Quaternary International 741 (2025) 109899

Contents lists available at ScienceDirect

Quaternary International

journal homepage: www.elsevier.com/locate/quaint

Effects of Lateglacial and Holocene climate change on southern Baltic environments: a plant sedaDNA and diatom sediment record

Laura Gedminienė [a,b,*], Kathleen R. Stoof-Leichsenring [c,**], Ulrike Herzschuh [c,d,e], Giedrė Vaikutienė [a], Miglė Stančikaitė [b], Žana Skuratovič [b], Domas Uogintas [b], Andrej Spiridonov [a]

[a] *Institute of Geosciences, Faculty of Chemistry and Geosciences, Vilnius University, M. K. Čiurlionio Str. 21/27, 03101, Vilnius, Lithuania*
[b] *State Scientific Research Institute Nature Research Centre, Akademijos Str. 2, 08412, Vilnius, Lithuania*
[c] *Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Polar Terrestrial Environmental Systems, Potsdam, Germany*
[d] *Institute of Biochemistry and Biology, University of Potsdam, Germany*
[e] *Institute of Environmental Science and Geography, University of Potsdam, Germany*

ARTICLE INFO

Keywords:
Lithuania
Plant sedaDNA
Pollen
Diatom
PCA
Sediment core

ABSTRACT

We combined multiproxy analyses of plant sedaDNA, diatom, and lithological data from two sediment cores to develop an uninterrupted Lateglacial and Holocene record from the Dūkštelis palaeolake, eastern Lithuania, and compared our findings to published pollen records. SedaDNA provides localised and taxonomically detailed insights into vegetation, surpassing the resolution of pollen data; however, its composition is strongly influenced by aquatic plants, a fact which limits the representation of terrestrial flora to some extent. Macrophyte sedaDNA and diatom data record shifts in lake productivity and water levels, while pollen data reflect a broader regional vegetation context, highlighting the complementarity of these methods.

Subalpine and lowland vegetation colonised the region during the Lateglacial. The presence of shrub taxa, like *Arctostaphylos uva-ursi* and *Arctous alpina* with colder-adapted species, like Dryadoideae and *Pyrola*, and herbs characteristic of lowlands in modern environments, like Trifoliaceae, *Mentheae*, Ranunculaceae, and *Plantago*, suggests an open but heterogenous environment with diverse microhabitats created under quickly changing geomorphological conditions. A gradual shift to a forested landscape began with the advent of riparian species like *Alnus* (~11300 cal yr BP), *Viburnum* (~10300–9200 cal yr BP), and deciduous trees including Ulmaceae, *Tilia,* and Fagaceae from ~11150, 10000, and 9900 cal yr BP, respectively. Early to Middle Holocene diatom and macrophyte data show that by ~10000 cal yr BP, the lake had shifted from a shallow mesotrophic-eutrophic state to a deeper eutrophic system. During the Middle to Late Holocene, sedaDNA data suggest a decline in forest vegetation as the lake evolved into a shallow wetland. At this stage, sedaDNA overrepresents species growing directly in and around the lake, and therefore potentially skewing the broader regional picture. In contrast, pollen data suggest a pronounced forest decline from ~3300 cal yr BP, likely linked to human activities such as forest clearance, which would increasingly shape the landscape from the Middle Holocene. Notable agricultural and pastoral impacts are indicated by the presence of species such as *Avena*, Brassicaceae, Plantago, and *Trifolium* starting ~3700 cal yr BP.

1. Introduction

To date, biological archives, including pollen, spores, non-pollen palynomorphs (NPP), diatoms, macrofossils, chironomids, etc., preserved in lake sediments and investigated under a microscope, have been considered among the most reliable indicators for tracking palaeoecological changes in the environment. Traditional palaeovegetation studies in the Baltic region, including Lithuania, have relied primarily on fossil pollen assemblages to reconstruct past vegetation history, migration, as well as to infer both natural (climatic) and anthropogenic

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This article is part of a special issue entitled: Quaternary Science Advances in the Baltic Sea Region published in Quaternary International.

* Corresponding author. Institute of Geosciences, Faculty of Chemistry and Geosciences, Vilnius University, M. K. Čiurlionio Str. 21/27, 03101, Vilnius, Lithuania.

** Corresponding author.

E-mail addresses: laura.gedminiene@gamtc.lt (L. Gedminienė), kathleen.stoof-leichsenring@awi.de (K.R. Stoof-Leichsenring).

https://doi.org/10.1016/j.quaint.2025.109899
Received 30 October 2024; Received in revised form 10 June 2025; Accepted 22 June 2025

influences on plant communities (Stančikaitė et al., 2019a; Šeirienė et al., 2021; Veski et al., 2012; Ozola et al., 2010; Borzenkova et al., 2015; Heikkilä et al., 2009). However, quantitative reconstructions of plant abundance require careful corrections for biases arising from differences in pollen productivity or dispersal among species (Githumbi et al., 2022; Serge et al., 2023). Also, it is very important not to overlook numerous factors, such as the size of a water body, shoreline, wind direction, and other properties such as sediment composition, relief, etc., which can affect the deposition, preservation, quantity and quality of fossil pollen (Garcés-Pastor et al., 2024; Alsos et al., 2024; Jia et al., 2022a, 2024).

Although pollen and macrofossil analysis has been effective thus far, this approach demands a considerable investment of time and human resources. Besides, pollen taxonomic resolution is often limited, being typically restricted to the genus or family level (Tian et al., 2023; Jia et al., 2022a; Alsos et al., 2016). While plant macrofossils can offer a somewhat more precise identification at the genus or species level, as well as better representing local vegetation (Birks and Birks, 2000), the scarcity of fossil finds usually restricts their utility. These limitations highlight the need for new approaches to unify and simplify analytical methods, offering better alternatives for palaeoenvironment studies.

One of the novel alternatives is the analysis of nucleic acids (DNA) preserved in sedimentary archives. There are plenty of terms and definitions used when studying these nucleic acids. Usually, it depends on factors such as the target of the research, the preservation quality of the DNA, and the methodologies employed (Capo et al., 2021). In simple terms, plant environment DNA, or sedimentary ancient DNA (sedaDNA), refers to older, often poorly preserved environmental DNA (eDNA) fractions buried in the sediments which originated from organisms that are no longer alive (Capo et al., 2021).

Since the pioneering studies of ancient DNA in lake sediments (Ogram et al., 1987), the number of publications in various DNA research fields has increased dramatically (Capo et al., 2021). The majority of sedaDNA studies evaluating vegetation responses to climate changes and human impacts during the postglacial period have been conducted in higher-altitude regions. Most of these studies are concentrated in the circumpolar Arctic and alpine regions of Eurasia and North America (Alsos et al., 2024; Von Eggers et al., 2024, and relevant papers from the sedaDNA Society track list, https://sedadna.github.io/, April 2025). However, similar studies in low- and mid-latitude regions, such as Central Europe, remain limited (Garcés-Pastor et al., 2024) and to date, no studies have employed the plant sedaDNA method in the Baltic countries.

Since this approach is relatively new compared to traditional microscope-based methods, the methodologies and technologies surrounding sedaDNA analyses are rapidly evolving and advancing. SedaDNA can improve researchers' ability to document past ecosystem dynamics and forecast ecosystem trajectories under climate change (Alsos et al., 2024; Von Eggers et al., 2024 and relevant papers from the sedaDNA Society track list, https://sedadna.github.io/April 2025). While the reliability of the sedaDNA method continues to improve, systematic comparisons with other established proxies can offer additional insights, enhancing its utility in palaeoecological research.

One of the objectives of sedaDNA is to retrieve the taxonomic composition of environmental samples using sequence data. Taxonomic identification of DNA sequences relies on comparing unknown sedaDNA sequences against a metabarcode reference database that contains comprehensive taxonomic information (Taberlet et al., 2018). However, some sedaDNA sequences remain unidentified (Tian et al., 2023). Current vascular plant reference databases, such as The European Molecular Biology Laboratory (EMBL) (Hamm and Cameron, 1986) and GenBank (Bilofsky et al., 1986), do not encompass all the species living on Earth. Most collections originate from Arctic and Boreal environments (Sønstebø et al., 2010; Willerslev et al., 2014). Thus, ongoing efforts and initiatives to expand and update reference libraries are essential to the improvement of metabarcoding applications and enhancing the interpretation of environmental DNA data.

The general metabarcoding approach involves collecting environmental samples, extracting DNA, amplifying target gene regions using specific primers during the PCR process, and then sequencing the amplified fragments. One of the most commonly used regions is the trnL (UAA) intron, a non-coding region of chloroplast DNA. The key advantage of the metabarcoding approach lies in the universality of the g-h primers (Taberlet et al., 2007), which are considered one of the most widely applied markers in vascular plant metabarcoding due to their robust amplification process and compatibility with highly standardised procedures. Although the P6 loop of the trnL (UAA) intron provides a lower degree of taxonomic resolution, due to its shortness compared to more advanced and longer genetic markers, it still offers a higher degree of resolution than traditional proxies (pollen, macrofossil), making it highly useful for working with highly degraded DNA, such as in sedaDNA samples.

Another issue that needs to be addressed is the preservation of sedaDNA in the environment, as its persistence is influenced by multiple factors. These include sediment composition (i.e. the amount of organic matter or clay), and various physical conditions such as catchment erosion rates, temperature, pH, pressure, water conductivity, oxygen level, and binding to the sediment components (Garcés-Pastor et al., 2024; Andersen et al., 2012; Parducci et al., 2013; Strickler et al., 2015). SedaDNA concentrations are also influenced by the proximity of plant growth to the sampling point, often leading to the detection of a higher percentage of local flora, which may even be overrepresented (Alsos et al., 2018). Keeping these methodological and physical preservation challenges in mind, data must be interpreted with caution. Several studies have compared sedaDNA data with traditional proxies such as pollen, plant macrofossils, and diatom records to address challenges related to preservation and interpretation (Capo et al., 2021). Generally, a higher taxonomic overlap between these proxies reflects local vegetation sources (Parducci et al., 2013; Tian et al., 2023; Revéret et al., 2023; Baisheva et al., 2023; Alsos et al., 2016). Identifying an ideal study site is crucial to the effective comparison of these proxies and the advancement of the application of sedaDNA methods (Capo et al., 2021). Such a site should ideally cover a complete sedimentation sequence without disruptions or heavy human impact while being small enough to trap pollen from local vegetation. The Dūkštelis palaeolake in eastern Lithuania meets these criteria and thus represents an excellent target for this approach.

According to previous studies (Gedminienė et al., 2025), the Dūkštelis region deglaciated during the Last Glacial Maximum, with the oldest pollen assemblages dating to the Early Bølling period. Although terrestrial vegetation was sparse at that time, it was highly diverse, reflecting the spread of herbaceous plants across a largely treeless landscape. During the second part of the GS-1 event, the vegetation experienced some unexpected perturbations, with short-term immigration of thermophilic plants. Uncertainties arise concerning a more prominent change around 3300 cal yr BP when bog development significantly impacts the vegetation. Additionally, the presence of thermophilic plant pollen and some unidentified macroremains found in the bottommost sediments has raised questions about whether the latter plants are of terrestrial or aquatic origin, as well as concerns regarding possible sediment redeposition. All the preceding suggests that some important aspects of the region's vegetation history may be missing in the pollen record. These uncertainties presented an intriguing opportunity for the application of the sedaDNA approach to this site to clarify the findings.

The application of a sedaDNA approach in this study will present a novel and promising alternative for palaeoenvironment research in Lithuania, offering enhanced taxonomic resolution compared to traditional methods. Against this backdrop, and alongside established proxies such as pollen, diatoms, and sediment lithology, this study aims to explore region's vegetation dynamics since the last glaciation, offering more detailed insights into both aquatic and terrestrial plant communities at the highest possible degree of taxonomic resolution. This will enable a more comprehensive view of ecological shifts, which is needed to understand the larger picture and the influence of climate on lake ecosystems and environment. The key objectives of this study are: 1) To document long-term vegetation and environmental changes in the region by comparing sedaDNA results with pollen data, thereby increasing taxonomical resolution and identifying differences between the two proxies. 2) To reconstruct lake development over time by concentrating on aquatic flora sedaDNA signals and diatom data while detecting the influence of aquatic vegetation on terrestrial vegetation records. 3) To determine the effects of human activities on the terrestrial and aquatic vegetation.

2. Material and methods

2.1. Study area

The Dūkštelis palaeolake is situated on the western margin of modern-day Lake Dūkštelis. It is located in what was once the marginal area of the Last (Weichshelian) glaciation (Guobytė and Satkūnas, 2011), in eastern Lithuania, approximately 20 km NNW from the centre of Vilnius, within the catchments of the River Riešė and River Dūkšta (Fig. 1). A detailed site description can be found in Gedminienė et al. (2025). The catchment of the lake is mostly covered with glaciolacustrine sediments (Lithuanian quaternary geological map M 1:200,000, geoportal.lt, 2024), forming a slightly elevated relief, which is surrounded by deep depressions; this extends from 54.80°N to 54.84°N and from 25.14°E to 25. 22° E, its elevation ranging from 156 to 172 m above sea level (m a.s.l.), increasing south-eastwards. Previously even steeper, the catchment slopes remain highly sensitive to changes in rainwater or snow cover. Erosion or wind transport can easily activate upper layer instability, and changes in vegetation cover can rapidly alter sediment delivery into the lake.

The more continental climate is mainly controlled by atmospheric circulation patterns, specifically an intensification of westerly air mass transfer, the intensity of cyclonic circulation and air mass advection, with greater annual temperature variations, colder winters, longer-lasting snow cover, and drier air (Bukantis, 2001; Rimkus et al., 2011). Average annual wind speed is 4 m/s, S-SW dominating. Average annual rainfall is about 700 mm, with about 80 mm falling during July, and 40 mm in January, while air temperatures vary around 17.5 °C in July and −4.5 °C in January (Lithuanian Hydrometeorological Service under the Ministry of Environment, Meteo.lt, 2023). The vegetation mosaic is characterised by a diverse mix of vegetation types, as an interface between the temperate broadleaf and mixed forests. The plant communities of mixed forests are generally dominated by deciduous trees such as birch and aspen species and coniferous trees such as Scots pine and spruce. Areas near rivers, streams, and other water bodies support a variety of moisture-loving plants. Wetlands and riparian vegetation are dominated by willows, alder, reeds, cattails, graminoids, umbellifers, and dropwort (*Filipendula*), also *Vaccinium* and *Sphagnum*. Open areas supporting a variety of grasses and wildflowers are also used for agriculture.

2.2. Fieldwork and sampling

A 12 m sediment core, DUK_D22, was obtained for sedaDNA studies from the Dūkštelis palaeolake (N 54°50′10″, E 25°9′59″, 156 m a.s.l.) in November 2022. The coring was accomplished using a Russian peat corer with a 1-m long inner chamber (∅5 cm) (Jowsey, 1966) from dry ground; sample depths are given in centimetres measured from the soil surface. The retrieved cores were carefully packed in U-shaped plastic tubes, wrapped to insulate them from contamination and further processed in a dedicated Laboratory of Quaternary Research at the State Scientific Research Institute Nature Research Centre (SSRINRC) in Vilnius. Previously, in 2014, a 13 m core, DUK_D, located 15 m from the DUK_D22 core, was collected from the same palaeolake using the same coring technique (as described in Gedminienė et al., 2025.) for a comprehensive set of palaeobotanical, lithological, and diatom analyses discussed in this paper. Despite the 1-m depth offset the two cores have highly comparable sediment patterns on the basis of their lithological profiles.

2.3. Laboratory analyses. Subsampling

Subsampling of the DUK_D22 core was conducted in a clean room facility at the Quaternary Research Laboratory at SSRINRC under strict hygiene protocols, ensuring removal of any sediments that had been in contact with plastic tubes. The core was subsampled at 2 cm intervals for different analyses. For the sedaDNA extraction, subsamples taken every 12 cm were directly packed into sterile 12.5 ml containers, sealed with Parafilm to prevent direct handling contact, and stored frozen at −20 °C. Of these subsamples, nine were chosen for a preliminary study to assess sedaDNA preservation across different lithological compositions and depths. Later, 63 subsamples were selected for a detailed study, spaced every 24–28 cm in the upper 1–600 cm interval and every 12 cm in the lower 600–1180 cm interval. In total, sedaDNA was obtained from 72 sediment subsamples of the DUK_D22 core.

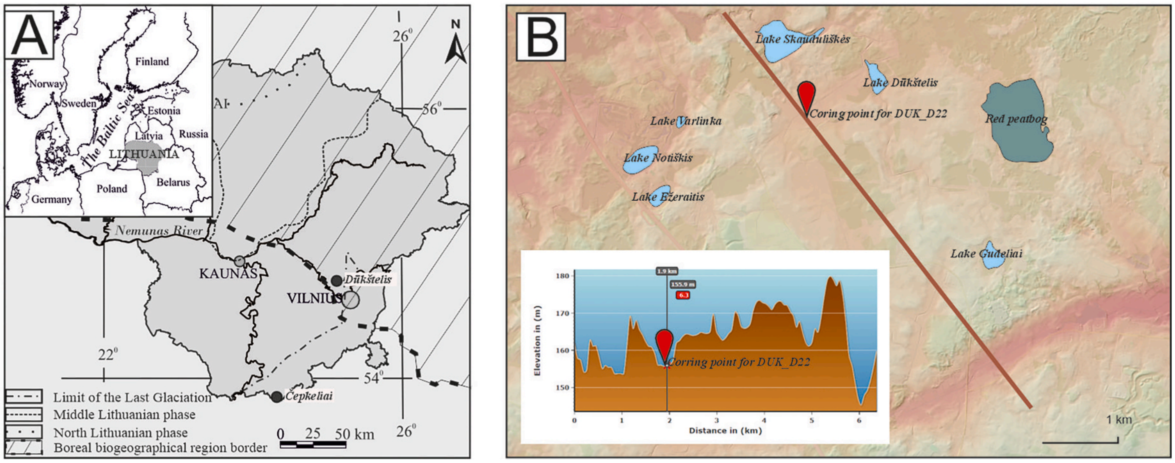

Fig. 1. Location of the study area (A) (setting of study site with limits of ice-marginal positions of the deglaciation of the Last Scandinavian Ice Sheet is shown with the dashed lines, and the border of temperate and boreal biogeographical region with the hatched background); Relief on the study area with the elevation profile adapted from geoportal.lt, 2024 (B). Compiled by L. Gedminienė and V. Minkevičius.

2.4. Dating and chronology

To obtain a robust DUK_D22 core sediment chronology, 9 bulk sediment subsamples were dated using the radiocarbon age dating method employing AMS techniques. Dating for this core was performed at the Centre for Physical Sciences and Technology in Vilnius, with calibration and modelling at the Laboratory of Nuclear Geophysics and Radioecology at SSRINRC. The chronology and age-depth model were compared with the age model of the DUK_D sediment core. Its age model was constructed with higher resolution, and results can be found in Gedminienė et al. (2025). Modelling of both cores was performed using the same methodology. The calibration of ^{14}C ages was performed using the OxCal v4.4.4 program (Bronk Ramsey, 2021), the age-depth model was constructed using OxCal 4.4.4 software (Bronk Ramsey, 2008).

2.5. Lithology and sedimentology

The sedimentological analyses of the DUK_D22 core were performed in the Laboratory of Quaternary Research at SSRINRC on 70 subsamples. Total organic matter (OM) and carbonates ($CaCO_3$) were measured using the loss-on-ignition method (Bengtsson and Enell, 1986) and expressed as a percentage of the dry weight. Magnetic susceptibility (MS) was assessed using the MFK1-B kappa bridge (AGICO, Brno, Czech Republic) equipment with a manual holder. Data was processed using SAFYR software, and values were reported in SI units ($*10^{-9}$, m^3/kg). The grain size was determined using a Fritsch Laser Particle Sizer “Analysette 22” (FRITSCH GmbH, Germany) for the fresh sediments, which allowed the determination of sand-, silt- and clay-sized particle proportions. Prior to this analysis, organic matter was not removed using any chemicals or by combustion. The differentiation in grain size was performed according to the Udden and Wentworth scale (Last, 2001) and presented as fractions of clay (<0.00195 mm), silt (0.0625–0.00195 mm), very fine sand (0.125–0.0625 mm), fine sand (0.125–0.25 mm), medium sand (0.25–0.5 mm) and coarse sand (0.5–2 mm). Lithological sediment composition measurement methodology and results for the DUK_D core can be found in Gedminienė et al. (2025).

2.6. SedaDNA approach

The DNA extraction and the setting up of the polymerase chain reaction (PCR) took place at the paleogenetic laboratory of the Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Potsdam. Germany. This facility is designed for sedimentary ancient DNA (sedaDNA) research and is located in a separate building devoid of any modern DNA or Post-PCR laboratories. To ensure cleanliness, the laboratory features an antechamber, separate preparation rooms for extractions and PCR setup, and individual UV workstations for each step. Cleaning of surfaces and plastic racks was performed with a dilution of hydrochloric acid and DNA-ExitusPlus™ (AppliChem). Detailed descriptions of genetic laboratory work, namely, sedaDNA extraction, polymerase chain reaction (PCR), purification, pooling, DNA sequencing, and basic bioinformatic analysis are presented in Huang et al. (2021), Baisheva et al. (2023); Stoof-Leichsenring et al. (2020).

2.6.1. DNA extraction and amplification

The extraction of sedaDNA was performed in two separate batches. A first single test batch contained 9 sediment samples equally distributed over the length of the core. The second main project contained seven batches of 9 samples each; in total, 72 sediment samples ranging between 1.2 and 5.5 g of sediment were used as input material from the entire sediment core. Despite all samples being of similar volume, samples from 900 cm downwards were heavier as they contained a smaller amount of OM compared to those from the upper layers. The DNA extraction was performed using the Dneasy PowerMax Soil DNA Isolation Kit (Quiagen, Germany) following the manufacturer protocol with slight modifications in the lysis step, in which 400 μl proteinase K and 100 μl DTT (5M) were added to the Bead solution and with a subsequent overnight incubation at 56 °C in a rotating incubator. One extraction blank (only extraction chemicals) was included for each batch of 9 samples and processed the same way as the sediment samples. After extraction, 1000 μl of the extract was concentrated to a final volume of 30 μl using the Genejet PCR purification kit (ThermoFisher Scientific). Before and after concentrations of DNA were quantified with a Qubit Fluorometer 2.0 (Invitrogen, USA) and samples were diluted to 3 ng/μl, which was used as the input to the PCRs. Amplifications were performed using the “*g*” and “*h*” universal plant primers (modified with a unique NNN-8bp tag for sample demultiplexing) for the P6 loop region of the chloroplast trnL (UAA) intron (Taberlet et al., 2007). Further, each PCR reaction contained 12.8 μl purified H_2O, 2.5 μl 10X PCR buffer, 2.5 μl dNTPs (2.5 mM), 1 μl BSA (20 mg/ml), 1 μl $MgSO_4$ (50 mM) and 0.2 μl Platinum™ *Taq* DNA-Polymerase High Fidelity (5U/μl). Except for polymerase and primers, all PCR chemicals were exposed to UV light for decontamination before use in the PCR mix.

Each PCR batch contained 12 preps: 9 sediment samples, one extraction blank, one extraction blank concentrated with Genejet, and one no template control (NTC) to monitor contaminations during PCR. Each sample and extraction blank were amplified in three independent PCR replicates with different primer tag combinations to allow an independent analysis of the PCR replicates. The PCR amplifications were carried out using a Biometra ThermoCycler (Biometra, Germany). The initial denaturation step was set at 94 °C for 5 min. This was followed by 40 PCR cycles, each consisting of denaturation at 94 °C for 30 s, annealing at 50 °C for 30 s, and elongation at 68 °C for 30 s, 72 °C for 10 min. Then, the presence and lengths of the PCR products were checked on a GelDoc Go Gel Imagine System (Biorad) using a 2 % agarose (Carl Roth GmbH and Co. KG, Germany) gel.

2.6.2. Purification, pooling, and DNA sequencing

The three PCR products from the sample (or blank) were merged and purified using a MinElute PCR Purification Kit (Qiagen, Germany) and quantified using a Qubit Fluorometer 2.0 (Invitrogen, USA). The purified PCR samples (total: 3 × 84) were pooled in equimolar concentrations for the next-generation sequencing service offered by Genesupport Fasteris SA in Switzerland. Sequencing was performed in paired-end mode (2 × 150 bp) on an Illumina NextSeq 500 platform (Illumina Inc.).

2.6.3. Bioinformatics and data filtering

After the Illumina sequencing, DNA sequence data was processed using ObiTools 3 (version 3.0.0) (https://git.metabarcoding.org/obitools/obitools3) (Boyer et al., 2016) with the following steps: first, forward and reverse reads were aligned and merged; second, sequences were sorted to samples according to the given primer tag combinations; third, data were cleaned for PCR and sequencing errors and finally assigned to the European Molecular Biology Laboratory (EMBL) (Kanz et al., 2005) taxonomic reference database, which was downloaded from the European Nucleotide Archive (ENA) website in June 2022. Using R software, the ObiTools3 output was filtered for DNA sequence types that had a 100 % match to the EMBL database and were taxonomically identified at the family level or lower (genus, species).

2.6.4. Further taxonomic filtering and functional grouping

The filtered ObiTools3 data were further analysed using Microsoft Excel. Preliminary (9) and detailed (63) samples were combined, arranging sediments according to sediment depth. Further, the following taxa were removed from the data set: i) taxa that occurred only once in the whole data set; ii); taxa assigned to higher taxonomic groups than family (i.e. order, class, division, etc.) iii) taxa that did not match Central European and regional vascular plant and bryophytes databases, i.e. taxa that are not naturally found in Central Europe. Plant sedaDNA sequences and the assignment of their taxonomical identification were double verified at the Nucleotide Sequence Database at the National Centre for Biotechnology Information (NCBI) (available at:

https://www.ncbi.nlm.nih.gov), but no taxonomic assignment changed. For the final selection of sequence types from both datasets, we retained only regionally occurring plant taxa, with the exception of Pinaceae. The occurrence of plant taxa was confirmed by diverse plant databases such as https://powo.science.kew.org/, https://floraveg.eu/, Neotoma Paleoecology Database (https://data.neotomadb.org/) and "The Global Pollen Project" (Martin and Harvey, 2017). After that we merged the "63" and "9" datasets and aggregated the read counts for each sequence type by scientific name, defining the final taxa in our dataset.

To denoise the dataset, sequences identified to the same best species, genus, and family were grouped into the corresponding categories at maximum taxonomic assignation. Then, the defined taxa were grouped according to the following functional vegetation categories, similar to when pollen data is grouped (Gedminienė et al., 2025), with the aim that both results could be compared: Quercetum mixtum (QM), Arboreal plant (AP), shrubs and bushes (Sh and SH), herb and grass plants (NAP), excluding human impact herbs (H), aquatic plants, green algae, and cyanobacteria. For each plant and plant group, percentages of the total sum (SUM) of all terrestrial (SUM = AP + QM + NAP + H + Sh + SH) taxa were recalculated. Shrubs and bushes here were divided into two groups to gain extra information. The SH group contains pioneers and early successional plants such as *Arctostaphylos uva-ursi*, *Hippophae*, *Arctous alpina*, and *Arctous*. The Sh group represents mid-to-late successional plants and is composed mainly of Salicaceae, *Viburnum*, *Lonicera*, *Juniperus,* and *Ribes*. The percentages of aquatic taxa, green algae, and cyanobacteria were recalculated based on the total sum (SUM) of all terrestrial taxa = 100 %. The aquatic macrophytes were classified using two different classifications: 1) hydrophytes (plants that develop their entire vegetative structures under water or on the surface of the water) and helophytes (plants that develop roots in water, but eventually develop a totally aerial vegetative and reproductive system); 2) emergent, floating-leaved, freely floating, and submersed macrophytes (Wetzel, 1983) regarding their attachment to the substratum. Diagrams were constructed and cluster analysis and subdivision to stratigraphical zones were performed using Tilia software and Constrained Incremental Sum of Squares CONISS (CONISS; Grimm, 1987).

2.7. *Pollen and spore analysis*

A detailed description of pollen and spore extraction methodology, as performed on the DUK_D core, and results, including composition and taxa abundances in the pollen data set at different periods, are presented in Gedminienė et al. (2025). Pollen and spore extraction followed the chemical procedures described in Berglund and Ralska-Jasiewiczowa (1986). The sediments were treated with 10 % HCl for carbonate removal, 10 % NaOH for organic and humic acid removal, and a heavy liquid for the separation of coarse particles. Pollen identification relied on Moore et al. (1991), Faegri and Iversen (1989), and the PalDat database (www.paldat.org).

2.8. *Diatom analysis*

Diatoms were analysed in 162 DUK_D core sediment samples. Sediments from a depth of 4–1298 cm were prepared in the laboratory using the techniques described by Battarbee (1986). The sediments were first treated with 10 % HCl to remove carbonates. After rinsing with distilled water, the sediments were treated with 30 % hydrogen peroxide to oxidise organic matter. After the reaction, the sediments were rinsed again with distilled water. The heavy liquid was used to concentrate diatom valves. Slides for microscopic analysis were prepared using the mounting medium Naphrax (refractive index 1.73). Diatom species were identified using a 'Nikon Eclipse 200' light microscope at × 1000 magnification.

Diatoms were identified at the species level primarily using European (Krammer and Lange-Bertalot, 1986, 1988, 1991a, 1991b; Lange-Bertalot et al., 2017) and North American (Spaulding et al., 2021) sources. Diatom species names were verified and updated according to the taxonomic nomenclature of the AlgaeBase database (Guiry and Guiry, 2024).

The species were classified into ecological groups according to their preferred habitats, planktonic and benthic (including both those unattached and attached to various surfaces in the lake), and trophic state – oligotrophic, oligotrophic–mesotrophic, mesotrophic, mesotrophic–eutrophic, eutrophic. The diatom checklists of Denys (1991), Van Dam et al. (1994), and the internet source for diatom identification and ecology "Diatoms of North America" (Spaulding et al., 2021) were the chief sources of information on the various diatom species' ecological requirements.

The TILIA program (Grimm, 2011) was used to present diatom data. Taxa with relative abundances of >1 % are presented in the diatom diagram. Species percentages (relative abundance) were calculated from the total sum of all valves counted in the sample. The ratio of planktonic to benthic diatoms (P/B) was calculated by dividing the sum of planktonic diatom valves by the sum of benthic diatom valves for each sample. The results of the stratigraphically constrained cluster analysis (CONISS; Grimm, 1987) are also presented in the diatom diagram.

2.9. *Ordination analysis*

Vegetation dynamics and patterns were visualised using ordination techniques. For pollen and sedaDNR analysis, response data are compositional and have a gradient of 1.6 SD and 2.5 SD units in length, respectively. Therefore, a linear method was recommended, and principal component analysis (PCA) was performed (Ter Braak and Šmilauer, 2012). The pollen data matrix contained information on 127 samples and the total abundance of pollen from 74 terrestrial taxa, while the DNR matrix contained information on 72 samples and 132 terrestrial taxa. All abundance data were log-transformed and centered by taxon. Additionally, the 20 most important taxa were displayed on the ordination graph. All ordination analyses were performed using Canoco v.5 software (Ter Braak and Šmilauer, 2012).

3. Results

3.1. *Lithological data and chronology*

A total of 9 AMS ^{14}C dates were used to develop the stratigraphic age-depth model for the DUK_D22 core (Table 1). Of these, only 6 dates were included in the final age-depth model (Fig. 2) to establish the chronological sequence. The three bottommost dates (FTMC-FV98-7, FTMC-FV98-8, and FTMC-FV-98-9) exhibited low agreement with the DUK_D core chronology and were excluded from the final model as outliers. Based on lithological evidence, which indicated a stable and stratigraphically consistent trend in the upper section of the core, radiocarbon dates directly above the lower section were used for linear extrapolation to model the age of the bottom sequence. The resulting age-depth model spans from >13690 ± 60 cal yr BP to 540 ± 20 cal yr BP and reveals a stable sedimentation rate (mean: 0.08 cm/year) for this interval. While a reduced sedimentation rate of about 0.05 cm/year was observed in the interval between 13320 ± 50 and 12600 ± 50 cal yr BP, the rate before >13690 ± 60 cal yr BP likely was much higher than it is represented in the diagram as it has a very different lithological composition.

We followed the stratigraphical subdivision of the Holocene and Lateglacial boundaries proposed by Lowe et al. (2008) and Walker et al. (2019), based on global stratotype ice cores. This includes the 11700–12850 cal yr BP interval for GS-1, with the Early to Middle Holocene boundary at 8236 cal yr BP, and the Middle to Late Holocene boundary at 4250 cal yr BP.

The lithology of the Dūkštelis palaeolake DUK_D22 core reveals significant variations across seven distinct litho- and bio-sedimentation zones, as identified through CONISS cluster analysis (Fig. 3).

Zone 1a (1190–1040 cm, before 13750 cal yr BP). Sediments are

Table 1
Dating results of DUK_D22 profile.

Lab Code	Dated interval, cm	Type	Age	pMC	Calibrated age range		cal yr BP	Modelled age range		Modelled age, cal yr BP
					cal yr BP		Median ±σ	cal yr BP		Median ±σ
					68,20 %	95,40 %		68,20 %	95,40 %	
FTMC-FV98-1	6–8	Soil; bottom sediment	538 ± 28	93.52 ± 0.32	625–520	630–510	540 ± 30	550–520	620–505	540 ± 20
FTMC-FV98-2	244–246	Soil; bottom sediment	2799 ± 29	70.58 ± 0.26	2940–2860	2995–2785	2900 ± 40	2960–2875	3000–2850	2920 ± 40
FTMC-FV98-3	524–526	Soil; bottom sediment	5244 ± 33	52.06 ± 0.21	6165–5930	6180–5920	5990 ± 70	6180–6085	6190–5955	6150 ± 50
FTMC-FV98-4	944–946	Soil; bottom sediment	10351 ± 39	27.56 ± 0.13	12450-12040	12470-11965	12200 ± 150	12325-12325	12390-12020	12190 ± 90
FTMC-FV98-5	984–986	Soil; bottom sediment	10821 ± 41	26 ± 0.13	12770-12725	12830-12725	12750 ± 30	12830-12735	12880-12725	12770 ± 40
FTMC-FV98-6	1024–1026	Soil; bottom sediment	11847 ± 46	22.88 ± 0.13	13770-13605	13795-13595	13690 ± 60	13630-13510	13685-13500	13550 ± 50
FTMC-FV98-7	1038–1040	Soil; bottom sediment	15788 ± 57	14.01 ± 0.1	19115-18965	19180-18900	19040 ± 70	Outlier	Outlier	13730 ± 70
FTMC-FV98-8	1094–1096	Soil; bottom sediment	31461 ± 157	1.99 ± 0.04	36065-35630	36185-35425	35830 ± 200	Outlier	Outlier	14460 ± 110
FTMC-FV98-9	1194–1196	Soil; bottom sediment	29182 ± 136	2.64 ± 0.04	34030-33550	34170-33290	33770 ± 230	Outlier	Outlier	15740 ± 190
–	1200	Bottom boundary, extrapolated data	–	–	–	–	–	–	–	15820 ± 200

composed of carbonaceous light grey silt, clayish, and coarsely laminated with fine sand layers. In this zone organic matter (OM) content is low, ranging from 3 to 8.2 % (increasing towards Zone 1b), while carbonate content reaches as high as 15 %. The grain size is dominated by silt (66.6–83.9 %), with clay-sized particles reaching up to 22 %, and minimal sand content. Magnetic susceptibility (MS) is high, with values ranging from 70.0 to 98.6 × 10^{-9} m^3/kg. This suggests sedimentation dominated by terrigenous minerogenic material and reflecting high-energy conditions with enhanced slope input from the catchment.

Zone 1b (1040–944 cm, 13750–12200 cal yr BP). Sediments transition to dark, finely laminated, silty-clayish gyttja. In general MS values decrease but still show greater variability (370.0–46.9 × 10^{-9} m^3/kg). There is an increased presence of medium and very fine sand, along with a significant proportion of clay (37.3–88.0 %). Loss-on-ignition (LOI) values indicate rising OM content (6.7–10.6 %) and a marked decrease in carbonate, suggesting more stable and slower sedimentation.

Zone 2 (944–750 cm, 12200–9400 cal yr BP). Sediments grade upwards from greenish-grey silty gyttja to dark green and brown, organic-rich gyttja, quickly oxidising. Lamination is not visually apparent. MS values decrease (30.7–2.4 × 10^{-9} m^3/kg), while fine and very fine sand content increase (22.3–31.3 %) with substantial silt and clay proportions. OM content rises rapidly from 18.9 to 40.2 %.

Zone 3 (750–622 cm, 9400–7500 cal yr BP). Organic-rich gyttja, dark brown, quickly oxidising dominates. MS values gradually become negative. Sediments consist of a mixture of various-grained sand, silt, and clay, with OM content constantly increasing (44.6–64.4 %). Between about 8600 and 8100 cal yr BP a temporal decline in OM is observed.

Zone 4 (622–435 cm, 7500–5100 cal yr BP) and Zone 5 (435–250 cm, 5100–3000 cal yr BP). Organic-rich, dark brown gyttja dominates. Both zones are characterised by consistently high OM content (60.7–71.4 %), with negative and gradually decreasing MS values. The sediments contain higher proportions of medium to very fine grains along with moderate amounts of silt and clay-sized grains, likely reflecting the presence of less decomposed organic matter rather than increased minerogenic input, as this is not indicated by other proxies. This suggests more stable sedimentation conditions, likely resulting from reduced catchment discharge. Around ~5100 cal yr BP, OM content temporarily declines, while silt and MS values increase.

Zone 6 (250–70 cm, 3000–1100 cal yr BP). Peat, medium decomposed, and brown in colour accumulates. This zone exhibits the lowest MS values. The sediments are dominated by very high OM content (79.0–93.8 %). However, the proportion of clay-sized particles (36.4–50.2 %) and silt-sized increases. This is likely due to the beginning of the accumulation of less decomposed peat rather than changes in minerogenic mater input. At a depth of about 150 cm, a temporal change is delineated with increased values of terrigenous material and coarser sediments.

Zone 7 (70–0 cm, from 1100 cal yr BP onwards). The uppermost zone is composed of poorly decomposed brown peat. There is a slightly increased proportion of sand of various grain sizes coinciding with an increasing trend in MS values, while OM content decreases. This change probably indicates an increased contribution of recent terrigenous matter input.

3.2. *Overview on pollen, other NPP, and sedaDNA sequence data*

During pollen analysis of a total of 127 samples from the DUK_D core, terrestrial plant taxa belonging to 31 families were identified, including 16 taxa at the family level, 43 at the genus level, and 10 at the species level (Table 2). Besides these, 15 water plant taxa, and 11 non-pollen palynomorphs (NPPs) including lichen, moss spores, and green algae were identified. Pollen assemblages and dominant taxon percentages during the whole sedimentation interval are described in Gedminienė et al. (2025).

The filtered sedaDNA “63” dataset contained a total of 7,445,373

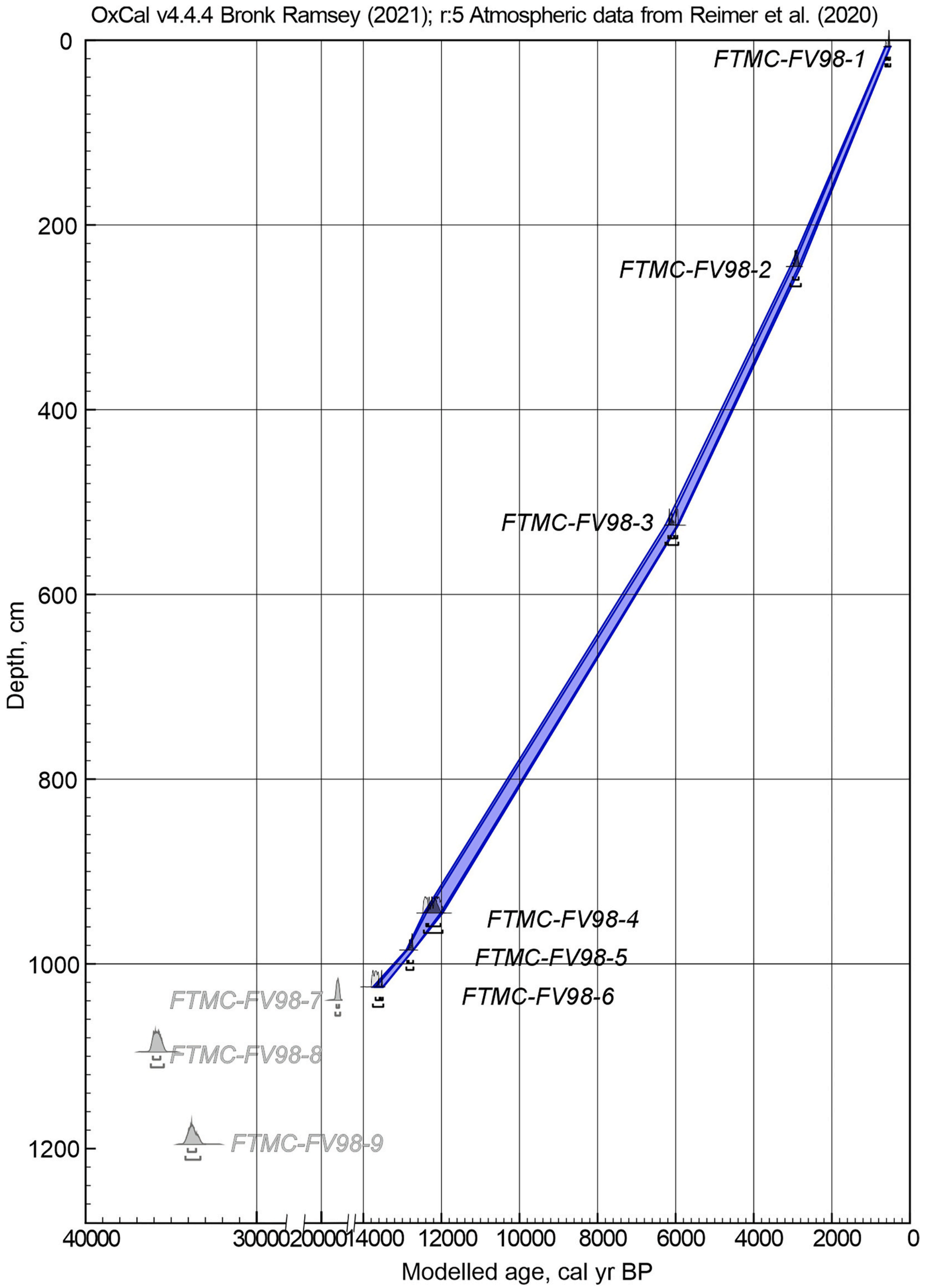

Fig. 2. Dūkštelis palaeolake age-depth model from DUK_D22 sediment core. Data included in the model are shown in black, while outliers, displayed in grey, were excluded from the final age-depth model.

read counts, of which 2 % were found in the extraction controls and 0.0008 % in the NTC. Among the 2 % of sequence reads in the blanks, there are only a very few blank controls which reached very high read counts for single sequence types, and particularly for higher family assignments like Fagaceae or Betulaceae (see Supplementary Data 1). Such amplifications never occurred multiple times in the blank PCR replicates and were therefore considered random PCR amplifications.

The filtered sedaDNA “9” dataset contained a total of 1,951,820 read counts, of which 0.7 % were found in the extraction controls and 0.0005 % in the NTC (see Supplementary Data 2). The final merged dataset contained 9,239,275 read counts recovered from the sediment samples, comprising 273 unique sequence types, which collapse into 155 unique taxa names including 132 terrestrial plants, 19 water plants, 4 taxa of green algae, 1 cyanobacteria identified to family, genus and sometimes species level (see Supplementary Data 3, 4). Fern and moss are found in both datasets but are not discussed in this research. The predominant

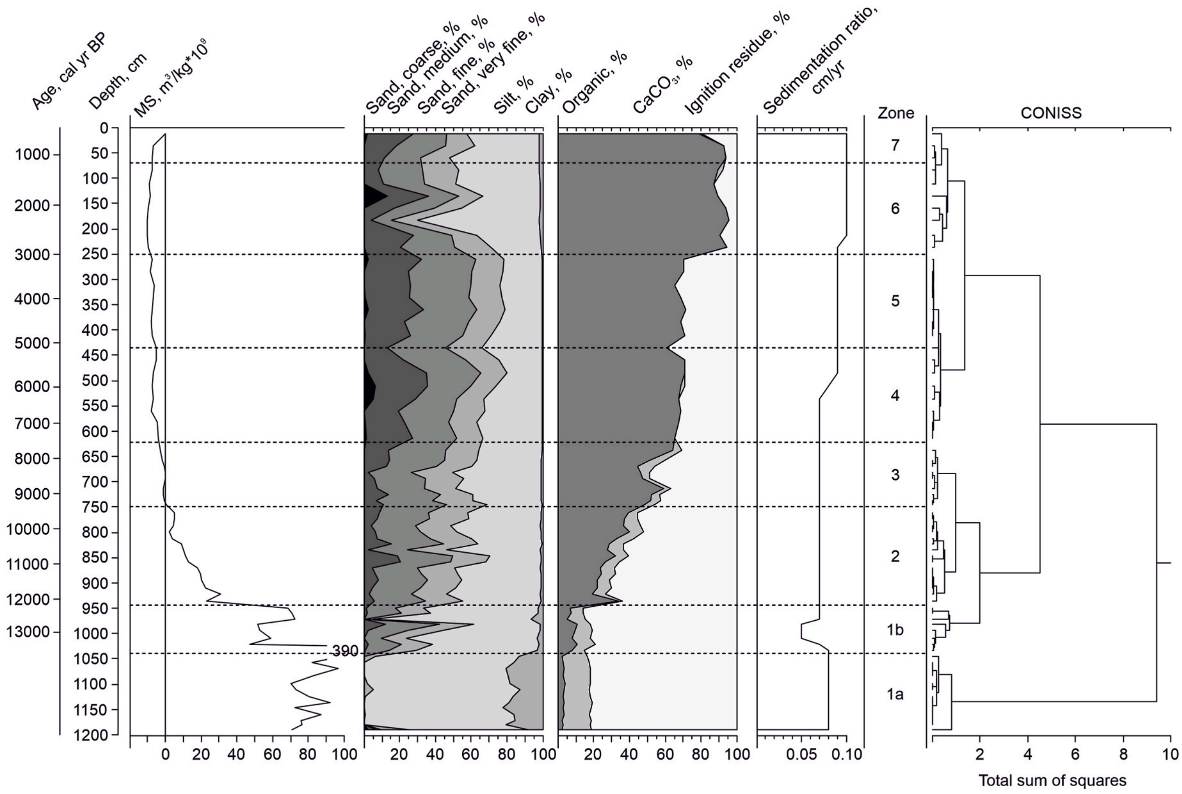

Fig. 3. The results of analyses performed on the Dūkštelis palaeolake DUK_D22 core, including magnetic susceptibility (MS), grain size, and loss-on-ignition (LOI), represented on an age-depth scale and alongside 7 zones.

terrestrial and aquatic plant groups listed in Table 2 illustrate the varying resolutions of pollen and sedaDNA analyses.

3.3. SedaDNA data

Only the most common plant types identified during sedaDNA analysis are plotted in diagrams (Fig. 4a–e**)**. Seven bio-sedimentation zones (DNA zones) were identified based on cluster analysis (CONISS; Grimm, 1987). Each zone represents a distinct time interval that reflects shifts in terrestrial vegetation and aquatic environments. These intervals capture transitions between open landscapes dominated by subalpine shrubs, herbs, and grasses (Fig. 4b–d), and periods of denser forests with increasing AP and QM taxa (Fig. 4a). Also, it discusses aquatic environment shifts away from glacial conditions with abundant wetlands to more open and temperate grassland ecosystems during warmer and drier periods, reflecting regional climate and hydrological changes (Fig. 4e). Periods of significant shrub and herb expansion, likely before 14000 cal yr BP, were followed by phases of forest expansion, with the dominance of temperate plants around 10000–7500 cal yr BP. These forested stages were subsequently replaced by periods of reduced tree cover and gradual transitions to grasslands. Water plants showed notable peaks during wetter periods, suggesting fluctuations in moisture levels. Most of the identified plant taxa are common in the region today. However, some taxa such as Juglandaceae, and Fagaceae, which were present in some samples before 3000 cal yr BP, are not currently common in the region. Shrubs and herbs like *Arctostaphylos uva-ursi*, *Arctous alpina*, Dryadoideae, *Saxifraga*, *Bartsia alpina*, and *Pyrola,* species typically found in tundra or alpine zones, but not regionally, were present in great numbers in Zone 1a, as well as being sporadically present in Zone 1b (Fig. 4b). Additionally, very high variability in the representation of certain families, particularly Asteraceae, Poaceae, Cyperaceae, Fabaceae, Orobanchaceae, etc. were observed at different depths within the core, offering highly enhanced taxonomic resolution compared to that achieved by pollen analysis (Table 2).

In the earliest part of the record, during the period covered by Zone 1a (before 13750 cal yr BP), shrubs (e.g., Saliceae, *Arctostaphylos uva-ursi*, *Arctous alpina*) and herbs (e.g. Dryadoideae, *Saxifraga*, *Bartsia alpina*, *Pyrola*, etc.) dominate, with values reaching 66 % (Fig. 4b). Grasses (e.g., Asteraceae family, *Mentheae*, *Ranunculus*, Brassicaceae) are less well represented, with a mean value of 30.1 % (Fig. 4c), while AP taxa (e. g., *Alnus*, Betulaceae) show a mean value of 6.25 % (Fig. 4a). Taxa such as Asteraceae, Brassicaceae, Poaceae are abundant, indicating a steppe-like environment with open vegetation. Some wetland and lowland herbs e.g. *Juncus,* Lamiaceae, Ranunculaceae, and Fabaceae are present, possibly indicating locally moist conditions. In the aquatic environment, submersed macrophytes, e.g. *Potamogeton*, *Potamogeton perfoliatus*, *Stuckenia*, and *Stuckenia filiformis,* dominate (Fig. 4e).

In Zone 1b (13750–11500 cal yr BP), there is a notable increase in AP taxa (mean values increase to 33.12 %) indicating the development of more forested landscapes. However, herbs and grasses begin to dominate (mean value 44 %) (Fig. 4c and d) over cold-adapted shrubs, reflecting a transition phase. There are signs of change, while Brassicaceae, and Asteraceae remain prevalent, the increase in *Ranunculus* and Polygonoideae along with the appearance of emergent macrophytes such as *Sparganium* and Typhaceae, suggest slightly wetter or more temperate conditions compared to Zone 1a. Shrub presence is less significant, SH decreases to 1.9 % and Sh decreases to 17.9 %. Although Betulaceae become more frequent, some samples also contain pioneer temperate forest trees, including *Fagaceae*, *Acer*, and Juglandaceae DNA. Water plant taxa decrease from 63 % to 47 %, with a reduction in submersed macrophytes (Fig. 4e). Freely floating and floating-leaved macrophytes appear, with an expansion of *Ceratophyllum demersum* and *Nymhoides peltata*, along with higher concentrations of green algae.

In Zone 2 (11500–9250 cal yr BP), AP max values (including Betulaceae) increase to about 73.2 %, vary at around ~30 %, indicating the expansion of mixed deciduous forests. The appearance of Ulmaceae,

Table 2

Most common terrestrial and aquatic plant types identified during pollen and sedaDNA analysis. *st stands for sequence type, used to distinguish between different genetic lineages, the number next to it shows variants within a species based on certain genetic sequences; **t stands for plant type identified during pollen analysis, the number next to it shows variants within a species.

Pollen**	SedaDNA*	Family
Terrestrial plants		
Alnus	*Alnus*	Betulaceae
Acer	*Acer* (st2)	Sapindaceae
Betula	Betulaceae (st2)	Betulaceae
Corylus	–	Betulaceae
Fagus	Fagaceae (st3)	Fagaceae
Quercus (t2)	*Quercus* (st2), *Quercus mongolica* var. *grosseserrata*	Fagaceae
Tilia	*Tilia* (st2)	Malvaceae
Ulmus	Ulmaceae (st2)	Ulmaceae
-	Juglandaceae	Juglandaceae
	Taxus	Taxaceae
Viburnum	*Viburnum* (st2), *Viburnum hanceanum*, *Viburnum odoratissimum*	Adoxaceae
Ericaceae, *Vaccinium, Calluna, Arctostaphylos*	*Arctostaphylos uva-ursi* (st3), *Arctous alpina* (st3), *Arctous*, *Vaccinium* (st2), *Pyrola* (st3)	Ericaceae
Salix	Salicaceae, Saliceae	Salicaceae
Hippophae	*Hippophae,* Elaeagnaceae	Elaeagnaceae
Juniperus	*Juniperus*	Cupressaceae
Apiaceae	Apioideae (st3)	Apiaceae
–	*Allium*	Amaryllidaceae
Asteraceae, *Centaurea, Cirsium, Artemisia,* Lactucaceae, *Anthemis arvensis*	*Achillea*, Anthemideae (st2), Asteraceae (st20), Asteroideae (st8), *Emilia,* Gnaphalieae, Heliantheae, *Hypochaeris cretensis*, Lactucinae, *Leontodon*, *Leucanthemella linearis*, Matricariinae, *Scorzoneroides*, *Tripleurospermum maritimum*,	Asteraceae
Boraginaceae	*Myosotis* (st2)	Boraginaceae
Brassicaceae	Brassicaceae (st4)	Brassicaceae
Humulus lupulus, Cannabaceae	*Humulus*	Cannabaceae
Caryophyllaceae, *Dianthus, Scleranthus, Lychnis*	Caryophyllaceae, *Cerastium*, Alsineae	Caryophyllaceae
Chenopodium	*Atriplex*, Chenopodioideae	Chenopodiaceae (Amaranthaceae)
Cyperaceae	*Carex castanea, Carex lasiocarpa, Carex pallescens, Carex* (st7), Carex subgen. Carex, *Schoenoplectus heterochaetus*	Cyperaceae
-	*Juncus* (st2), Juncaceae	Juncaceae
Helianthemum	*Helianthemum*	Cistaceae
Fabaceae, *Ononis*	*Astragalus (st2)*, *Lathyrus pratensis*, *Medicago*, Hedysareae (st2), Trifolieae, *Onobrychis viciifolia*, *Oxytropis*, *Trifolium* (st3), *Vicia*	Fabaceae
	Ribes	Grossulariaceae
Mentha, Stachys	*Galeopsis*, *Lamium*, Lamiaceae (st6), Mentheae (st4)	Lamiaceae
Lythrum	*Lythrum salicaria, Trapa*	Lythraceae
–	*Linum*	Linaceae
Onagraceae	*Chamaenerion angustifolium*, Epilobieae	Onagraceae
–	*Bartsia alpina, Euphrasia frigida* (st2), *Euphrasia tricuspidata*, *Euphrasia*, *Melampyrum*, *Odontites*, *Pedicularis* (st6)	Orobanchaceae
Plantaginaceae, *Plantago*	*Callitriche hermaphroditica*, *Hippuris, Plantago* (st2), *Veronica* (st2), *Veronica longifolia*	Plantaginaceae
	Armeria	Plumbaginaceae
Poaceae	*Bromus* (st3), Dactylidinae, *Festuca sinensis*, *Helictochloa*, *Holcus*, *Phragmites australis* (st2), *Poa*, *Poa ligulata,* Poaceae (st2), Poeae (st5), Poeae Chloroplast Group 2 (Poeae type) (st3), Poodinae incertae sedis, Pooideae,	Poaceae
Graminae (avena), Gramineae, *Secale cereale*, *Triticum*	*Avena,* Poeae Chloroplast Group 1 (Aveneae type) (st3), Hordeinae, Triticeae, *Triticum aestivum*	Poaceae
Rumex, Polygonaceae, *Rheum*	Polygonoideae (st3), Rumiceae, *Polygonum*	Polygonaceae
Polygonum persicaria	*Persicaria*	Polygonaceae
	Lysimachia	Primulaceae
Ranunculus flammula *Ranunculus acris* Ranunculaceae	*Caltha* (st2), *Ranunculus* (st7), *Ranunculus auricomus*, *Ranunculus ficariifolius*, *Ranunculus reptans*	Ranunculaceae
Thalictrum	*Thalictrum*	Ranunculaceae
Filipendula	*Filipendula ulmaria* (st2)	Rosaceae
Rosaceae	*Crataegus*, Colurieae, Dryadoideae, Fragariinae, *Prunus*, Rosaceae, Rosoideae,	Rosaceae
Potentilla	Potentilleae (st2), *Potentilla* (st3)	Rosaceae
Rubus chamaemorus, *Rubus*	*Rubus*	Rosaceae
–	Rubieae (st2), Rubioideae (st2)	Rubiaceae
Galium verticillatum	*Galium* (st2)	Rubiaceae
–	*Saxifraga* (st4), *Saxifraga kotschyi*	Saxifragaceae
Urtica	*Urtica*	Urticaceae
–	Caprifoliaceae (st2), Knautia, Lonicera	Caprifoliaceae
	Convolvulaceae (st2)	Convolvulaceae
Water plants		
–	*Phragmites australis*	Poaceae
	Ceratophyllum demersum	Ceratophyllaceae
Scheuchzeria palustris	–	Scheuchzeriaceae
Elodea	–	Hydrocharitaceae
Typha	*Sparganium* (st2), Typhaceae	Typhaceae
Cyperaceae	*Schoenoplectus heterochaetus*	Cyperaceae
Menyanthes	*Nymphoides peltata*	Menyanthaceae
Myriophyllum verticillatum, Myriophyllum alterniflorum, Myriophyllum	*Myriophyllum*	Haloragaceae
Nymphaea, Nuphar	Nymphaeaceae (st2)	Nymphaeaceae
Potamogeton	*Potamogeton* (st2), *Potamogeton crispus*, *Potamogeton perfoliatus* (st3), *Potamogeton praelongus*, *Stuckenia* (st2), *Stuckenia filiformis* (st3), *Stuckenia vaginata*	Potamogetonaceae
Trapa Natans	*Trapa*	Lythraceae
Equisetum	*Equisetum* (st4)	Equisetaceae
Urticularia	*Utricularia*	Lentibulariaceae

Acer, *Tilia*, and the establishment of Fagaceae suggest a rapid shift toward a more densely forested landscape. Values of QM vegetation increase to 26 % in the upper part (Fig. 4a). Herbs and grasses decline significantly to about 27 %, with minimum percentages in some samples as low as 6.5 %. Although shrubs and bushes (Sh) increase to 34–60– %, the disappearance of cold-adapted species such as *Arctous* and *Pyrola* is noticeable, but the emergence and continuous rise of *Viburnum* mark the beginning of a transitional phase from tundra-dominant landscape to a more diverse shrubland or open woodland (Fig. 4b). The presence of *Lamiaceae* and Asteraceae suggests that patches of open land or

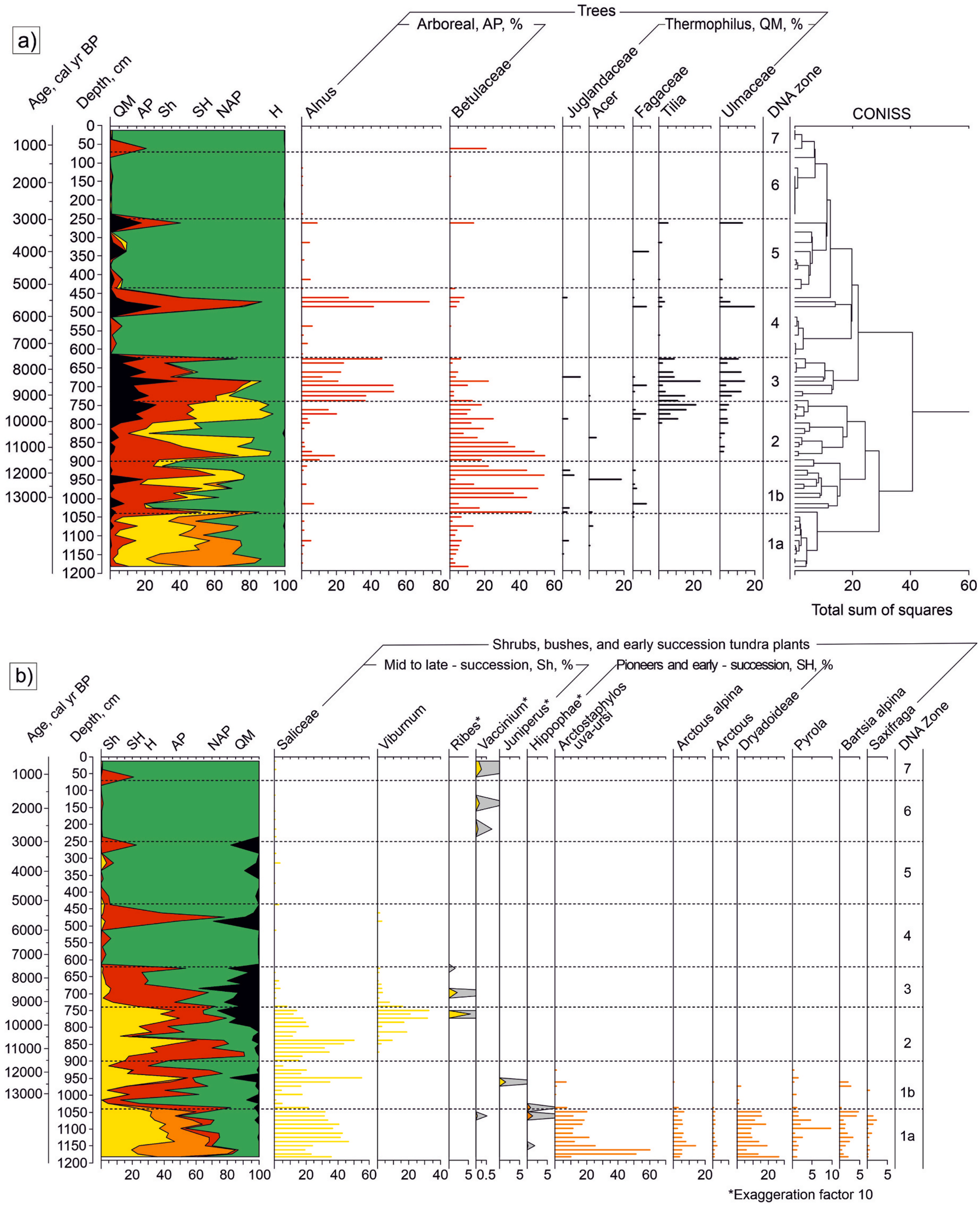

Fig. 4. Stratigraphic diagrams highlighting the relative abundance (%) of selected sedaDNA taxa from the Dūkštelis palaeolake (core DUK_D22): a) trees; b) shrubs and bushes; c) grasses and herbs; d) Poales; e) aquatic plants, green algae, and cyanobacteria. The leftmost panel presents the total (100 %) sum diagram of all taxon groups. Abbreviations: QM - Quercetum mixtum, AP - Arboreal plants, NAP – non-arboreal plants (herbs and grasses), Sh - mid-to late-successional shrubs and bushes, SH - pioneer and early-successional shrubs, H - human impact herbs. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

disturbed areas may have persisted. An increase in the number of sedges and rushes, and wet meadow grasses (i.e. *Juncus*, *Carex*, *Filipendula ulmaria, Caltha and Ranunculus*) points to the expansion of wetland or riparian habitats (Fig. 4c). From the middle of this zone, floating submersed macrophytes decrease, while freely floating, and floating-leaved macrophytes increase, along with a higher presence of emergent macrophytes (Fig. 4e).

In Zone 3 (9250–7500 cal yr BP), forests dominate the landscape, with AP taxa reaching their highest levels, increasing to 42 %, highlighted by a peak in QM species showing an increase up to ~38 %. *Alnus* and Betulaceae are prominent, while Fagaceae, Ulmaceae, and *Tilia* also increase and reach peak values, marking a more diverse forest canopy

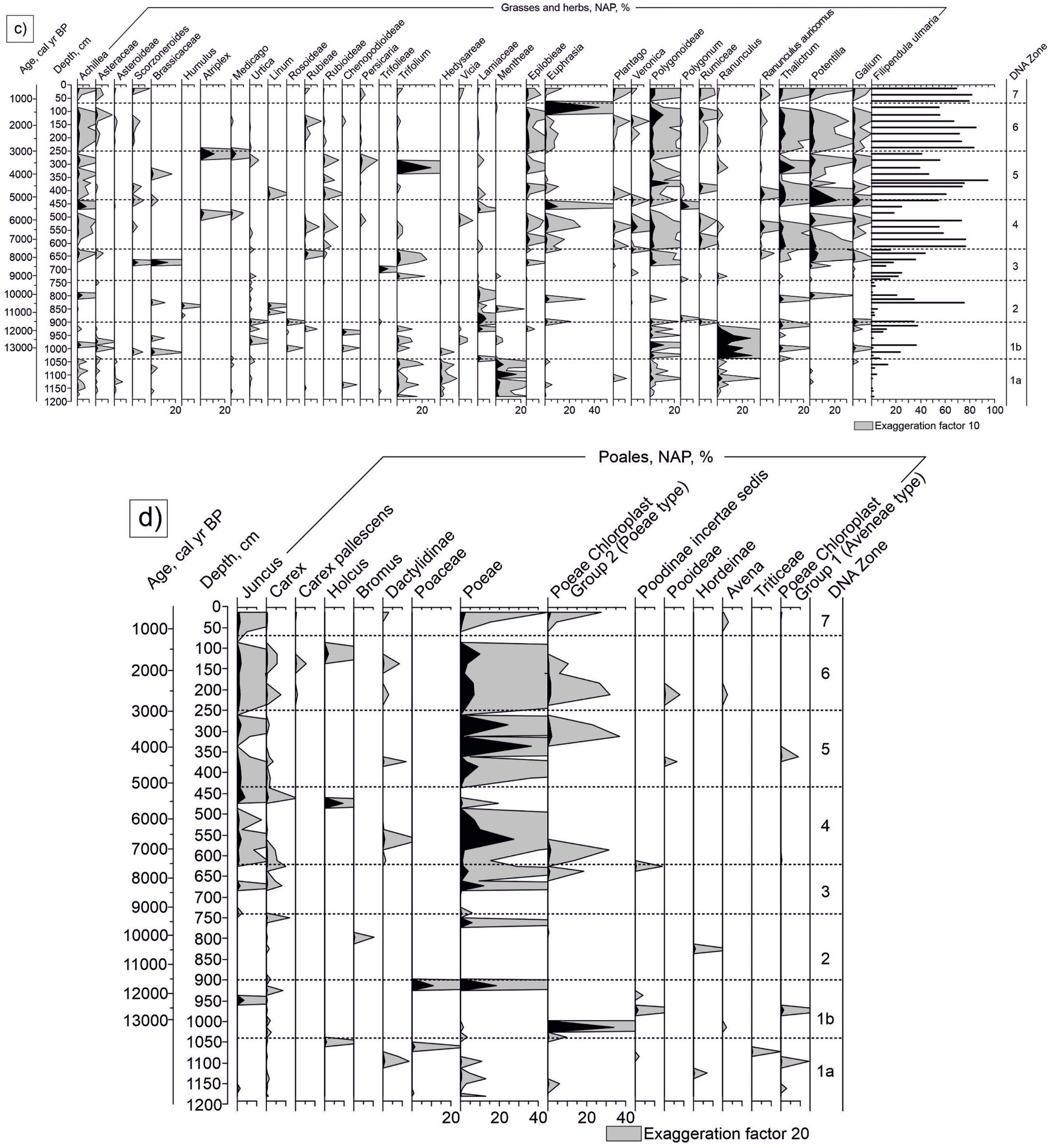

Fig. 4. (*continued*).

(Fig. 4a). The presence of shrubs decreases almost instantly, but herbs and grasses gradually re-emerge starting at 15.9 % at the beginning of the zone and increasing to 67.8 % later. Taxa such as *Asteraceae* and *Brassicaceae* remain present, likely representing localised open areas. The increase in *Potentilla*, *Filipendula ulmaria, Urtica, Galium*, Trifolieae, and various species of Polygonoideae suggests the presence of nutrient-rich soils. The appearance of different plant families from the order of Poales points to diversification within the grass family, likely reflecting changes in habitat structure, potentially driven by fluctuating moisture levels (Fig. 4d).

In Zone 4 (7500–5100 cal yr BP), a reduction to 21 % in mean values of AP taxa is observed (Fig. 4a). Herbs vary around 73 %, reaching a maximum of 99.4 %. Although the dominance of plants of the order Poales plays an important role in vegetation composition, a significant increase in *Filipendula ulmaria*, *Thalictrum, Potentilla,* and Polygonoideae suggests a resurgence of sedges and wetland vegetation (Fig. 4c). The

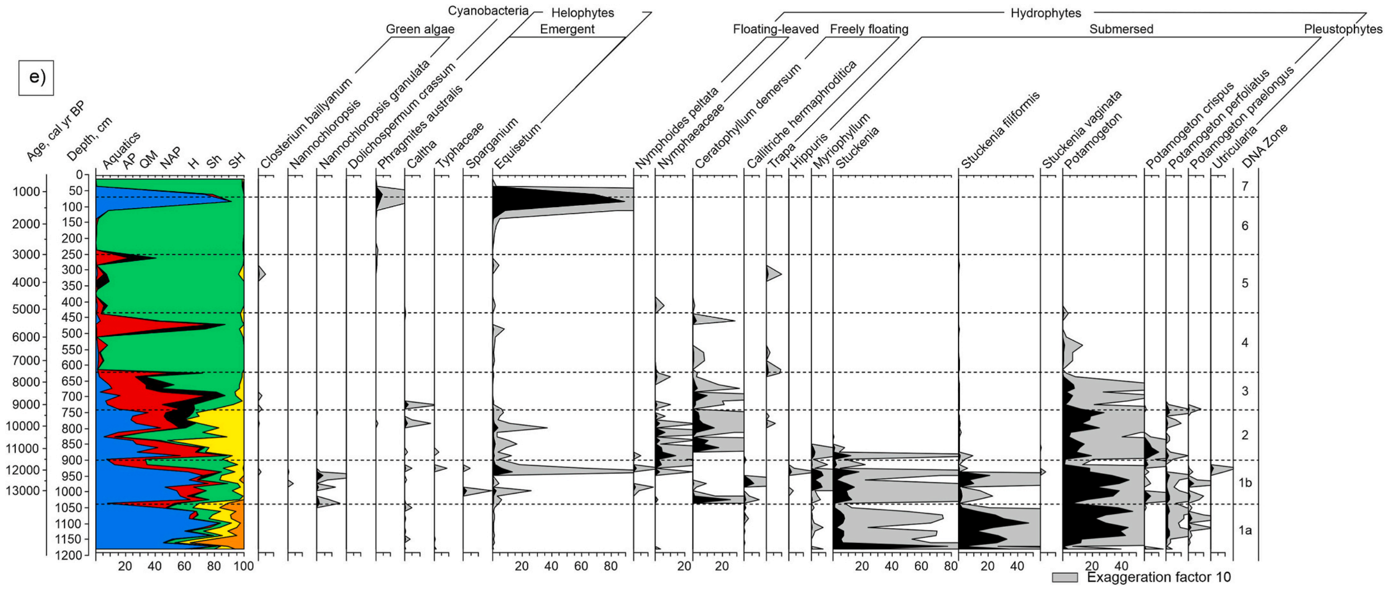

Fig. 4. (*continued*).

herbaceous taxa show an increase, with more representation from *Galium*, *Ranunculus*, and *Urtica*, suggesting localised openings in the forest canopy or disturbances that favoured these species. There is a clear presence of *Plantago, Achillea,* and *Euphrasia*, both of which are indicators of pasture and disturbed areas. The mixed forests remain dominant, with a continuing presence of Juglandaceae, Fagaceae, and *Tilia*, especially in the upper part of the zone- However, the overall percentages of tree taxa are poorly expressed and usually remain very low. At the top of the zone, the reappearance of *Alnus*, Betulaceae, and Ulmaceae is observed, likely pointing to an event lasting a few centuries (Fig. 4a). Within the end of this zone, submersed macrophytes disappear, and freely floating macrophytes decline significantly (Fig. 4e).

In Zone 5 (5100–3000 cal yr BP), the decline in AP taxa continues, with mean values dropping to about 4 %, followed by a pronounced, but brief comeback at the end of the zone (Fig. 4a). This suggests a turn towards a more open landscape or possible deforestation events, either as a result of climate change or early human activities. The increasing trend coincides with the increasing presence of *Equisetum*, similar to that observed in Zone 4 (Fig. 4e). Percentages of herb and grass taxa continuously increase, reaching about 91 %, with Poeae dominating in particular. Additionally, high percentages of *Filipendula ulmaria*, *Potentilla*, *Galium*, *Thalictrum*, *Ranunculus*, Polygonoideae, and Brassicaceae, taxa commonly associated with disturbed ground or pastureland, are detected (Fig. 4c). Hydrophytes decrease significantly, with only a few representatives such as *Trapa* and Nymphaeaceae (Fig. 4e), while submersed hydrophytes disappear.

In Zone 6 (3000–1100 cal yr BP), herbs and grasses dominate, reaching a maximum of 99.9 %, with almost no tree taxa detected in the sedaDNA analysis. Herbaceous taxa such as *Plantago*, *Galium*, and various Asteraceae taxa are abundant, and there is a rapid increase of *Euphrasia* and Epilobieae in the upper part of the zone. The presence of *Filipendula ulmaria, Potentilla, Thalictrum,* and Polygonoideae suggests wetland or riparian environments in certain parts of the landscape (Fig. 4c). Increased finds of *Phragmites australis* and Equisetum appear at the end of this zone (Fig. 4e).

In Zone 7 (1100 cal yr BP and later), the landscape is dominated by open habitat vegetation, including various members of the Asteraceae family, *Plantago*, *Potentilla*, *Galium*, *Urtica*, Ranunculaceae, and several finds from agricultural plants, likely indicating continued or expanding human land use. The dominance of *Phragmites*, *Filipendula ulmaria*, *Epilobium,* and Juncus suggests localised wetlands or moist conditions. This vegetation composition is similar to the current local flora. Despite their presence in patches around the palaeolake today, the high concentration of Betulaceae, observed only in one sample, and some *Alnus* are detected in the sedaDNA records.

3.4. Diatom data

The diatoms were analysed over the entire length of the DUK_D sediment sequence from 0 to 1300 cm, though the diagram specifically represents the 1096–486 cm depth interval. The upper (486–4 cm) and lower (1298–1096 cm) sections of the sediment sequence contain only occasional diatom valves, and these samples are not included in the diatom diagram. The final chronological sequence for this core, consisting of 17 dates, is described in Gedminienė et al. (2025). The uppermost part of the sediment core, 0−15 cm, consists of vegetative parts of plants. There was very low diatom content, mainly acidophilous *Eunotia praerupta* Ehrenberg, *Eunotia incisa* W.Smith ex W.Gregory, aerophilic *Hantzschia amphioxys* (Ehrenberg) Grunow (Van Dam et al., 1994) and benthic *Amphora ovalis* (Kützing) Kützing, *Cavinula scutelloides* (W.Smith ex W.Gregory) Lange-Bertalot. At a depth of 15–310 cm, peat is present, and only occasional diatom valves were detected. The sediment interval at a depth of 310–486 cm is composed of gyttja and there was low diatom content, mainly planktonic *Aulacoseira granulata* (Ehrenberg) Simonsen and benthic *A. ovalis* (Denys, 1991). The bottom sediments at a depth of 1096–1296 cm consist of clay and occasional valves were found, mainly benthic *Cymbellafalsa diluviana* (Krasske) Lange-Bertalot and Metzeltin (Sizemore et al., 2023), *C. scutelloides* and *A. ovalis* (Denys, 1991).

The sediment interval 1096–486 cm consists of gyttja which is rich in diatom valves. Diatom species were classified into five local diatom assemblage zones (LDAZ) according to cluster analysis and characteristic diatom assemblages (Fig. 5).

LDAZ I, 1096–1030 cm, 11700–11000 cal yr BP. This zone is characterised by the prevalence of benthic diatoms (35–93 %), mainly *Pseudostaurosira brevistriata* (Grunow) D.M.Williams and Round, *Staurosira construens* Ehrenberg, *Staurosira venter* (Ehrenberg) Cleve and J.D. Möller, and *Staurosirella lapponica* (Grunow) D.M.Williams and Round. Planktonic species make up 6–64 % of the total and the most common are *Lindavia radiosa* (Grunow) De Toni and Forti, *Lindavia ocellata* (Pantocsek) T.Nakov et al.*,* and *Cyclotella distinguenda* Hustedt. Mesotrophic–eutrophic diatoms are abundant (39–64 %), but the eutrophic group also makes up a large proportion of the total (Fig. 6). The P/B ratio is low (0.1–1.8).

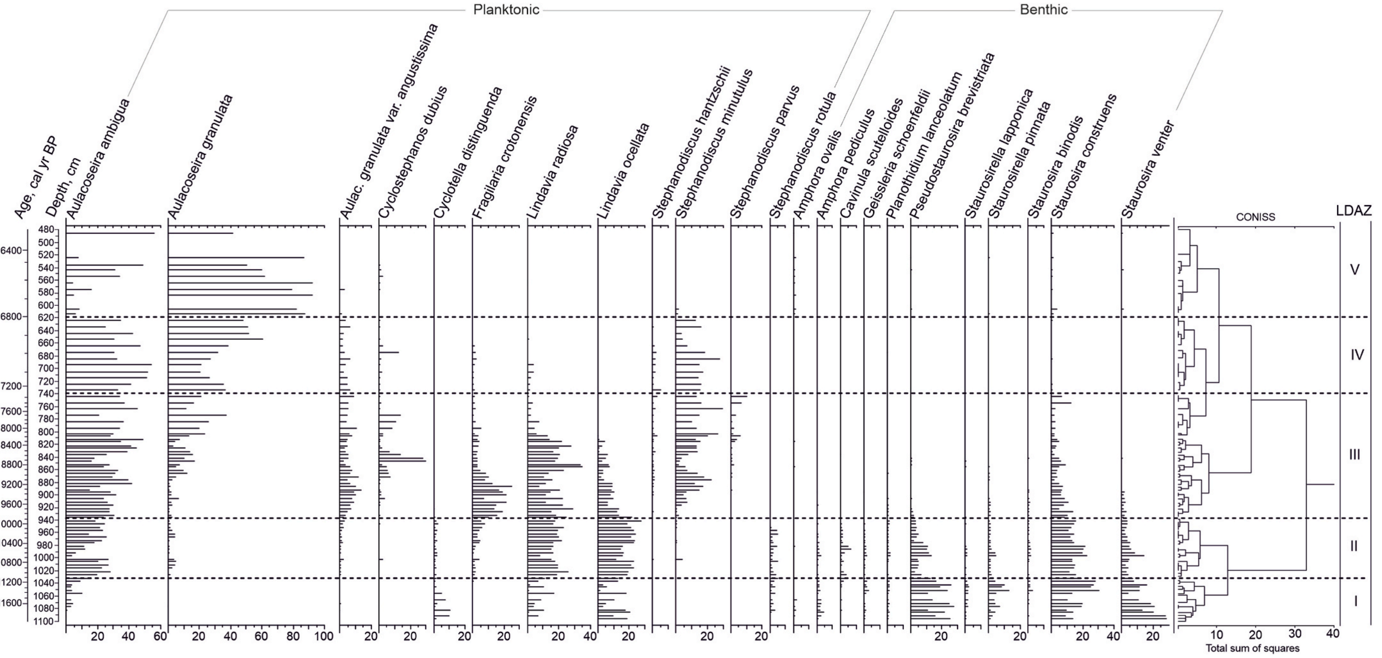

Fig. 5. Relative abundance (%) of selected diatom taxa from the Dūkštelis palaeolake (core DUK_D). LDAZ – local diatom assemblage zone.

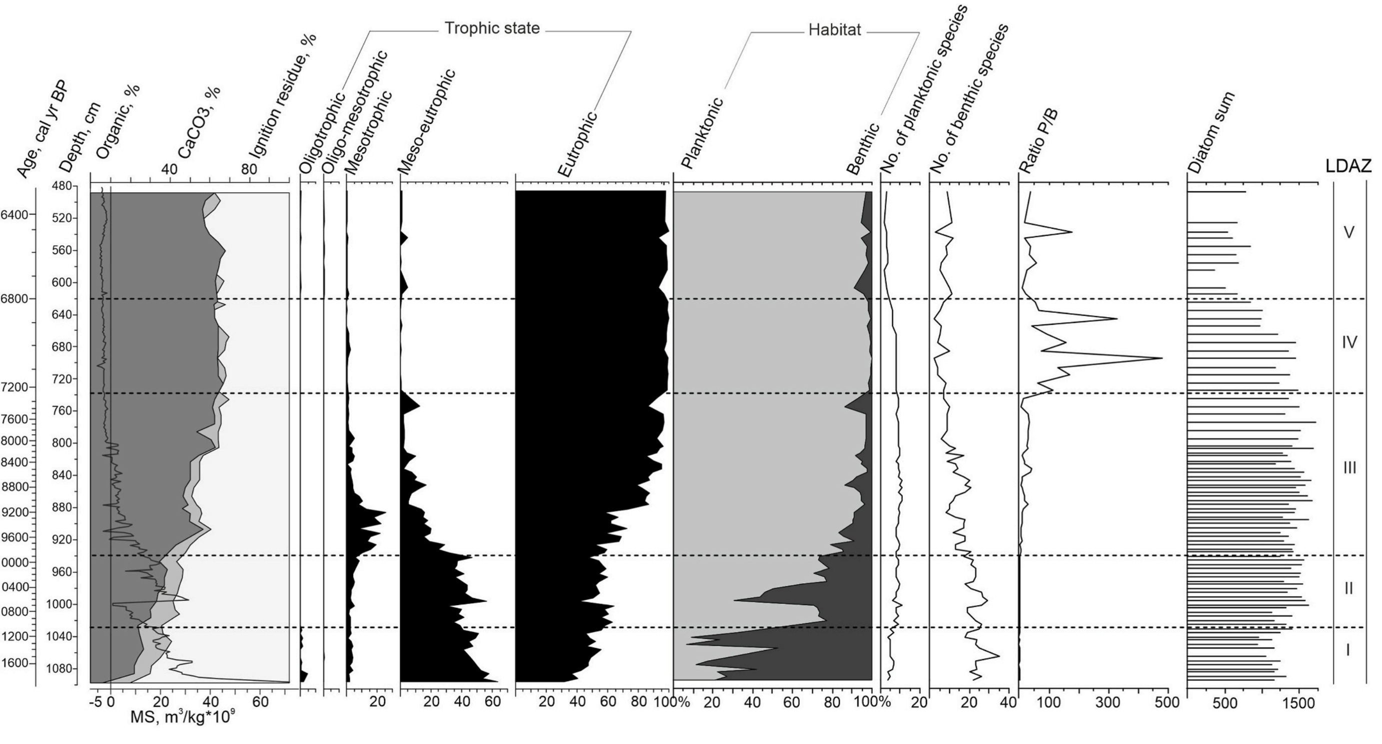

Fig. 6. Diagram of diatom ecological groups classified by trophic state and habitat. The leftmost panel presents magnetic susceptibility (MS), and loss-on-ignition (LOI) from the Dūkštelis palaeolake (core DUK_D).

LDAZ II, 1030–940 cm, 11000–9900 cal yr BP. Benthic diatoms predominate, mainly *S. construens*, *S. venter*, and *P. brevistriata*, as in the zone below. However, there is a gradual decrease in these species proceeding upwards in the zone. Planktonic diatoms increase to a frequency of 43–78 % and are dominated by *L. radiosa*, *L. ocellata,* and *Aulacoseira ambigua* (Grunow) Simonsen. A predominance of eutrophic (47–63 %) and mesotrophic-eutrophic diatoms is observed. The P/B ratio remains low (0.4–3.4).

LDAZ III, 940–740 cm, 9900–7250 cal yr BP. The content of benthic diatoms decreased to 3–26 %, while previously dominant species now only make up a few percent of the total. A significant increase in planktonic diatoms is characteristic of this zone. Planktonic diatoms are dominated by *A. ambigua*, *Cyclostephanos dubius* (Hustedt) Round, *Fragilaria crotonensis* Kitton, *L. radiosa,* and *Stephanodiscus minutulus* (Kützing) Cleve and Möller. Eutrophic diatoms increase gradually upwards in the zone and reach 96 %. The number of planktonic diatom species increases significantly, and the P/B ratio increases up to 3–37.

LDAZ IV, 740–620 cm, 7250–6800 cal yr BP. This zone is characterised by an increase in planktonic diatoms up to 97–99 %. The planktonic diatoms are dominated by *A. ambigua*, *A. granulata,* and *S. minutulus*. A decreased content of benthic diatoms as well as the number of benthic taxa is also observed. Eutrophic diatoms make up 98–99 % of the entire zone. The P/B ratio increased significantly and varies in a range of 42–482.

LDAZ V, 620–480 cm, 6800–6300 cal yr BP. The percentage of planktonic diatoms remains high, 97–98 %, as in the lower zone. Two planktonic species dominate – *A. granulata* and *A. ambigua*. The abundance of eutrophic diatoms is as high as in the lower zone and makes up 93–99 %. The number of planktonic taxa decreased, and the number of benthic taxa increased slightly. The P/B ratio decreased and varies over a range of 10–179.

3.5. *Statistics, ordination analyses, and data comparison*

The two sediment cores from which the sedaDNA and pollen proxies were derived had a 1-m depth difference, making correlation necessary. Alignment of the cores was achieved by synchronising them based on the dating, matching LOI and MS data, using CONISS cluster analysis, which allowed their subdivision into the seven zones with the greatest lithological similarity. Because the sedaDNA data and MS from the sediment interval at a depth of 1200–944 cm showed considerable variation, this interval was further subdivided into two subzones: Zone 1a and Zone 1b. Noticeable differences between the cores were observed, likely due to localised sedimentation processes and a minor degree of spatial heterogeneity within the palaeolake basin, which may have influenced the preservation and representation of environmental gradients in each core. The same ordination methodology was applied to both the pollen data (Gedminienė et al., 2025) and the sedaDNA data to compare the proxies and to reveal primary patterns of vegetation dynamics in each zone. According to the ordination based on pollen data, the first PCA axis explains 41 % of the total variation, the second explains 10.7 %, and the cumulative explained variation of the first two axes is 51.7 % in the dataset (Fig. 7), meaning the first two principal components summarise over half of the variability in the pollen data. According to the ordination based on sedaDNR data, the first PCA axis explains 23.65 % of all variation, the second – 17.62 %, and the cumulative explained variation of the first two axes is 41.27 % in the data set (Fig. 8). This suggests that pollen data may represent clearer or stronger vegetation-environmental gradients, making interpretation more straightforward, while sedaDNA data reflect greater complexity, noise, or more diverse signals, possibly due to their higher taxonomic resolution or different source areas, requiring additional components for a fuller explanation. However, both ordinations reveal broadly consistent patterns of vegetation succession and zonation through time in relation to the overall agreement on the temporal progression and differentiation of vegetation zones, despite the differences in dominant taxa and resolution. This procedure provided a visualization of reliably comparable datasets which allowed us to observe noticeable differences at certain corresponding depths.

In pollen data (Fig. 7), plants with lower pollen productivity are underrepresented, and vegetation is predominantly characterised by arboreal taxa, such as *Quercus*, *Alnus*, *Picea*, and *Ulmus*, and therefore such analysis primarily reflects regional environment changes. The stratigraphic zones show clear shifts in forest composition and density over time, with a distinct clustering of zones along the principal components. In contrast, the sedaDNA data (Fig. 8) display a greater representation of herbaceous and shrubby taxa, including *Arctostaphylos uva-ursi*, *Dryadoideae*, and *Saxifraga*, indicating a stronger signal from local, ground-level vegetation, providing finer-scale resolution of understory and non-arboreal plants. The sedaDNA zones also show distinct clustering but with more variability within zones, possibly due to the heterogeneous nature of DNA preservation and deposition in different lithology and under various physical conditions, also higher sedaDNA sensitivity to shorter-term environment fluctuations.

Environmental gradients represented by the axes for pollen data (Fig. 7) suggest two important ecological factors in shaping regional plant communities. The first axis likely represents a climate gradient from colder to warmer conditions, showing a transition from pioneer species like *Betula*, *Pinus*, and *Salix* (1st and 2nd zones), to deciduous trees like *Quercus*, *Ulmus* and *Tilia*, including a notable increase in *Carpinus betulus* in warmer, more humid climates. Interpreting the second axis is more complex as it reflects both regional and local environmental gradients. It likely reflects a moisture gradient, as there is a transition between species that thrive in drier conditions (e.g., *Juniperus*, *Artemisia*, Caryophyllaceae) and species that prefer more humid conditions (e.g., *Alnus*, *Quercus*), indicating changes in local water availability or soil moisture.

SedaDNA results (Fig. 8) reflect more local environmental conditions than pollen data (Fig. 7). The first PCA axis likely represents a gradient of climate or vegetation succession, similar to the pollen data. The presence of *Arctostaphylos uva-ursi*, *Dryadoideae*, and *Saxifraga* early in Zones 1a and 1b may reflect colder, tundra-like conditions, while the appearance of Betulaceae on the opposite side likely reflects a later successional stage with more woody (forest) vegetation as climate conditions improved. On the other hand, it may represent the openness of habitats where there was a change from open vegetation in terms of shrubs and grasses in Zones 1a and 1b to a more closed vegetation in Zones 3, 4, and 5, and a slight recovery to more open habitats with grasses predominant at the upper part of Zones 5, 6 and 7. This change

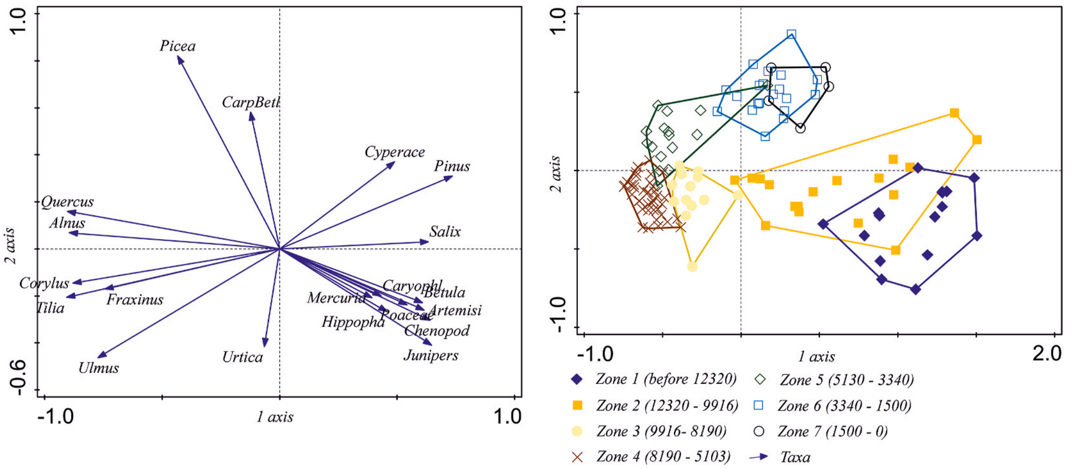

Fig. 7. The results of the principal component analysis (PCA) representing 20 of the most important pollen taxa displayed on the ordination graph and the terrestrial pollen data indicating possible environmental gradients within the zones from the Dūkštelis palaeolake (core DUK_D).

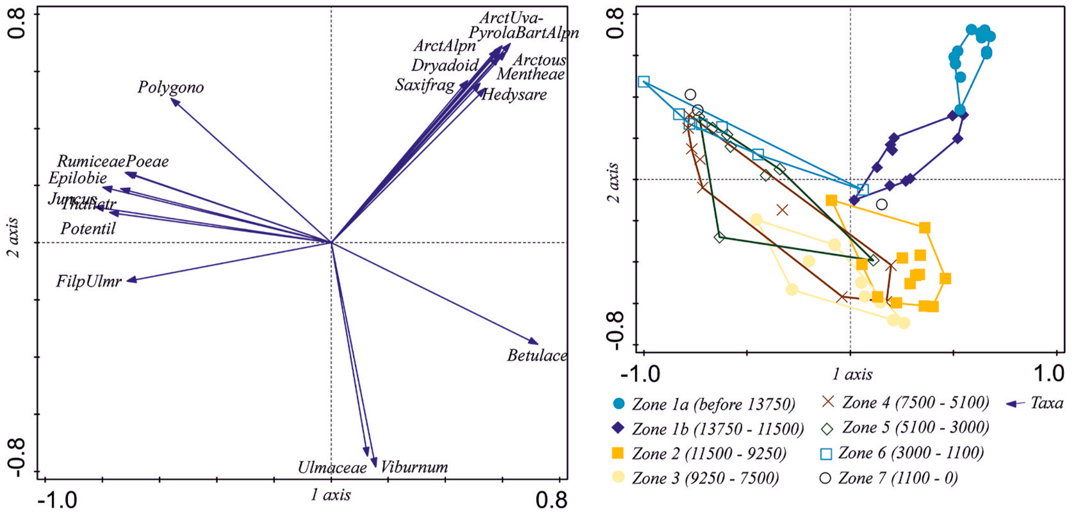

Fig. 8. The results of the principal component analysis (PCA) representing 20 of the most important sedaDNA taxa displayed on the ordination graph and the terrestrial sedaDNA data indicating possible environmental gradients within the zones from the Dūkštelis palaeolake (core DUK_D22).

traces more local factors because during pollen analysis presence of dwarf shrubs is very rare. The second axis (Fig. 8) could be related to heat and moisture availability, local habitat differences, or the altitude. Cold and dry environments in Zones 1a and 1b change to wetter in Zones 2, 3, 4, and 5. Some species like *Pyrola*, *Arctostaphylos uva-ursi*, *Dryadoideae*, and *Saxifraga* may suggest drier or specific higher altitude conditions, while others like *Rumiceae, Juncaceae,* and *Filipendula ulmaria* indicate a preference for wetter conditions.

4. Discussion

The integration of the sedaDNA approach with traditional, pollen, diatom, and lithological analyses enabled a higher-resolution reconstruction of past vegetation compared to pollen analysis alone (Table 2). The observed differences are discussed in this paper primarily in conjunction with previous records from the Dūkštelis palaeoake (Gedminienė et al., 2025). As sediment properties have some degree of heterogeneity over the lake basin, some differences between the proxies are expected; however, the main patterns remained consistent and complementary. This approach effectively identified species growing near and in the lake and was particularly useful for detecting species that produce less pollen, like herbaceous plants, shrubs, and aquatic macrophytes. In contrast, pollen analysis reflected a broader environmental context, but at the cost of underrepresenting non-tree taxa, that is, those which do not produce large amounts of pollen. For example, wind-pollinated trees like *Betula* and *Corylus* may be well represented in pollen records due to long-distance dispersal but can be underdetected in sedaDNA because their DNA is less likely to accumulate in lake sediments compared to that of aquatic or shoreline plants. Conversely, lower-ground taxa such as Arctostaphylos uva-ursi, Dryadoideae, Pyrola, and Saxifraga are poorly represented in pollen diagrams but show high values in sedaDNA data, highlighting the complementary nature of these proxies.

Diatoms, supplemented by lithological proxies and macrophytes from sedaDNA, revealed changes in water depth, oxygen levels, trophic state, and sedimentary processes – factors that were crucial for the preservation of sedaDNA, pollen, and diatoms. Combining quantitative pollen influx data with sedaDNA read abundance, alongside cross-validation approaches, can improve confidence in vegetation reconstructions, covering potentially missing broader ecological patterns. Moreover, understanding the differential preservation and transport mechanisms affecting both proxies is essential to optimise their combined use in paleoecological studies.

4.1. Subalpine ecosystem combined with patches of wet lowlands during the Lateglacial

Our observation highlights an intriguing scenario in which two contrasting vegetation types coexist in the same environment in the Lake Dūkštelis region after the last deglaciation, a phenomenon which may reflect a transitional or “no modern analogue” ecosystem. These kinds of ecosystems likely developed in response to climatic and geomorphological conditions that no longer exist, leading to unique, patchy landscapes where subalpine and lowland vegetation types could thrive simultaneously in close proximity. In Arctic regions, such an extinct Pleistocene steppe-tundra biome is also known as the “mammoth steppe” (Garcés-Pastor et al., 2024). The sedimentation period, which lasted until about 13800 cal yr BP, is characterised by cold and harsh conditions (Veski et al., 2012; Gedminienė et al., 2025), with vegetation similar to Late Pleistocene tundra or subalpine ecosystems. This is partially consistent with the findings of this study with the presence of shrub taxa like *Arctostaphylos uva-ursi*, *Arctous alpina,* and colder-adapted species (e.g., Dryadoideae, *Pyrola, Saxifraga*) (Fig. 4b, Zone 1a). While these represent cold, scarcely vegetated environments with limited soil, the simultaneous high representation of herbs not characteristic of modern subalpine ecosystems (e.g., Trifoliaceae, *Mentheae*, Ranunculaceae, *Plantago*, various Asteraceae, Poaceae taxa, and Saliceae) in the same spectra is observed, suggesting an existence of lowlands with relatively lower environmental stress. The clustering of such a different taxa within the same zone (Fig. 8) supports the hypothesis that even small elevation changes can create microclimatic gradients affecting the vegetation, as seen in studies of altitudinal zonation (Sundqvist et al., 2013; Robbins and Matthews, 2010). This dynamic and heterogeneous environment, formed following the glacial retreat, created diverse microhabitats which are well documented in the Lateglacial and Early Holocene periods (Williams et al., 2004; Overpeck et al., 1992), identifying climate change and unstable conditions which led to vegetation assemblages that do not have direct modern counterparts. In our case, pronounced altitudinal gradients may have fostered wetter, herb-rich lowlands and drier, sparsely vegetated elevated terrains. Pollen data for this period showed an increase in shrubs and herbs, with notable representation of trees like *Alnus*, *Betula*, and *Pinus*, suggesting a regional forest spread (Gedminienė et al., 2025.).

In the earliest part of our record, the lake sediments, highly carbonated and laminated with silty-sandy layers, suggest an unstable environment reflecting the dynamic runoff regimes from the shoreline. Relatively high MS values indicate minerogenic matter input from the surroundings. This instability and the unfavourable cold conditions of the postglacial were limiting factors in diatom preservation, although our results indicate that the water basin formed immediately after glacial retreat. Submersed macrophytes like *Stuckenia filiformis* and *Potamogeton* suggest clear, nutrient-rich, shallow, and oligotrophic water environments, likely no deeper than 7–10 m (Wetzel, 1983). These plants have high light requirements, as reflected by their Ellenberg-type light indicator value, which reaches category 7.6 (Tichý et al., 2023; https://floraveg.eu/). The sparse presence of *Myriophyllum* implies some shallow zones, while steep shorelines probably limited plant growth to narrow areas, with little to no vegetation in deeper areas due to reduced light and nutrients. Occasional valves of freshwater benthic diatoms support the macrophyte data in leading us to the conclusion that sedimentation took place in the shallow zone of the lake. Pollen preservation was also poor, as suggested by low influx rates (Gedminienė et al., 2025).

In contrast, conditions for sedaDNA preservation were favourable until about 13750 cal yr BP. A lacustrine environment which contained high carbonate concentrations (Fig. 3), and reduced bioturbation due to colder waters, likely supported sedaDNA integrity (Garcés-Pastor et al., 2024). Low values of PCR inhibitors (Parducci et al., 2019) most probably also contributed to the sedaDNA preservation. These results are similar to findings from the Tibetan Plateau lacustrine sediments, where sedaDNA assemblages of alpine meadows provided consistent but higher taxonomic resolution than pollen (Tian et al., 2023).

Between 13750 and 11500 cal yr BP (Zone 1b), a continuous shift towards forested environments occurred, though herbs and grasses still dominated (Veski et al., 2012; Borzenkova et al., 2015). Meantime, more detailed pollen data (Gedminienė et al., 2025) suggests several climatic reversals, particularly between 12800 and 11700 cal yr BP during so-called GS-1 event (Lowe et al., 2008; Walker et al., 2019). Here the supposition of warming phases is supported by great variability in Salicaceae taxa and occasional appearances by temperate trees such as Fagaceae, *Acer*, and even Juglandaceae in the sedaDNA data (Fig. 4a). Concurrently, colder phases saw a resurgence of species suited to cold, dry conditions, such as *Arctostaphylos uva-ursi, Pyrola*, *Bartsia alpina*, Dryadoideae, and *Juniperus* (Fig. 4b, end of Zone 1b - beginning of Zone 2). The drier conditions are also supported by increased clay and silt levels, increased MS values, and decreased OM concentrations (Fig. 3, upper part of Zone 1b). These rapid turnovers align with other GS-1 records (Druzhinina et al., 2015; Veski et al., 2012; Šeirienė et al., 2021; Stančikaitė et al., 2022b), where colder episodes (Renssen et al., 2015) returned landscapes to treeless tundra, as indicated by pollen spectra dominated by *Betula sect. albae*, *B. nana*, *Pinus*, *Salix*, *Artemisia*, Poaceae, Cyperaceae, Chenopodiaceae and Dryas (Ozola et al., 2010).

Assumptions of a warm climate episode (Gałka et al., 2015), detected using fossil pollen and the Modern Pollen Analog Technique (MAT) (Gedminienė et al., 2025.), during the end of the GS-1 event, raised doubts if thermophilic taxa pollen could be regionally transported, leaving the extent of warming during the middle GS-1 as a matter for speculation. SedaDNA data confirms these interpretations, with the presence of thermophilic plant taxa (e.g. Juglandaceae, Fagaceae, *Acer*), the quick spread of *Filipendula ulmaria, Equisetum*, *Typhaceae,* and the appearance of green algae, etc., supporting the idea of significant warming and rapid habitat change to a non-alpine regime (https://floraveg.eu/) during this time.

Aquatic environments also exhibit noticeable changes within this transitional zone until about 11700 cal yr BP. *Stuckenia filiformis* declined, while the more eutrophic species *Ceratophyllum demersum* and *Potamogeton crispus* appeared, indicating a temporal shift towards deeper water levels (Wetzel, 1983). Correspondingly, the light requirements decreased, with *Ceratophyllum demersum* having an Ellenberg-type light indicator value of 6.2 and *Potamogeton crispus* 5.9, reflecting adaptation to lower light conditions in deeper or more turbid waters (Tichý et al., 2023; https://floraveg.eu/). Such change likely expanded the growth zones on the shorelines, creating favourable conditions for emergent macrophytes (Last and Smol, 2001). These temporal changes (Gałka et al., 2015), along with higher coarse sediment levels and increased MS values (Fig. 3), likely appeared due to hydrological shifts, which exposed new shorelines, augmented sediments with coarser matter and oxygen, negatively impacting diatom (Battarbee et al., 2002) and sedaDNA preservation (Capo et al., 2021).

4.2. Transition towards a more temperate and forested landscape in the Early Holocene with fluctuating water levels

Between 11700 and 9000 cal yr BP, the onset of the Early Holocene marks a significant shift towards a more temperate and forested landscape. A change from a cold and relatively dry climate to suddenly warmer and more humid during Early Holocene is discussed in studies of the Baltic Sea basin, western Russia, north-eastern Poland (Borzenkova et al., 2015; Veski et al., 2012; Wohlfarth et al., 2007). A short cooling phase occurred approximately 250 years after the final drainage of the Baltic Ice Lake (at about 11530 cal yr BP, Borzenkova et al., 2015), with the coldest part of Preboreal oscillation at about 11400 cal yr BP. Only from about 11270 cal yr BP, there was a sudden climatic improvement within the territory of present-day Lithuania (Borzenkova et al., 2015). A shift to a warmer and more humid climate can also be inferred from the increase in organic matter in lake sediments. Though sedaDNA data indicates an increase in Betulaceae, the early expansion of Ulmaceae, *Tilia*, and Fagaceae (~11150, 10000, 9900 cal yr BP) suggests a gradual shift towards more diverse deciduous forests under warmer conditions. Additionally, the establishment of riparian species i.e. *Alnus* (~11300 cal yr BP; 9800–8600 cal yr BP), Salicaceae (peak values at about 10800–10650 cal yr BP), and *Viburnum* (~10300–9200 cal yr BP) reflects a continuously fluctuating water regime (Fig. 4, Zone 2).

Diatom assemblages dominated by benthic taxa are indicative of relatively shallow, clear-water lake environments, as water transparency is one of the main factors of benthic diatom growth (Heinsalu et al., 2008). The mesotrophic-eutrophic taxa *L. radiosa* and *L. ocellata* indicate low and moderate nutrient enrichment (Van Dam et al., 1994). These taxa and the abundant *P. brevistriata* have relatively high oxygen requirements (>75 % saturation; Van Dam et al., 1994), suggesting well-oxygenated water conditions during this interval. It was also found that planktonic *Cyclotella* species become more abundant in deeper lakes during the longer ice-free periods (Reavie et al., 2017). The content of planktonic and benthic diatoms varies over a wide range, indicating variable water levels, although the P/B ratio remains very low, suggesting a relatively shallow environment. Such conditions of a low trophic lacustrine environment and changeable water level were common in the SE Baltic region (Gryguc et al., 2013; Pędziszewska et al., 2015; Druzhinina et al., 2020; Spiridonov et al., 2021; Vaikutienė et al., 2025) during the Early Holocene gradual warming in Europe (Davis et al., 2003). Overall, during the Early to Middle Holocene, emergent macrophytes, such as *Sparganium*, members of the Typhaceae, and *Filipendula ulmaria* thrived in the newly expanded wetlands or riparian zones, due to the development of a littoral zone, increasing precipitation and rising water levels. However, several periods of climatic instability, at about 11700, 11150, 10800, and 10000 cal yr BP, as indicated by variability in Betulaceae, Salicaceae, *Viburnum*, and *Filipendula ulmaria,* align with Early Holocene Oscillations and illustrate complex climate-ecology interactions (Borzenkova et al., 2015; Gałka et al., 2015). The transition towards a deeper eutrophic state is marked by the reappearance of floating macrophytes such as *Ceratophyllum demersum at* about 11000 cal yr BP; however, this increase in water depth led to the expansion of the riparian zone in which *Filipendula ulmaria* started to spread. More significant eutrophication and lake deepening started from ~10000 cal yr BP. Meantime, following this period, a shift in diatom life strategy from benthic taxa to planktonic (a gradual increase in the P/B ratio at about 9200 cal yr BP) and the gradual replacement of planktonic mesotrophic-eutrophic *Lindavia* sp. to eutrophic *A. ambigua*, *A. granulata*, *S. minutulus* and *C. dubius* (Bradshaw et al., 2002; Van Dam et al.,

1994) until ~8400 cal yr BP, clearly signifies a rising lake level and nutrient content associated with the ongoing warming of the Early Holocene. A similar gradual replacement of mesotrophic-eutrophic *Lindavia* sp. diatoms by eutrophic *Aulacoseira* sp. has been observed in two other lakes of the SE Baltic region (Druzhinina et al., 2023; Vaikutienė et al., 2025).

These changes are statistically supported, as species adapted to wetter environments (i.e. *Filipendula ulmaria*, *Juncus*, *Thalictrum*, and *Alnus*) cluster on the same side of the second axis in the PCA (Fig. 8). Additionally, this axis may reflect local landscape variability, such as proximity to water bodies, or soil fertility. The placement of species like *Salix* and Cyperaceae might suggest a wetland or riparian environment, potentially capturing subtle shifts in hydrological conditions or microhabitat preferences. Clustered around 8200–7800 cal yr BP, six samples shift to the opposite side of the PCA second axis, marking a distinct short-term transition to a drier environment with reduced nutrient availability. This shift aligns with a well-documented 8.2 ka cooling event (Rasmussen et al., 2007). Concurrently, changes in terrestrial and aquatic plant composition, including a decline in thermophilic taxa (*Alnus*, *Corylus*, *Tilia*), a rise in NAP and overall diversity, coupled with a slight temperature decline, align well with a significant ecological reversal, as reported in Gedminienė et al. (2025).

Further expansion of forest cover, dominated by mixed deciduous species such as Ulmaceae, Fagaceae, and *Tilia*, aligns with continuous warming. Dense forest canopies left little room for understory plants like *Viburnum*, which had previously been more widespread. This transition towards a fully forested ecosystem aligns with the warm, moist conditions characteristic of the beginning of the Holocene Thermal Maximum (Gedminienė et al., 2025; Borzenkova et al., 2015).

4.3. High lake productivity and its gradual eutrophication in the middle to Late Holocene

During the Middle to Late Holocene (from ~7500 cal yr BP), the high level of organic matter, reaching up to 60 % (Fig. 3), indicates increased biogenic productivity, likely driven by warmer temperatures, longer growing seasons, and extended ice-free periods. This elevated productivity, as perceived by LOI %, persisted until about 3500–3000 cal yr BP. Meanwhile, sedaDNA and pollen data indicate several environmental shifts toward increased productivity in the lake's riparian zone and gradual eutrophication.

The diatom assemblage composition is characterised by a significant decrease in species variety, and in the content of benthic diatoms, indicating a specific environment, favourable for several taxa growth. The increased P/B ratio and total prevalence of planktonic eutrophic *Aulacoseira* sp. suggest that the lake level rose during the Middle Holocene (7300–6300 cal BP). Planktonic taxa (*A. ambigua*, *S. minutulus*, and *A. granulata*) become dominant. Their moderate oxygen requirements (>50 % saturation; Van Dam et al., 1994) imply reduced oxygen levels in the water column compared to the earlier period. The diatom assemblages are dominated by eutrophic planktonic *A. ambigua* and *A. granulata* (Van Dam et al., 1994) and support the notion from pollen data that the lake became nutrient-enriched, as the *Aulacoseira* sp. is characteristic of nutrient-rich environments (Kiss et al., 2012). A similar abundance of the planktonic eutrophic taxa *Aulacoseira* sp. was found in SW Lithuania (Vaikutienė et al., 2025) and Estonia (Punning et al., 2008), possibly reflecting a significantly warmer climate during the Middle Holocene. Meantime, the significant decline in freely floating macrophytes and very low occurrences of hydrophytes from around 6800 cal yr BP suggests either drier conditions or significantly reduced areas of open water. This likely reflects intensified wetland formation in riparian zones and forest recovery dominated by Alnus, which is highly tolerant to wet, fen-type environments.

While pollen data more clearly capture dense forest cover (i.e. *Corylus*, *Tilia*, *Fraxinus*, *Quercus,* and *Carpinus*) (Gedminienė et al., 2025.), sedaDNA provides a detailed localised view, revealing a broader diversity of herbs, grasses, and aquatic plants from the lake's immediate vicinity. However, sedaDNA may skew the broader regional picture, potentially underreporting certain arboreal species, especially tree taxa. This discrepancy likely arises from sedaDNA's overrepresentation of taxa growing directly in and around the lake (Alsos et al., 2018; Garcés-Pastor et al., 2024; Capo et al., 2021). In our research, we see that the transition to the Late Holocene was marked by a decline in forest cover, with fewer broadleaved trees, a growing presence of shrubs (Salicaceae), along with the expansion of herbaceous plants, particularly Poaceae and *Filipendula ulmaria*. The scattered appearance of *Alnus* and increased *Betula* (~5700 and 4200 cal yr BP) in tree pollen spectra (Gedminienė et al., 2025) is simultaneous with the global cooling trends and rising precipitation levels in most of Poland, central Europe, Finland, and regions of Sweden (Borzenkova et al., 2015). The authors of Borzenkova et al. (2015), Seppä and Poska (2004) and the references within these articles state that these climatic changes are probably related to decreased summer solar radiation due to astronomical factors, though the causes of superimposed oscillations remain the subject of debate. These natural changes likely limited forest expansion and reduced the presence of thermophilic species.

The rapid, repeated spread and recession of emergent macrophytes and riparian taxa, i.e. *Filipendula ulmaria*, *Juncus*, and Rumiceae, highlight hydrological and topographical variations, occurring on timescales of roughly half a millennium. These cyclical water level changes were likely driven by broader climatic influences (Galbraith et al., 2016; Stančikaitė et al., 2022a) rather than seasonal shifts alone during the Middle and Late Holocene. Changes in hydrology and the increasing number of frequent cold spells and heavy precipitation events (Gedminienė et al., 2025) probably had a direct impact on the lake's catchment and riparian vegetation dynamics. Under conducive conditions to wetland and riparian zone development between ~1600 and 1080 cal yr BP, *Phragmites australis* spread rapidly, forming dense stands that often outcompete native plants and reduce overall biodiversity. Due to its high transpiration rates, *Phragmites* australis can lower local water levels by transpiring more water than native vegetation, leading to a gradual drop in lake or wetland water levels (Xu et al., 2011). While *Phragmites australis* stands can trap sediments and stabilise shorelines, reducing erosion, they may also contribute to sediment accumulation and vertical accretion. The spread of this taxon, along with *Juncus* and *Equisetum* possibly altered shoreline morphology. Such a change towards increased sedimentation led to the rapid riparian zone elevation and wetland formation which becomes more visible from about 3500 to 3000 cal yr BP.

Conversely, the disappearance of freely floating macrophytes like *Trapa* and *Nymphaeaceae*, along with the scarcity of diatom remains, confirms a rapid shrinkage of deep-water habitats. These rapid changes are visible in the upper layer of sediments which consists predominantly of peat (>90 % organic matter). Peat formation usually creates an acidic environment unfavourable to most diatoms. Occasional valves of acidophilous *Eunotia* sp. and aerophilous *Hantzschia amphioxys* (Van Dam et al., 1994; Lange-Bertalot et al., 2017), and the appearance of *Vaccinium* taxa confirm a drying environment and peatbog development. These trends likely reflect a combination of reduced water levels and drying, possibly influenced by human-driven landscape modification.

4.4. Potential impacts of early human habitation on the Dūkštelis Lake environment

Archaeological studies in the Dūkštelis Lake area have concentrated on tracing early human presence through flint tool typology and interdisciplinary methods (Gudaitienė, 2014; Gudaitienė, 2015; Gudaitienė, 2016; Gudaitienė, 2017; Gudaitienė, 2018; Rimkutė, 2013). The cultural and chronological periodization of early human communities has primarily been defined by the typological division of flint artefacts and their degree of patination. In over 40 archaeological sites across Lithuania, flint artefacts were attributed to the Ahrensburgian and

Swiderian cultures (covering the Late Palaeolithic to Early Mesolithic archaeological periods), based on the typology (Šatavičius, 2016; Juodagalvis and Balakauskas, 2012; Gudaitienė, 2018). The oldest flint artefacts from the Dūkštelis archaeological site located on the lakeshore are also typologically linked to the Late Swiderian communities (Gudaitienė, 2018), suggesting these were the earliest groups to travel through and inhabit the region during GS-1 and the beginning of the Early Holocene (Preboreal) periods (~12000–10000 cal yr BP). These groups likely utilised the lake's resources seasonally, as evidenced by structures interpreted as huts and hearths alongside burnt bone and charcoal discovered in cultural layers near the palaeolake (Gedminienė et al., 2014; Gudaitienė, 2018).

While this timeline is supported by a wealth of archaeological evidence indicating small-scale seasonal settlements, the harsh climatic conditions during GS-1 and most of the Preboreal likely limited long-term settlement. Arboreal trees, shrubs, and bushes dominated the S–SE part of Lithuania at this time (Gedminienė et al., 2025; Stančikaitė et al., 2019b; Juodagalvis and Balakauskas, 2012), and the abundance of grazing for reindeer and other game animals attracted hunter-gatherers in their wake.

Ecologically, the presence of disturbance-indicator taxa such as *Plantago, Euphrasia,* Asteraceae, Trifolieae, Rumiaceae, and Polygonoideae, during this period is difficult to attribute solely to human activity, as these species can also reflect climate-driven vegetation shifts and localised forest openings. However, when combined with microcharcoal records, lithological data, pollen and spore (Gedminienė et al., 2025), and flint finds, it is plausible that small-scale human activities, such as hunting and localised burning, began influencing the landscape from ~12000 cal yr BP. More substantial vegetation changes, including increased openness and shifts in species composition, become evident from about 8000 to 7500 cal yr BP.

During the Middle to Late Holocene, bioproxies reveal greater localised disturbances, likely caused by events such as windthrow or fire. Increased microcharcoal concentrations and significant finds of *Pteridium, Juniperus*, and Ericaceae support this interpretation (Gedminienė et al., 2025; Juodagalvis and Balakauskas, 2012; Stančikaitė et al., 2019b). The increase in taxa like Asteraceae, Trifolieae, Brassicaceae, *Potentilla*, *Galium, Plantago*, and *Urtica*, which also thrive in open, disturbed areas, supports the possibility of human activities creating openings in the forest canopy, possibly for animal husbandry. However, these signs alone are insufficient to conclusively attribute local fires to human activity.

While pollen data provide some evidence of early land-use practices, including deforestation and limited agriculture, sedaDNA data offers less insight into human-environment interactions. Unfortunately, the significant aquatic and wetland plant sedaDNA signal from about 7500 cal yr BP onward makes it difficult to discern human impacts on regional vegetation, as the scattered occurrence of certain taxa does not represent the overall landscape. This complicates the detection of human-induced vegetation changes at the regional scale using sedaDNA alone, underscoring the need to integrate multiple proxies.

Pollen data indicate deforestation in the Dūkštelis region beginning around ~5400 cal yr BP, marked by the decline in thermophilic trees (*Alnus*, *Ulmus*, *Tilia*, and *Corylus*). Deciduous species such as *Quercus*, *Fraxinus*, and *Carpinus* show a decline slightly later. Such a decline, despite small differences in its timing, aligns with broader trends observed across NW Europe (Gedminienė et al., 2025; Heikkilä and Seppä, 2010; Stančikaitė et al., 2019a, 2019b; Druzhinina et al., 2023). From ~3700 cal yr BP, the landscape saw further openings, likely driven by a combination of climate cooling, successive marshland, and riparian zone expansion, and intensified human activity such as agriculture, grazing, and deforestation. Disturbance-tolerant herbaceous taxa became dominant as forest cover declined. However, vegetation shifts marked by species like *Avena*, Brassicaceae, *Trifolium*, *Atriplex*, and *Medicago* suggest an increasing influence of human land use, agriculture, and grazing, which became more prominent in shaping the region's vegetation, though the signal of the impact remains minor. Human activity during the Neolithic, Bronze Age, Iron Age, and later periods is well-documented in Lithuania, Latvia, Belarus, and the Kaliningrad region, with extensive archaeological evidence of settlements, traces of hearths, stone structures, and hundreds of artefacts (Stančikaitė et al., 2019b; Juodagalvis and Balakauskas, 2012; Druzhinina et al., 2023). At Dūkštelis, potsherds spanning multiple periods, from early hand-built to wheel-thrown pottery, and 20th-century debris further attest to prolonged human occupation. The site also yielded 19th–20th century artefacts, including Imperial Russian uniform buttons with double-headed eagles, iron fragments, and unfired rifle cartridges, likely linked to military activity. However, ploughing and farm construction had severely damaged the NE and N parts of the settlement (Gudaitienė, 2019). Despite some damage to archaeological contexts, all findings provide a valuable framework within which to correlate human presence with ecological changes observed in bioproxy records.

4.5. *Limitations of the sedaDNA approach*

The preservation of DNA in sediments depends on various environmental factors during deposition, including water temperature, conductivity, and pH (Jia et al., 2022b). After deposition, oxygen levels (Mejbel et al., 2022) and properties, like mineral content, of the sediments and catchment geology further influence DNA integrity (Sand et al., 2024; Freeman et al., 2023; Kanbar et al., 2021). Under less beneficial conditions the DNA can be degraded more easily, which leads to random PCR amplifications and reduced reproducibility of PCR results. Further, the presence of inhibitors in the sediments, like humic acids and complex organic compounds, can hinder successful amplification, decreasing the taxonomic diversity in the amplified PCR product.

In our core, DNA preservation appears stronger until about 13750 cal yr BP. During this period, sedaDNA preservation was likely enhanced by a high-carbonate lacustrine environment, stable pH levels, and reduced bioturbation from colder waters. This interpretation is supported by high carbonate content (determined via LOI analysis) and the presence of shallow-water, oligotrophic plants such as *Stuckenia filiformis* and *Potamogeton,* which thrive in clear, carbonate-rich conditions. The stability of these environments likely minimised sedaDNA fragmentation, while lower concentrations of PCR inhibitors in early sediments improved amplification success.

In contrast, sediments younger than 7500 cal yr BP show poorer sedaDNA preservation, particularly for terrestrial species. Increased organic matter (OM) and high levels of humic acids, evidenced by rising LOI values, acted as potent PCR inhibitors. Concurrently, the expansion of eutrophic aquatic plants such as *Potamogeton, Potamogeton crispus*, and *Ceratophyllum demersum*, adapted to nutrient-rich, turbid waters, likely contributed to inhibitor accumulation. These factors skewed sedaDNA datasets toward the overrepresentation of aquatic and wetland taxa (e.g., *Equisetum*, *Phragmites australis*, Poales, *Filipendula ulmaria*), which proliferated near the lake margins during the water-level rise. The increased prevalence of aquatic and wetland species in the DNA data likely reflects vegetation in and near the lake margin, as these plants were closer to the DNA deposition site. Proximity to the deposition site further amplified their DNA signal, while terrestrial species farther from the shoreline were underrepresented.

To overcome these challenges, methodological adjustments are crucial. Techniques such as using inhibitor-resistant polymerases or pretreating samples to remove inhibitors can enhance sedaDNA recovery and improve the accuracy of palaeoenvironmental reconstructions. Until these methods are fully optimised, traditional analyses, i.e. pollen, diatom, macrofossil, lithological studies, etc., should be used in parallel to identify discrepancies and address the limitations of sedaDNA analysis in reconstructing past plant communities.

5. Conclusions

- SedaDNA offers more localised insights into the vegetation dynamics of the lake's immediate environment, while pollen data reflects a broader regional context, highlighting the complementary nature of both methods. Sediment composition, sedimentation conditions, and domination of aquatic or wetland plants significantly impact sedaDNA results, especially terrestrial flora.
- Lateglacial vegetation includes subalpine and lowland taxa, suggesting that diverse habitats were shaped by unique climatic and quickly changing geomorphological conditions. Early Holocene climatic warming favoured the migration of mixed deciduous forest species, like Ulmaceae, *Tilia*, and Fagaceae, while hydrological fluctuations supported the expansion of wetlands and riparian zones.
- The dynamic of the aquatic environment reflects an interplay of water depth, nutrient levels, and climatic influences over time. Initially clear, shallow, oligotrophic waters supported the growth of submersed macrophytes; as water levels deepened during the GS-1 stage, emergent macrophytes expanded along shorelines. Conditions evolved towards mesotrophic to eutrophic shallow water states around 11000 cal yr BP. By the Middle to Late Holocene, cyclical water level variations driven by broader climatic factors impacted both aquatic and riparian vegetation, marking a final transition towards a more terrestrialised environment.
- Supplemented with archaeological evidence, palaeoecological data suggests that early human habitation in the Dūkštelis region could have begun influencing the landscape as early as ~12000 cal yr BP. However, intensified human activity, including agriculture and the grazing of their animals, became evident from ~3700 cal yr BP, further reducing forest cover and promoting disturbance-tolerant species, marking a significant shift in vegetation due to human land use, though the signal of the impact is very minor.

CRediT authorship contribution statement

Laura Gedminienė: Writing – original draft. **Kathleen R. Stoof-Leichsenring:** Writing – review & editing, Software, Methodology, Formal analysis, Writing – original draft, Resources, Investigation. **Ulrike Herzschuh:** Resources, Writing – review & editing, Funding acquisition. **Giedrė Vaikutienė:** Visualization, Investigation, Writing – original draft, Methodology, Formal analysis. **Miglė Stančikaitė:** Funding acquisition. **Žana Skuratovič:** Writing – original draft, Investigation, Methodology, Formal analysis. **Domas Uogintas:** Visualization, Methodology, Formal analysis, Writing – original draft, Software, Investigation. **Andrej Spiridonov:** Supervision.

Data availability

The Supplementary Data files 1 and 2 provide the raw sequence counts in replicates from both sequencing runs. The final filtered and grouped dataset is found in the Supplementary Data 3 and 4.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

The authors confirm that neither the manuscript nor any parts of its content are currently under consideration or published in another journal.

All authors have approved the manuscript and agree with its submission to journal "Quaternary International".

Acknowledgments

We would like to express our sincere gratitude to the editors and reviewers, who have put considerable time and effort into their comments on this paper. The study was supported by grants from the Research Council of Lithuania (LMTLT) No. S-PD-22-77 and No. S-MIP-17-133. Special thanks to Hannah Schmidt and Sarah Gwen Olischläger, who helped in the DNA lab at Helmholtz Centre for Polar and Marine Research, AWI, Potsdam, Germany. Thanks to Vytautas Minkevičius for assisting in the creation of the study site figure. Thanks to Jūratė Karosienė for her valuable advice on aquatic plant ecology. Thanks to Gabrielė Gudaitienė, whose archaeological research prompted a strong interest in investigating this region.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quaint.2025.109899.

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