richness (per 500 pollen grains) and plant richness (in three 50 × 50 km plots) are used as response variables. Six climate variables (annual precipitation, mean annual temperature, precipitation seasonality, temperature seasonality, isothermality, windspeed) and six landscape variables (lake area, elevation, elevation variation, openness, landscape diversity, human population density) are used as explanatory variables. Quadratic terms of all explanatory variables are tested. Log-transformation is used for annual precipitation, windspeed, lake area and human population density to ensure a uniform data distribution. Both richness data and explanatory variables are standardised to zero mean and unit variance to enable comparison of model estimates. Backward selection of explanatory variables is used and only significant ($p < 0.01$) variables retained in the models. Marginal pseudo-R^2 (reflecting the variation explained by fixed variables) and conditional pseudo-R^2 (reflecting the variation explained by both random and fixed variables) are calculated for the models according to Nakagawa and Schielzeth (2013). In models describing pollen richness, plant richness is also used as an explanatory variable. To test whether the relationship between pollen and plant richness is influenced by climate or landscape configuration, a separate model-selection procedure is used to test for interactions between plant richness and environmental variables in explaining pollen richness.

Linear mixed effect models with pollen richness as response, environmental variables as fixed variables, and "Region" as a random variable do not have significant spatial autocorrelation in the errors. However, errors of the LME models with plant data as the response remain spatially autocorrelated. To clarify the proportions of variation explained by purely spatial variation, climate, and landscape variables, we use variation partitioning (Borcard, Legendre, & Drapeau, 1992). Moran's eigenvector map (MEM) approach (Griffith & Peres-Neto, 2006) is used to characterise the spatial structure in the data. In the MEM approach, orthogonal, linearly independent (MEM) eigenvectors are calculated from a spatial weighting matrix. Based on permutation tests, a set of MEM variables significantly ($\alpha < 0.05$) contributing to minimising the global Moran's I is chosen and used as explanatory variables in variation partitioning. In addition to spatial descriptors (the MEM variables), explanatory datasets characterising climate (annual precipitation, mean annual temperature, precipitation and temperature seasonality, isothermality, windspeed) and landscape (elevation, variation in elevation, openness, landscape diversity, human population density) are used in variation partitioning. In the case of pollen richness, plant richness is considered as an additional explanatory variable.

The LME analysis and variation partitioning are primarily used to test the effect of climate, landscape and spatial variables on total pollen and plant richness. However, similar analyses are followed up for other richness variables (Andersen-transformed pollen richness, tree and shrub richness in pollen and in plants, herb and grass richness in pollen and in plants, richness of wind-pollinated taxa in pollen and in plants, richness of non-wind-pollinated taxa in pollen and in plants). The results of these analyses are presented in Appendix S3 (LME models) and Appendix S4 (variation partitioning).

The statistical software R (R Core Team, 2017) was used for all statistical analyses with packages "nlme" (Pinheiro, Bates, & DebRoy, 2018) for LME models, "vegan" (Oksanen et al., 2017) for variation partitioning, and "spdep" (Bivand & Piras, 2015) for MEM calculations.

3 | RESULTS

3.1 | Pollen richness as a predictor of plant richness

Total pollen richness is relatively weakly associated with plant richness ($r = 0.53$, $p < 0.001$) (Table 1, Figure 2a). The Andersen transformation improves the pollen–plant richness correlation

TABLE 1 Pearson correlation coefficients between richness calculated from pollen data (columns) and plant data (rows), R_{po} – pollen richness, R_{pl} – plant richness

Pollen→ Plants ↓	**Richness (R_{po})**	**R_{po} Andersen-transformed**	**R_{po} Families**	**R_{po} herbs and grasses**	**R_{po} trees and shrubs**	**R_{po} wind-pollinated**	**R_{po} non- wind-pollinated**
Richness (R_{pl})	0.53	0.63	0.51	0.18	0.79	0.81	−0.07
R_{pl} pollen types	0.52	0.62	0.52	0.16	0.8	0.81	−0.08
R_{pl} families	0.48	0.58	0.51	0.13	0.77	0.76	−0.09
R_{pl} herbs and grasses	0.52	0.62	0.5	0.17	0.78	0.8	−0.07
R_{pl} trees and shrubs	0.59	0.68	0.59	0.24	0.83	0.82	0.02
R_{pl} wind-pollinated	0.47	0.57	0.44	0.12	0.74	0.75	−0.11
R_{pl} non-wind-pollinated	0.54	0.64	0.53	0.19	0.8	0.81	−0.05

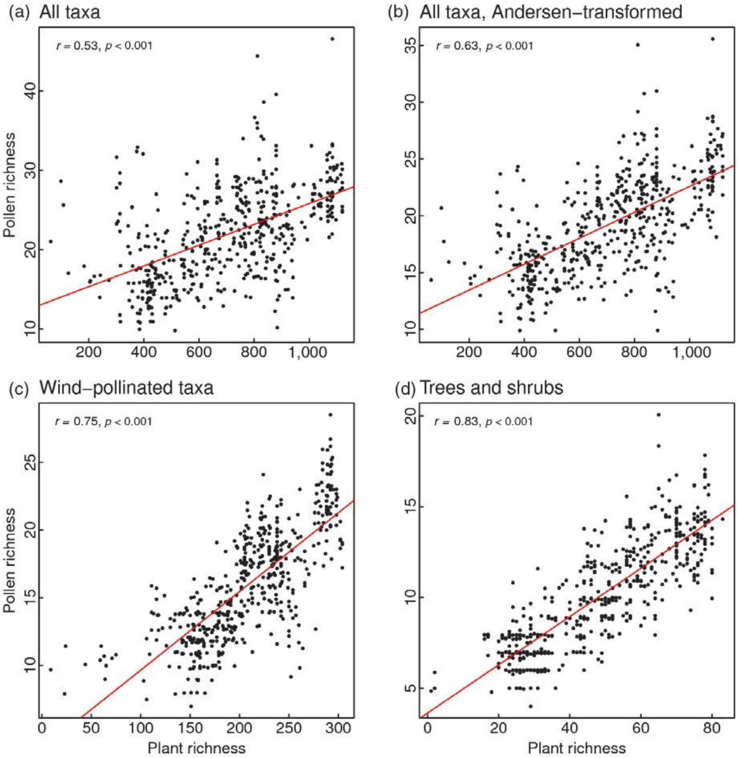

FIGURE 2 Correlations between pollen richness and plant richness in different taxon groups: (a) all taxa, (b) all taxa, pollen Andersen-transformed, (c) wind-pollinated taxa, (d) tree and shrubs. Pearson correlation coefficient and its *P*-value are shown on each figure

($r = 0.63$, $p < 0.001$) (Table 1, Figure 2b). While pollen richness of wind-pollinated taxa is a relatively good predictor of plant richness of wind-pollinated species ($r = 0.75$, $p < 0.001$; Figure 2c), there is no significant correlation between richness estimates of taxa that are not wind-pollinated ($r = -0.05$, n.s) (Table 1). The highest correlation is found between pollen and plant richness of trees and shrubs ($r = 0.83$, Table 1, Figure 2d). In addition, pollen richness estimates of wind-pollinated taxa and of trees and shrubs appear to be good predictors of all the plant richness estimates included in the study with correlation coefficients above 0.75 (Table 1).

3.2 | Pollen and plant richness in relation to climate and landscape variables

Linear mixed effects models show that while the environmental variables explain most of the variation in plant richness (marginal pseudo-$R^2 = 0.92$), the relationships between pollen richness and environment are less well determined (marginal pseudo-$R^2 = 0.58$) (Table 2).

Mean annual temperature is the strongest predictor of both pollen and plant richness (Figure 3a,b, Table 2) with more taxa at higher temperatures. The LME models with other richness estimates indicate that mean annual temperature is clearly the strongest predictor of both pollen and plant richness irrespective of the taxon group considered (Appendix S3). While plant richness is significantly associated with all the climate variables tested, the relationships between pollen richness and climate are weaker (Table 2). However, three temperature-related climate variables—mean annual temperature, temperature seasonality and isothermality—have significant interaction terms with plant richness in explaining pollen richness (Table 2, Figure 4). The relationship between pollen and plant richness is less determined at lower mean annual temperature values (Figure 4a) and the pollen–plant richness association is even negative at high latitudes (Figure 4b). When using the Andersen-transformed pollen richness or tree and shrub richness, interactions between plant richness and climate are fewer and are less determined but still statistically significant (Appendix S3 Table S3.1, Figure 4c,d).

Because all 21 pooled pollen samples (including pollen data from several lakes) are from northern latitudes, we checked whether the pooling of the data might have caused the interaction effects—with pooled pollen samples having higher beta-diversity and thereby higher pollen richness. We calculated the LME interaction model including all original 633 pollen samples and pollen richness rarefied to the lowest pollen sum of 134. The interaction terms with plant richness were significant for annual mean temperature ($p < 0.001$) and for temperature seasonality ($p < 0.001$), but the interaction between plant richness and isothermality was not significant (Appendix S3 Table S3.6).

Of the landscape variables, elevation is similarly associated with both plant and pollen richness with more taxa at higher

TABLE 2 Results of linear mixed effect (LME) models with total pollen richness (per 500 pollen grains) and plant richness as response and "Region" as a random variable. All variables are standardised to zero mean and unit variance to enable comparison of model estimates. The results are post backward selection of variables. Symbol "n" denotes a unimodal quadratic association, "u" denotes u-shaped association, and ×denotes interaction with plant richness in pollen richness model. The significance of the variables is indicated as follows: ***p < 0.001, **0.001 < p<0.01, *0.01 < p<0.05, n.s p > 0.05. Marginal pseudo-R^2 (reflecting the variation explained by fixed variables) and conditional pseudo-R^2 (reflecting the variation explained by both random and fixed variables) are given for each model

	Pollen richness				**Plant richness**	
	LME with quadratic associations		**LME with plant richness interactions**		**LME with quadratic associations**	
Variable	**Estimation**	***t*-value**	**Estimation**	***t*-value**	**Estimation**	***t*-value**
Plant richness	+0.09	1.16 n.s	0.40	6.15***	–	–
Climate						
Annual precipitation			+0.44	7.33***	+0.11	3.47***
Mean annual temperature	+0.94 u 0.18	9.70*** 4.39***	+0.16 × +0.36	1.96* 5.92***	+0.79 u 0.21	18.09*** 11.78***
Precipitation seasonality					−0.05	−3.09**
Temperature seasonality			+0.11 × +0.20	1.20 n.s 4.40***	+0.10 n 0.15	3.29** −7.39***
Isothermality	−0.16	−3.29**	−0.06 × −0.14	−1.28 n.s −2.97**	−0.02 n 0.1	−1.03 n.s −7.44***
Windspeed					−0.18 −0.04	−8.42*** 4.64***
Landscape						
Elevation	+0.23 u 0.09	4.80*** 4.16***			+0.2 u 0.05	9.39*** 5.43***
Elevation variation	+0.25	3.92***			−0.02 n 0.08	−0.60 n.s −3.61***
Openness	+0.24 u 0.18	5.74*** 5.42***	+0.25	4.88***		
Landscape diversity			−0.11	−3.30**	+0.05 u 0.03	2.62** 2.56*
Human population					+0.31 n 0.04	10.75*** −2.73**
	Marginal R^2 = 0.58 Conditional R^2 = 0.68		Marginal R^2 = 0.51 Conditional R^2 = 0.68		Marginal R^2 = 0.92 Conditional R^2 = 0.95	

elevations (Table 2). Other landscape variables have different relationships with pollen and plant richness: openness is only associated with pollen richness (Figure 3c,d) and human population density is only associated with plant richness (Figure 3e,f). While landscape diversity is positively associated with plant richness, the relationship with pollen richness tends to be negative (Table 2). Lake area is not significant in any of the models and is not included in the results tables.

When plant richness is included as an explanatory variable in the model together with all the environmental variables, plant richness is significantly associated with pollen richness only after interactions with climate variables are accounted for (Table 2). In the case of Andersen-transformed pollen richness, richness of trees and shrubs and richness of wind-pollinated taxa, the corresponding plant richness is significant also in the models without the interaction terms (Appendix S3).

The results of variation partitioning show that the largest proportion of variation in both pollen and plant richness is explained jointly by the climate, landscape and spatial variables (80% for plant richness, 22% for pollen richness; Figure 5). The share of variation explained by climate and landscape independently of the spatial variables is larger for pollen richness (12.5%) than for plant richness (2.3%) (Figure 5). For pollen richness of herbs and grasses and taxa not wind-pollinated, landscape variables explain relatively large individual shares of variation (7.0% and 6.5% respectively) (Appendix S4; Figures S4.3b and S4.5b). The amount of variation in pollen richness explained only by plant richness is low (<1%) for all richness estimates (Figure 5, Appendix S4). However, the total amount of variation explained by plant richness including the variation explained jointly with other variables varies from 3% (for richness of herbs and grasses and richness of non-wind-pollinated taxa) to >55% (richness of trees and shrubs and richness of wind-pollinated taxa).

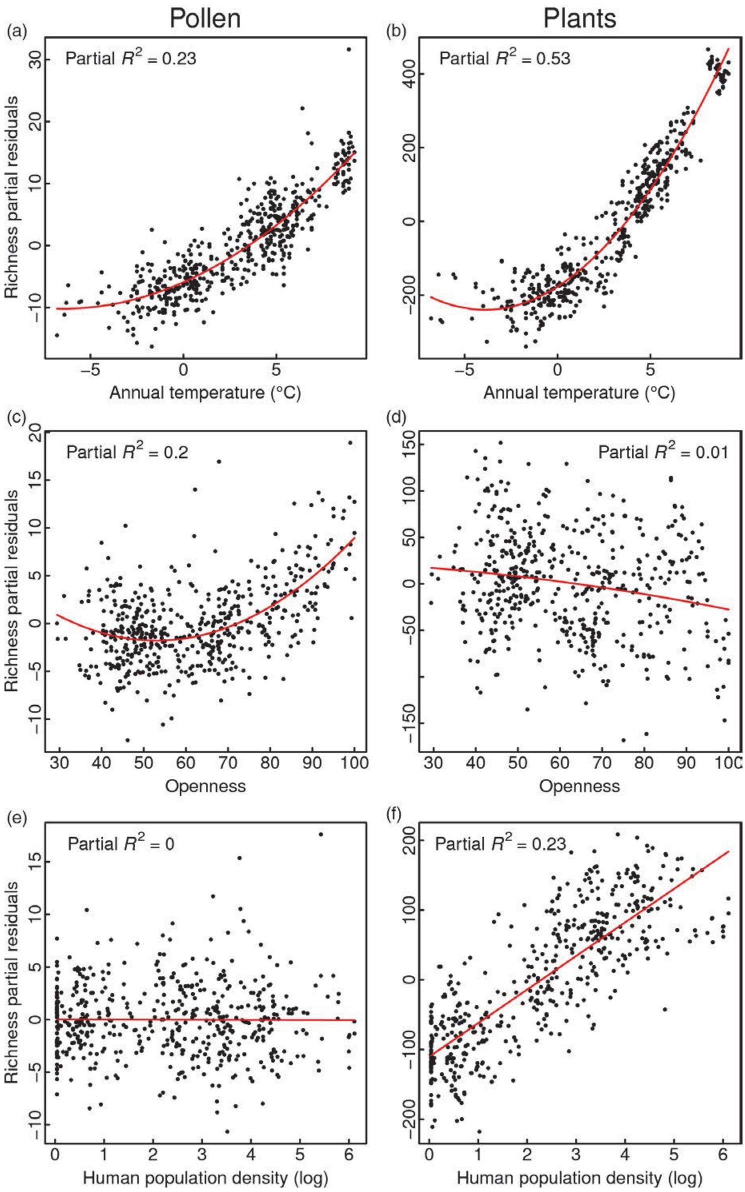

FIGURE 3 Relationships between richness and selected environmental variables in pollen (left column) and in plants (right column): annual mean temperature (a, b), openness (c, d), human population density (e, f). Partial regression plots of linear regression analysis are given with all the other significant environmental variables accounted for (see Table 2)

4 | DISCUSSION

4.1 | Pollen richness in relation to plant richness

The often used rarefaction-based total pollen richness has a relatively low but significant positive correlation with total plant richness ($r = 0.53$, $p < 0.001$). The most serious critiques against using pollen richness as a proxy of past plant richness relate to the pollen-representation bias sensu Odgaard (1999, 2008) where the high pollen producers decrease the probability of finding rare pollen types and thereby influence the estimated richness. Several different methods have been proposed to minimise the pollen-production bias (cf. Birks, Felde, Bjune et al., 2016). Using pollen-representation values (i.e. Andersen, 1970) or pollen productivity estimates (e.g. Broström et al., 2008) to downweight the high pollen producers prior to rarefaction analysis is one option that has been used by several authors (Felde et al., 2016; Matthias et al., 2015). In our analysis, we test the use of Andersen-transformed pollen richness and although it improves the pollen–plant richness correlation ($r = 0.63$, $p < 0.001$) it

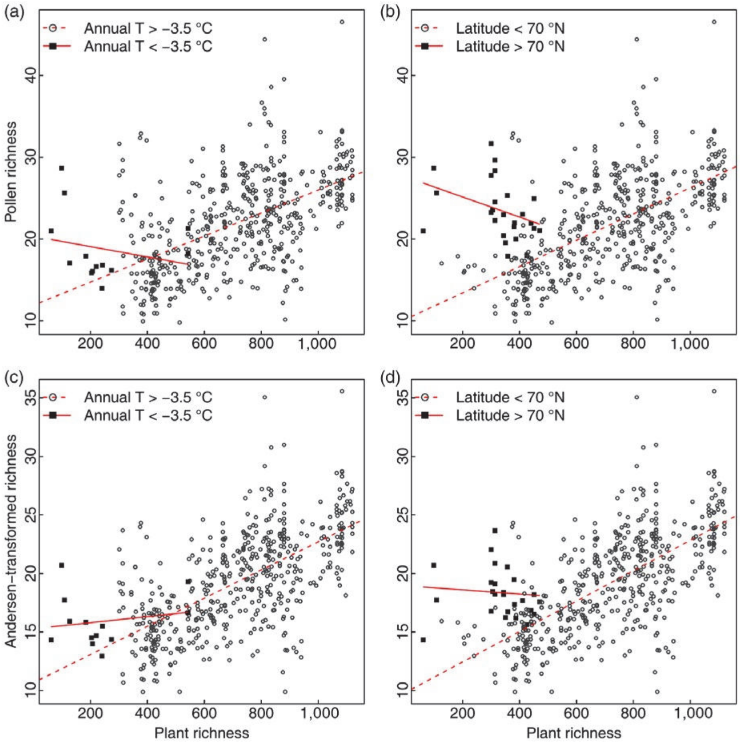

FIGURE 4 Interactions of pollen–plant richness relationships with mean annual temperature (a, c) and with latitude (b, d). The results are given both for pollen richness (a, b) and for Andersen-transformed pollen richness (c, d)

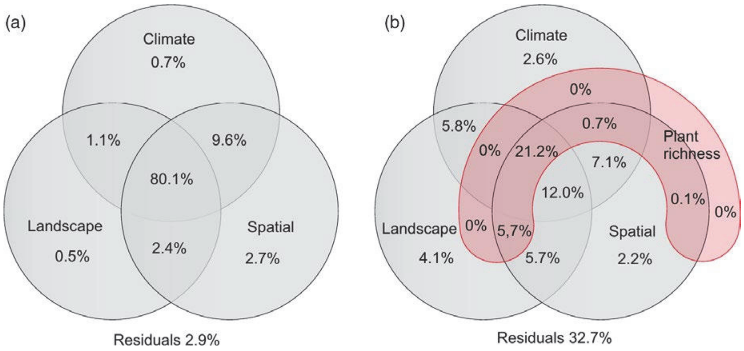

FIGURE 5 Results of variation partitioning for plant richness (a) and pollen richness (b). Explanatory datasets characterise climate (annual precipitation, mean annual temperature, precipitation and temperature seasonality, isothermality, windspeed), landscape (elevation, variation in elevation, openness, landscape diversity, human population density) and spatial autocorrelation (spatial eigenvector [MEM] variables). In the case of pollen richness (b), plant richness is considered as an additional explanatory variable

does not completely remove the interaction effects of the richness relationship with climate and latitude. The pollen data are limited by the original pollen counts in the samples and any transformation can only work within the limits of the original counts. To overcome this problem, methods adjusting the maximum pollen count during the counting process have been proposed—allowing pollen counts to be developed relative to the evenness and richness of the specific sample rather than a fixed number (Keen et al., 2014). Our analyses together with earlier studies (Felde et al., 2016; Matthias et al., 2015) suggest that methods accommodating pollen-representation bias in pollen richness studies warrant further attention and should become as widely used as pollen-production transformations in land-cover reconstruction studies (e.g. Mazier et al., 2015; Mehl & Hjelle, 2015; Roberts et al., 2018).

The studies that investigate pollen–plant richness relationships often use the pollen type–based plant richness to reduce the influence of taxonomic bias where some pollen taxa include considerably more species than others (Felde et al., 2016; Goring et al., 2013; Meltsov et al., 2011). For example, the whole family Cyperaceae is included as one pollen type, while the main tree species can be separated at the genus or species level. In our dataset, translating the plant data into pollen types or using family-level richness does not improve the correlation between the pollen and plant richness estimates, indicating that taxonomic bias is more-or-less constant across the whole range of the data.

In our results, the correlation between plant and pollen richness greatly improves when only trees and shrubs are considered (*r* = 0.83). Similar to our study, Flenley (2005) showed that the palynological richness of woody taxa follows well the latitudinal gradient of tree and shrub species. As with tree and shrub richness, pollen richness of wind-pollinated taxa is a good indicator of corresponding plant species richness (*r* = 0.75). Many of the tree and shrub taxa in our study are wind-pollinated (Appendix S1) and thus the two richness measures largely overlap. Similar to the pollen data in large databases such as the European Pollen Database (Davis et al., 2013; Giesecke et al., 2013) or the Neotoma Paleoecology Database (Williams et al., 2018), our pollen dataset combines the work of multiple analysts and the dataset loses taxonomic precision due to the merging of certain morphologically difficult pollen taxa. The lack of correlation between pollen and plant richness among insect-pollinated taxa or among herbs and grasses may be related to this “analyst effect” but is likely to be additionally influenced by landscape configuration (c.f. Appendix S4, Figures S4.3 and S4.5) and the spatial scale of the plant data used. Changes in the diversity of insect-pollinated taxa can be detected with good pollen-taxonomic precision, consistent effort in pollen taxonomy, and high pollen sums (>1,000 grains) (Meltsov et al., 2011). The RSAP for European small lakes is usually estimated to be 1,000–2000 m from the lake (Hjelle & Sugita, 2011; Nielsen & Sugita, 2005; Poska, Meltsov, Sugita, & Vassiljev, 2011), which is a much finer spatial resolution than the resolution of the plant data in our study. Therefore, to understand better the relationship between plant and pollen richness of both wind-pollinated and non-wind-pollinated taxa, the plant dataset should include several nested spatial scales.

Weng et al. (2006) suggest that the wind-pollinated and insect-pollinated pollen taxa should be treated separately in pollen richness studies. Our results strongly support this and we recommend that richness of trees and shrubs or richness of wind-pollinated taxa are good choices when using pollen richness to reflect major changes in past plant richness over broad spatial scales and in studies involving data from different sources. According to our results, pollen richness of trees and shrubs and of wind-pollinated taxa are also good indicators of broad-scale total plant richness (*r* = 0.79 and *r* = 0.81 respectively) because in northern Europe the plant richness of trees and shrubs and the richness of wind-pollinated taxa are, in turn, highly positively correlated with total richness. However, as the relationship between wind-pollinated and non-wind-pollinated taxa is not constant across the globe (Regal, 1982), studies from other regions or global studies of pollen–plant richness are needed to confirm the trends demonstrated here.

A series of earlier studies have found similar positive correlations between pollen and plant richness in Europe (Birks, 1973; Felde et al., 2016; Matthias et al., 2015; Meltsov et al., 2011; Odgaard, 2008). However, investigations from the tropics (Gosling et al., 2018; Jantz, Homeier, & Behling, 2014) or from temperate western North America (Goring et al., 2013) have not found such positive correlations. Evaluating pollen–plant diversity relationships not only depends on the nature of pollen data but also on the spatial scale and quality of plant data (Birks, Felde, Bjune et al., 2016). In the present study, we use the best available regional-scale plant database that has a relatively coarse spatial resolution (50 × 50 km) and both pollen and plant data reflect the well-known latitudinal richness gradient relatively well (Figure 4). Goring et al. (2013) showed the relationship between pollen richness and fine-scale (20 × 20 m) plant richness to be slightly negative. The scale of the plant data is much finer than the estimated relevant source area of pollen for similar-sized lakes (1,000–2,000 m; Hjelle & Sugita, 2011; Nielsen & Sugita, 2005; Poska et al., 2011). This further emphasises the importance of finding relevant spatial scales when interpreting pollen richness in terms of plant richness.

4.2 | Climate influence on pollen and plant richness

In the plant data, the richness pattern is very strongly spatially autocorrelated and the purely spatial variables are the best descriptors of the richness gradient (Figures 1 and 5a). This is related to the relatively coarse spatial resolution of the data (50 × 50 km) where the influence of local-scale variables (including landscape diversity and structure, microclimate) is smoothed out and the climate and landscape variables explaining the richness patterns covary with the spatial variables. Climate variables explain 91.5% of the variation in plant richness (Figure 5), confirming the importance of water-energy variables for determining richness patterns over broad geographic scales (Hawkins et al., 2003). However, the proportion of variation explained jointly by climate, landscape and spatial variables is extremely high (80.1%) indicating that it is difficult to separate the effects of landscape and climate variables at this spatial resolution. The low vascular plant richness in the northeastern part of the study area (NW Russia) may be an artefact because both Atlas Florae Europapeae (Jalas & Suominen, 1972; Jalas et al., 1996, 1999; Kurtto et al., 2004) and Atlas of North European Vascular Plants (Hultén & Fries, 1986) concentrate on European species and may lack species with more eastern distributions (Ronk, 2016). However, the west–east richness decrease is also reflected by the pollen data (Figure 1) and the LME models suggest that the gradient is positively related to isothermality both in plants and in pollen (Table 2) indicating that large diurnal temperature oscillations and/or high continentality have a negative influence on plant and pollen richness.

Climate and landscape variables have distinctive independent effects on pollen richness regardless of spatial patterns and plant richness (Figure 5b), indicating that climate and landscape variables influence pollen richness directly and not only through plant richness. Numerous studies of pollen-production estimates across Europe have demonstrated considerable variation in pollen production for the same taxa in different regions (e.g. Broström et al., 2008; Mazier et al., 2012). This is also likely to influence pollen richness estimates when the detection probability of taxa decreases due to less favourable flowering conditions and reduced pollen production. The significant interactions of the plant–pollen richness relationship with climatic variables and latitude indicate that pollen richness at conditions corresponding to present-day high latitudes (>70°N, mean annual temperature <−3.5°C) in sedimentary studies should be treated with caution because the richness values may be heavily influenced by long-distance transport of extra-regional pollen. Pollen data from high latitudes often have low pollen sums because of the scarcity of pollen. Pooling pollen data from several lakes (as we have done in 21 pooled samples) increase the overall pollen-source area and might be the reason behind the unproportionally high pollen richness in low temperatures and high latitude (Figure 4). However, the analysis with pollen richness from the original samples (without pooling) indicates that the interaction of pollen–plant richness correlation with temperature is not an artefact of our data handling but is also evident when pollen richness is based on low pollen sums (Appendix S3 Table S3.6). Low temperatures in high latitudes (and elevations) may have a negative influence on local pollen production increasing the proportion of long-distance pollen in the samples (van der Knaap, 1990; Seppä, 1998). The relatively high pollen richness in the late-glacial described in several studies (Berglund, Gaillard, Björkman, & Persson, 2008; Birks & Line, 1992; Reitalu et al., 2015) might therefore be influenced by long-distance pollen dispersal from outside the region.

4.3 | Influence of landscape variables on pollen and plant richness

Among the landscape variables, openness and elevation have positive correlations with pollen richness and, as discussed above, earlier studies have also shown that both variables can have a positive effect on pollen richness (but not necessarily through an increase in plant richness) (Felde et al., 2016; Meltsov et al., 2011; Odgaard, 2008). In two modern pollen–plant richness studies from the tropics, where there is no clear link between pollen and plant richness, the gradient of openness is involved: Gosling et al. (2018) described the diversity from closed evergreen forests to wooded savanna and Jantz et al. (2014) involved elevational gradients. Openness, at high elevations or latitudes, in naturally open dry areas or human-influenced landscapes is known to have a positive effect on pollen richness through the increased pollen-source area in open conditions (Felde et al., 2016; Seppä, 1998; Sugita et al., 1999) and through higher pollen evenness that allows more taxa to be detected (Odgaard, 2008). Our results also demonstrate that openness has a positive effect on pollen richness but not on plant richness (Figure 3) indicating that openness interacts with the pollen–plant richness relationship. These results call for caution in interpreting pollen richness from open areas and for the development of methods that take into account differences in pollen production and source area, for example calculating pollen diversity from pollen accumulation rates (van der Knaap, 2009), employing varying pollen sums depending on pollen production (Keen et al., 2014), or using expert knowledge to exclude extra-regional pollen (van der Knaap, 1990).

The individual effects of landscape variables are especially high for pollen richness of herbs and grasses and for pollen richness of non-wind-pollinated taxa, further confirming that in our dataset these groups of pollen taxa are influenced by different factors and/or on different spatial scales than the plant species richness used in our study.

Late-Holocene pollen diversity studies from Europe often highlight human impact as having a positive influence on pollen richness where land-clearance for agriculture and anthropogenic disturbance are creating habitats for more taxa that cannot grow in forested areas (Berglund et al., 2008; Colombaroli et al., 2013; Felde et al., 2018; Giesecke et al., 2012; Reitalu et al., 2015). It is, therefore, somewhat surprising that there is no association between human population size and pollen richness in the LME models (Figure 4e), while population size is significantly positively correlated with plant richness (Figure 4f). In our dataset, the human population size is strongly positively correlated with mean annual temperature ($r = 0.9$, $p < 0.001$, Appendix S2) and the effects of climate and human impact are not clearly separable. We also test the LME model without mean annual temperature, and then human impact is included in the model and it is significantly positively linked with pollen richness. The modern data used in our study are not directly comparable with the situation during the last 4,000 years when temperatures were decreasing slightly (Renssen et al., 2009) but the human impact was increasing considerably.

5 | CONCLUSIONS

Our results offer the first regional-scale comparison of pollen and plant richness from Europe and allow the evaluation of the relative importance of different environmental variables on both pollen and plant richness. Differences in pollen production among taxa influence the pollen richness estimates and the development of better methods for reducing pollen-production bias should therefore get more attention in further methodological studies. Pollen richness values may be overestimated in open landscapes, such as arctic tundra, high elevations and areas of intensive agriculture where the extremely low local pollen production increases the proportion of taxa from outside the region.

We suggest that pollen richness of trees and shrubs or of wind-pollinated taxa are good indicators of broad-scale plant richness changes over thousands of square kilometres. The pollen richness of insect-pollinated herbaceous plants is more likely to be influenced by local landscape-scale factors and should be interpreted separately from the wind-pollinated taxa. Our results confirm that pollen data can provide insights into past plant richness changes, and thus make it possible to investigate vegetation diversity trends over long time-scales and under changing climatic and habitat conditions outside the scope of contemporary ecological studies.

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AUTHORS' CONTRIBUTIONS

T.R. designed the study and wrote the paper with the input from H.J.B.B., H.S. and all other co-authors; H.J.B.B., A.E.B., T.G., I.M., S.M.P., J.S.S. and H.S. provided the pollen-analytical data; A.H. prepared the gridded plant distribution dataset; V.V. and T.R. harmonised the pollen taxonomy and divided the plant data into pollen types; A.E.B. and T.R. prepared the climate and environmental datasets; T.R. and A.E.B. did the statistical analyses with suggestions from H.J.B.B.

DATA ACCESSIBILITY

The original pollen counts are available from the European Modern Pollen Database http://wp.unil.ch/davisgroup/research (Davis et al., 2013). Coordinates of pollen-sample lakes, the dataset of plant species associated with each of the 511 pollen samples and pollen and plant richness calculations are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.m4s45t4 (Reitalu et al., 2019).

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SUPPORTING INFORMATION

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

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