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Influence of Geological and Soil Factors on Pine, Birch, and Alder Stability During the Holocene Climate Change in Central Latvia, Northeastern Europe

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Abstract: Understanding the past dynamics of vegetation in response to climate change is crucial for predicting future ecological outcomes. This study has two primary objectives: (1) to reconstruct the vegetation history of the coastal region around Lake Lilaste in Central Latvia during the Holocene and (2) to assess the impacts of climate change on forest composition through the analysis of pollen data and radiocarbon dating. The results indicate that dominant tree species, particularly pine (*Pinus*), have shown remarkable resilience despite significant climate fluctuations. Pine's adaptation to the sandy, mineral-poor soils surrounding the lake likely underpins its sustained dominance, while the influence of climate change on overall tree biomass is more notable. Our results suggest that vegetation may be more susceptible to future climate variability, yet the region's geological and soil conditions continue to favor pine, birch (*Betula*), and alder (*Alnus*) populations. While human activities have influenced the region during the last millennia, their impact has been more pronounced in areas further from the lake. This study underlines the importance of long-term forest dynamics and emphasizes that the soil and geological and geographical setting must be considered for climate change assessments.

Keywords: pollen analysis; radiocarbon dating; forest composition; Holocene; sandy substrate; climate warming

Academic Editor: Bas Van Geel

Received: 30 September 2024
Revised: 8 November 2024
Accepted: 11 December 2024
Published: 2 January 2025

Citation: Stivrins, N.; Jarmakovica, M. Influence of Geological and Soil Factors on Pine, Birch, and Alder Stability During the Holocene Climate Change in Central Latvia, Northeastern Europe. *Quaternary* **2025**, *8*, 2. https://doi.org/10.3390/quat8010002

1. Introduction

The forest plays a significant role in providing ecosystem services that benefit society, including biodiversity, wood production, recreation, hydrology, and climate regulation [1,2]. The relevance of anthropogenic impacts in the context of climate change is becoming an increasingly pressing issue for both society and science [3–6]. In light of climate goals and the rising demand for renewable materials, the utilization of natural resources is expected to increase, particularly to meet the growing need for timber and the expansion of forested areas. Forest vegetation represents a vital natural resource in Latvia, covering 53% of the country's territory. This extensive forest area highlights the importance of researching forest vegetation dynamics and developing well-considered forest management plans [7–9].

Changes in environmental conditions are influenced not only by annual mean temperature and precipitation but also by seasonal variations and extremes, which significantly affect vegetation phenology and plant productivity. For example, fluctuations in winter and spring temperatures have been linked to vegetation development [10–13]. During drought years, the growth of boreal forests has been primarily hindered by temperature [14]. As the climate continues to change, understanding past climate and vegetation data—including trends, drivers, and consequences—serves as a crucial resource for assessing potential future forest composition [15,16]. Some studies suggest that to establish a robust next generation of trees, it is crucial that the species planted today are climatically suitable for the entirety of the twenty-first century [17]. Species such as beech, oak, and ash are generally more resilient to changing conditions, while others, including larch, silver birch, and Norway spruce, exhibit a higher vulnerability to shifting climates [18].

Given the importance of forest ecosystem services, it is essential to understand how climate change may impact forests in Latvia by the end of this century, when average temperatures are projected to be at least 2–3.5 °C warmer than present. Geological evidence indicates that the Latvian territory experienced similar climatic conditions during the Middle Holocene, characterized by air temperatures that were 2–3.5 °C higher than those today [19]. The features of historical climate and environmental variability are preserved in the natural record, which varies in data resolution and the temporal extent of the information it conveys [20].

The aim of this study is to reconstruct past vegetation changes in a sandy coastal region of Central Latvia to understand how climate change during the Holocene has influenced forest composition. Gaining long-term insights into these shifts is essential for assessing which tree species may become dominant and which are likely to decline in the future. Given that sandy soil areas are currently utilized primarily for forestry rather than agricultural purposes, it is anticipated that similar land management practices will continue to be relevant in the future. The study site was selected to determine whether the climate serves as the primary factor influencing forest dynamics, or whether other potential agents also play significant roles. This study specifically aims to consider local soil and geological factors, which have often been overlooked in research that focuses exclusively on the role of the climate in shaping forest composition in the pan-Baltic region [21–24]. We hypothesize that climate change did not significantly alter the long-term composition of dominant tree species, such as pine, birch, and alder, within the forest during the Holocene. Furthermore, we propose that soil and geological factors played a more critical role in maintaining the long-term stability of these species than the climate did.

To characterize vegetation during the Holocene, pollen analysis is used in this study, allowing the reconstruction of past vegetation relationships that allow for the identification of dominant trees in a given area. Pollen is one of the most abundant microfossils preserved in sediment archives, such as lakes, whose sedimentary assemblages are related to regional and local vegetation. Pollen analysis is the primary method for determining past vegetation responses to climate change and human impact [25–27]. At the same time, we are aware that pollen can travel from a wider area; therefore, our reconstructions describe more regional vegetation than that strictly local. Lake sediments accumulate relatively slowly but continuously (there may be breaks in sediment accumulation in peatlands and soils), preserving information from a specific time (younger sediments accumulate on top of older sediments), which allows for reconstructing the evolution of terrestrial vegetation and environmental changes over time. In this study, we selected Lake Lilaste as the main study site characterizing vegetation dynamics during the Holocene. Lake sediments were chosen as a primary data source due to their relatively stable depositional environment, which has been less affected by, for example, wave-induced water or wind erosion [20]. Lake Lilaste is large, and such sites tend to reflect the regional relative forest cover [28,29].

2. Study Area

Lake Lilaste (183.6 ha) is located in the Coastal Lowland (Figure 1) at an altitude of 0.5 m a.s.l., with a catchment area of 140 km^2. The average water depth is 2 m, but the max depth is 3.2 m. It is a flow-through lake with river Melnupe entering the lake on the eastern side, connected with Lake Dunezers in the south, and it has an outlet to the Baltic Sea (Riga Bay) on the northwestern part. The average mean temperature is +8 °C, the summer mean air temperature is +18.5 °C, and the winter mean air temperature is −2.5 °C. The average amount of annual precipitation is 650 mm. Rather poor soils comprise the area within 4 km, including Pv (Luvisols/Alisols), 83% of all soils; Tp (Hemic histosols), 11%; Pg (Dystric Arenosols/Alisols/Dystric cambisols, retisols, regosols), 3%; and Vg (Gleysols), 3%. Vegetation and landcover within 4 km comprise coniferous forest, 54% of all areas; sparsely vegetated areas, 11%; transitional woodland-shrub, 8%; mixed forest, 7%; broad-leaved forest, 3%, beaches, dunes, and sands, 2%; inland marshes, 3%; and peat bogs (wetland), 2% [29]. The total tree stock within 4 km is 945,037 m^3. The area around Lake Lilaste is surrounded by Holocene eolian sediments—sand—influenced by the location of the lake in the area of the seaside plain, where the southeastward flow of wind drift occurs and a zone of eolian sediment accumulation is formed. The direction of the wind-driven debris flow is indicated by the dunes and foredunes. The relief consists of undulating plains and undulating dune hills, ranging in height from 10 to 20 m. Quaternary sediments within 4 km comprise lgQ3ltv (glaciolacustrine sand and silt with sand), 61.6%; vQ4 (eolian sand), 17.7%; mQ4ltv (marine sand), 8.4%; aQ4 (alluvial sand), 7.7%; and bQ4 (peat), 4.5%. Lake Lilaste is located in a coastal area and its development has been influenced by the stages of the Baltic Sea [30,31].

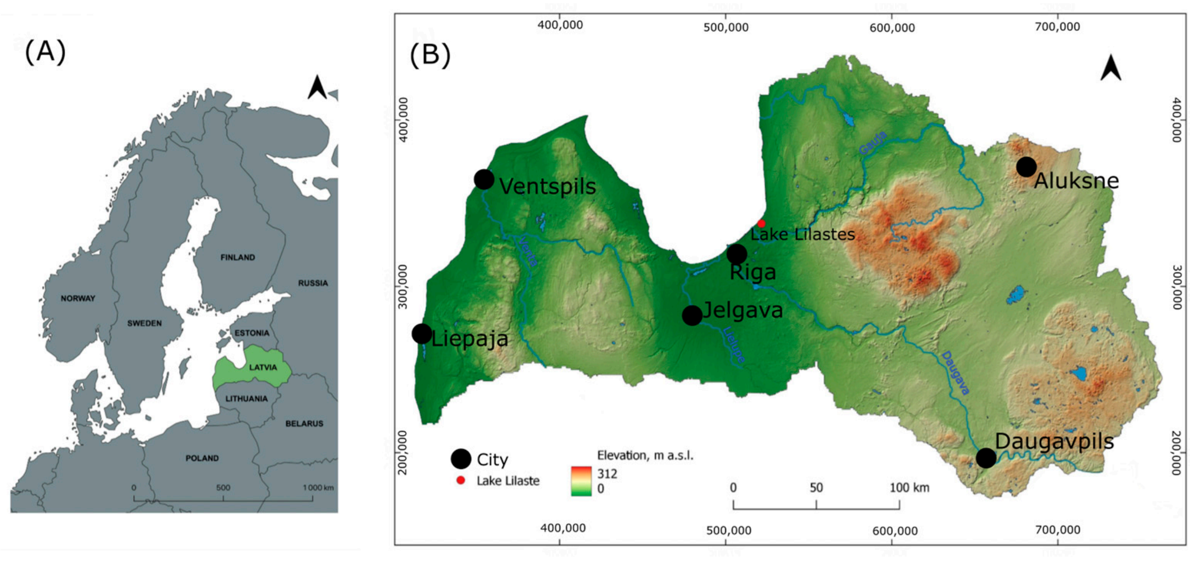

Figure 1. Location of the Lake Lilaste site in northeastern Europe (**A**); location of study site (Lake Lilaste) in Latvia (**B**).

3. Materials and Methods

3.1. Sampling and Chronology

Lake Lilaste was sampled through ice in February 2013. Altogether, 10.40 m of lake sediment was obtained. We used chronological data (spheroidal fly ash particles, ^{14}C; Table 1) previously published by Grudzinska et al. [30] and applied the latest IntCal20 calibration data set [32], producing a new age–depth model in the R environment [33] using the Clam package version 2.6.1. [34].

Table 1. Data used to build a chronology for Lake Lilaste (according to the original data from [30]).

Depth, cm (From Water Surface)	Lab Code	Date	Dating Method
218	SFAP	−55–−70 cal BP	Spheroidal Fly Ash Particles
380	Poz-63856	2385 ± 30	^{14}C AMS
515–520	Tln-3500	3793 ± 60	^{14}C conventional
540–545	Tln-3497	3920 ± 55	^{14}C conventional
660	Poz-63857	4880 ± 30	^{14}C AMS
878	Poz-57601	6370 ± 40	^{14}C AMS
1050	Poz-63858	7810 ± 35	^{14}C AMS
1222	Poz-48438	9630 ± 60	^{14}C AMS
1240	Poz-48439	9710 ± 50	^{14}C AMS

3.2. Pollen

In total, 51 samples were analyzed for pollen. To provide information on vegetation changes during the Holocene epoch, samples were prepared at 200-year intervals to obtain a sequential representation of long-term vegetation changes. Sample counts started at a depth of 1145 cm, corresponding to 9800 cal BP (Early Holocene), and the uppermost sample layer was at a depth of 202 cm, corresponding to −60 cal BP (Late Holocene). Hence, sampling intervals were measured based on the chronology of the age–depth model. Before chemical treatment, tablets containing *Lycopodium* spores (one tablet per subsample) were added to sediment subsamples to estimate the concentration of pollen grains per cm^3 [35]. Subsamples of 1 cm^3 and 1 cm thickness were treated using the standard pollen preparation method procedure. The acetolysis method [36,37] to remove polysaccharides was used for each sample (hot water bath for 3 min). The prepared samples were stored in glycerin. At least 500 terrestrial pollen grains per sample were counted to the lowest possible taxonomic level using published pollen keys and a personal reference collection. The percentage of terrestrial taxa was estimated using arboreal and nonarboreal pollen sums (excluding sporomorphs of aquatic and wetland plants). The pollen accumulation rate was estimated by multiplying pollen concentration per sample with the mean sediment accumulation rate, providing an approximate indication for past tree biomass variability [38].

Pollen results were visualized using the RStudio environment (v. 2024.04.0+735) using the *riojaPlot* package version 01-20. Principal Component Analysis (PCA) showing the variation and relationships in the data was generated in PAST version 4.15 [39]. Prior to PCA, the data were transformed (normalized) using the Box–Cox statistical transformation, which transforms variable values so that they resemble a normal distribution, as otherwise, values that are significantly high due to one species/taxon might produce incorrect/biased PCA results [40].

4. Results

4.1. Chronology

We did not recognize any rapid breaks or thickening in sedimentation. In conclusion, sediment accumulation was not disturbed and there was a continuous sedimentation of gyttja during the Holocene in Lake Lilaste (Figure 2). Basal sediments consist of clayey silt with sand (1260–1245 cm), sand layers with wood (1245–1226 cm), gyttja with detritus (1226–1218 cm), lacustrine marl (1218–1193 cm), silty gyttja (1193–1130 cm), calcareous gyttja (1130–1110 cm), and organic rich homogenous gyttja (1110–200 cm; 200 cm is the top of the sediment surface as the water depth was 200 cm at the sampling point) [30].

Based on the sediment accumulation results, a higher accumulation rate occurred from 8280 cal BP, which roughly coincides with the start of Middle Holocene and marks beginning of the Holocene Thermal Maximum. The period from 7610 to 6770 cal BP stands out in terms of the intensity of the sediment accumulation rate, with an annual accumulation of about 0.14–0.15 cm. Although these values were higher than the rest of the indices, it is not clear what is behind this increase in sedimentation, as there can be multiple reasons for this. The average sediment accumulation rate in Lake Lilaste during the Holocene was ~0.1 cm per year. Chronological confidence ranges (95%) span from 123 to 295 yr (on average, 196 yr). Weighted averages before the present were used (cal BP; 0 = CE 1950). Chronological zonation followed the common stratigraphic subdivision of the Holocene [41]: Early Holocene (Greenlandian Age; warm and moist climatic conditions), 11,700–8200 cal BP; Middle Holocene (Northgrippian Age; warm and dry), 8200–4200 cal BP; and Late Holocene (Meghalayan Age; cool and moist), last 4200 cal BP.

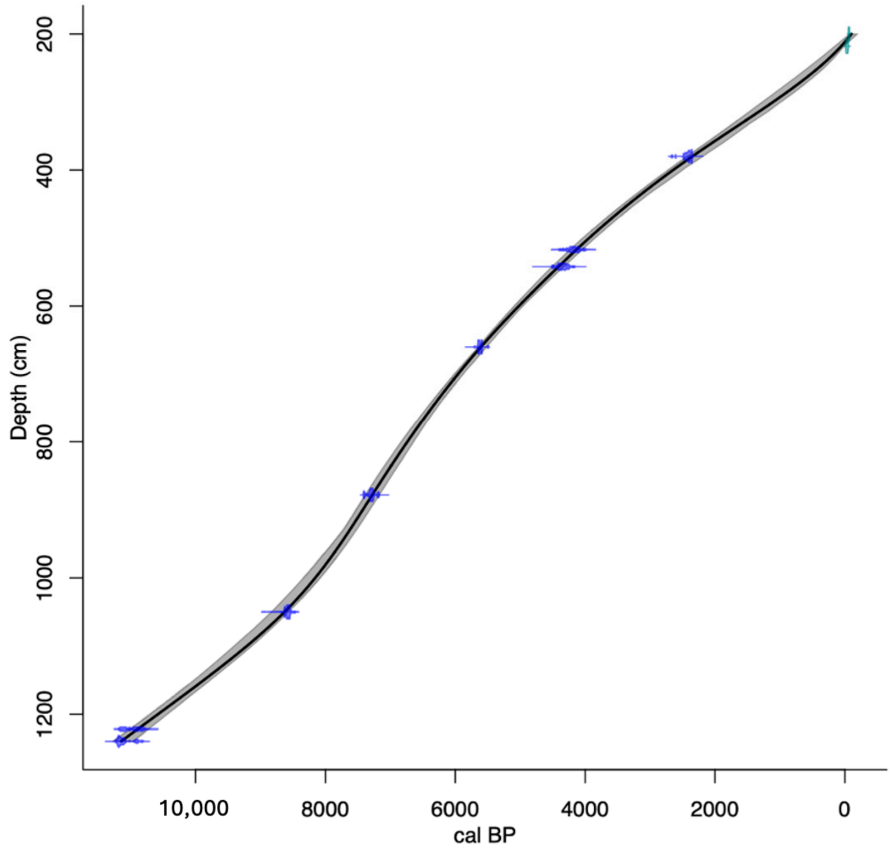

Figure 2. Age–depth model for the sediment sequence of Lake Lilaste. The gray area indicates a reconstructed 95% chronological uncertainty band. The ^{14}C dates are indicated in blue and spheroidal fly ash particles are in light blue.

4.2. Pollen

A total of 12 tree, 9 shrub and small shrub, 5 ruderal, and 13 grass and herbaceous genera/families were identified. The dominant taxa were trees—pine (*Pinus*), spruce (*Picea*), birch (*Betula*), and alder (*Alnus*) (Figure 3). Pine was dominating in the vicinity of Lake Lilaste during the Holocene (percentage values from 28 to 57%). The average amount of birch was 20%, with a maximum (34%) in the Early Holocene. The average percentage of spruce in the vegetation was 9% at its lowest, with a peak in the Middle Holocene. The maximum amount of hazel (*Corylus*) was reached between 8490 and 7100 cal BP. Early Holocene vegetation was characterized by pine, birch, alder, and spruce as the dominant trees around the site. The Middle Holocene had the highest broadleaved tree appearance within the Holocene. *Quercus* appeared in the region from 7000 cal BP. *Ulmus* had its highest values during the Middle Holocene, and, starting in the first half of the Late Holocene, substantially declined (Figure 3). Overall, Late Holocene is characterized by a decline in broadleaved trees.

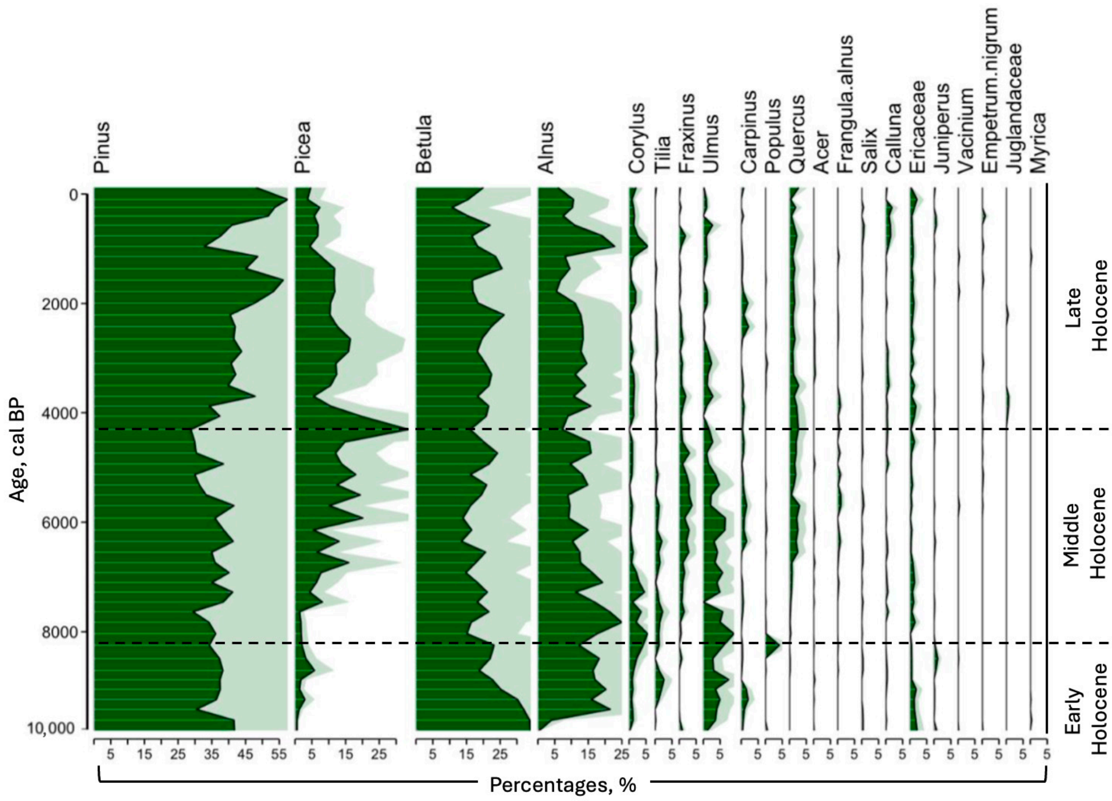

Figure 3. Lake Lilaste tree and shrub pollen percentages. Light green—an exaggeration at ×10 for pollen data expressing the change in plant taxa dynamics (this applies to following figures as well).

The amount of herbs and deciduous plants around Lake Lilaste was comparatively lower than that of trees and shrubs (Figure 4). Grasses (Poaceae) were the dominant component of the vegetation, with percentages ranging from 0.7% to 9%. The peak abundance of grasses occurred during the Early Holocene, and rather high values were also reached in the first half of the Middle Holocene. Pollen analysis also revealed the presence of *Humulus* as early as the Early Holocene; however, the highest values were reached only in association with human impact (Figure 5). Although our analyses show human-related *Humulus* as early as the Early Holocene, it is important to underline that these taxa can occur in natural conditions as well. The presence of *Secale cereale* (rye), *Avena* (oat), and *Centaurea cyanus* (cornflower) was recorded in the Late Holocene, with percentages ranging from 0.1% to 1%.

Regarding the Principal Component Analysis (Figure 6), the first two components of the PCA explain 31.4% of the total variation. Each Holocene subdivision (Early, Middle, and Late) shows a tendency to cluster separately, indicating that vegetation composition differed across these time periods. Despite the dominance of certain tree taxa being relatively stable throughout the Holocene, the observed variation in the PCA is primarily driven by changes in the remaining vegetation. The Middle Holocene cluster is closely associated with broadleaved trees, while the Late Holocene cluster exhibits positive correlations with human-influenced, cultivated plants. The PCA does not show distinct correlations with pine and birch, as these taxa were abundant and dominant throughout the entire Holocene. PCA shows that there were some assemblage similarities as few samples overlapped clusters. The Late Holocene, one the other hand, showed a rather distinct gradient, with little to no overlap in similarities. According to the PCA results, compositional change had a distinct trajectory from natural boreal-type vegetation in Early Holocene to a minor broadleaved admixture in Middle Holocene and natural–human hemiboreal vegetation in Late Holocene.

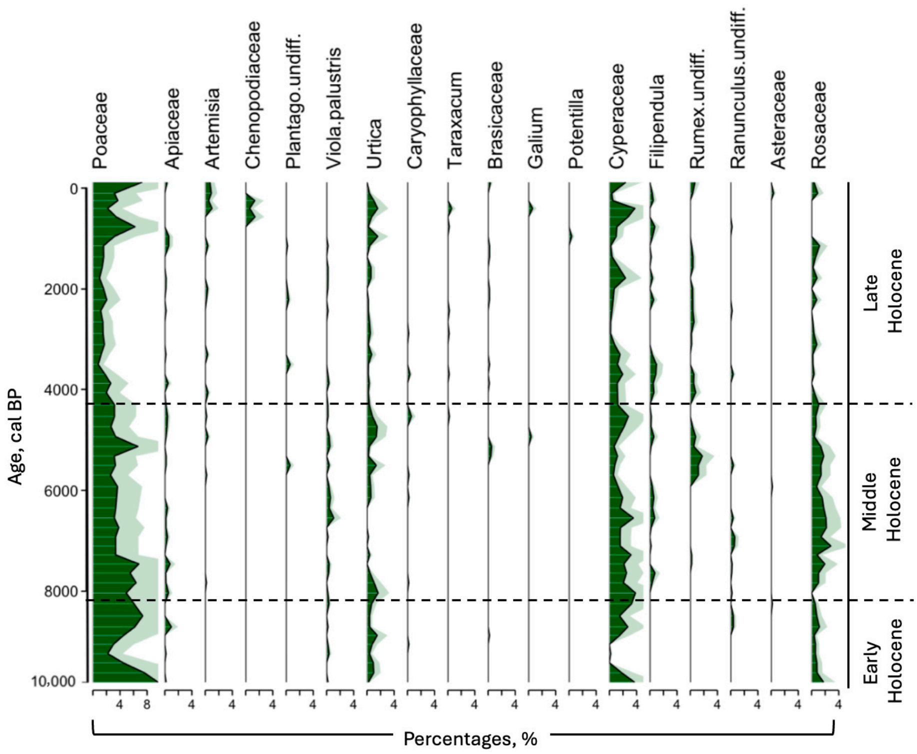

Figure 4. Lake Lilaste herb pollen.

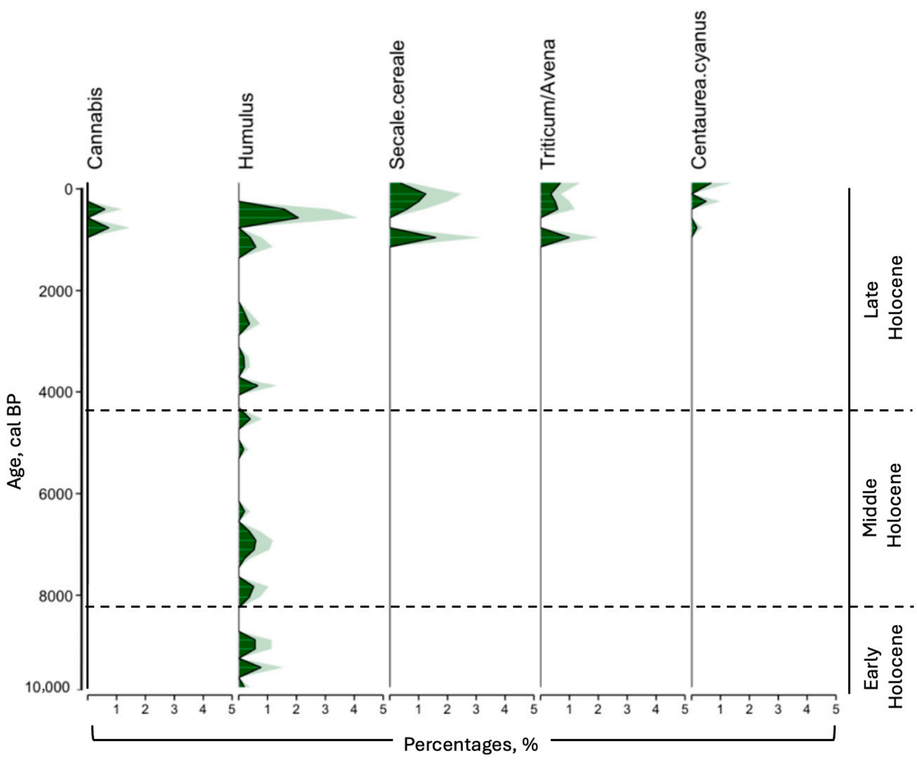

Figure 5. Lake Lilaste naturally occurring and cultivated plant pollen.

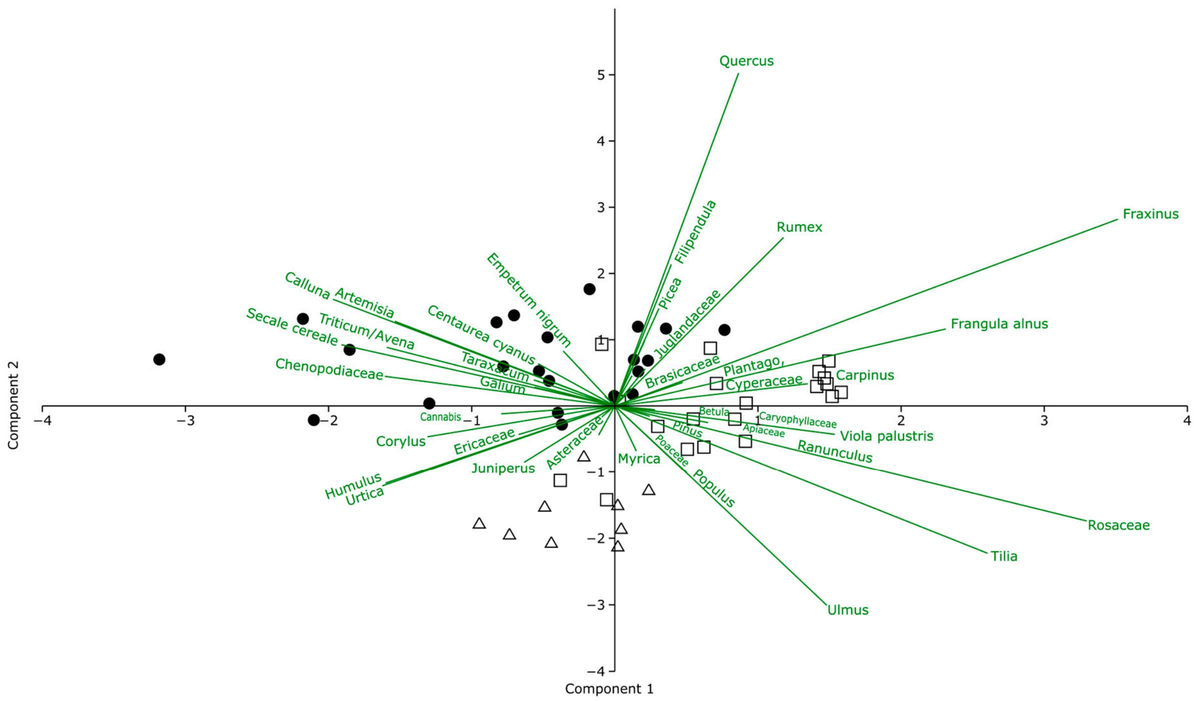

Figure 6. Principal Component Analysis of Lake Lilaste pollen. Triangles indicate Early Holocene, squares indicate Middle Holocene, and filled circles indicate Late Holocene.

5. Discussion

Our findings suggest that, with the exception of spruce, the composition of dominant tree species in central Latvia has remained relatively stable throughout the Holocene. In contemporary Latvian forests, the most prevalent tree species include Scots pine (*Pinus sylvestris*), comprising 33%; Norway spruce (*Picea abies*) at 19%; birch (*Betula pubescens* and *pendula*) at 30%; and black and gray alder (*Alnus glutinosa*, *incana*) making up 10%. Although *Picea* has been present in Latvia since the Late Glacial [21,42,43], it reached its highest relative abundance during the Middle and Late Holocene. *Picea* is one of the dominant tree species in Eurasia and it has expanded across Northern Europe in a somewhat asynchronous manner [44]. The spread of spruce in Central Latvia may have been influenced by interspecific competition with other tree species. It is likely that *Picea* competed with *Corylus* and *Tilia*, as indicated by the mirrored patterns of increasing and decreasing percentages between these species (Figure 3). According to Seppä et al. [44], the decline in *Tilia* populations during the Middle Holocene was not primarily driven by climate, but rather by competitive replacement due to overlapping ecological niches with *Picea*.

Vegetation changes in the study area were observed (Figure 6), but they were less significant than expected. During the Middle Holocene, broadleaved trees exhibited limited maximum distribution ranges and represented only a minor component of the overall vegetation (Figure 3). This period corresponds with warm and dry climatic conditions, as well as the peak expansion of broadleaved trees in the Baltic region [19]. In contrast, other studies examining long-term vegetation changes across different regions in Latvia report more substantial variations in pollen ratios within sediment records than our findings. For instance, the study on Lake Kūži [45] shows a rapid and sustained increase in hazel, alder, lime, and elm populations during the Middle Holocene. *Tilia*, specifically, has been present in Latvia since 9500 cal BP [43,45]. Although other studies suggest an earlier and more pronounced shift in broadleaved tree populations during the Middle Holocene, our findings indicate only minor variability in broadleaf representation (Figures 3, 6 and 7). A key difference between our study and others is the predominant Quaternary sediments and soil types in the study sites. Previous studies appear to have concentrated on sites situated in regions with till, clay, and silt sediments [19,44–46], where the soil and geological conditions are conductive to the growth of broadleaved trees. In contrast, our study site is located in a sandy region characterized by nutrient-poor soils, which may limit the growth and competitiveness of broadleaved trees compared to conifers. Sandy, nutrient-poor (xeric) mineral soils play a crucial role in sustaining specific forest types and associated ecological processes [47,48]. For instance, Tweiten et al. [48] investigated the influence of soil, climate, and fire in the pine and oak forests of northern Wisconsin, demonstrating that climate change impacts vegetation differently depending on soil type.

The low abundance of broadleaved species at Lake Lilaste likely accounts for the absence of a distinct 8.2 ka cooling event signal, which has been previously identified in Latvia [19,44] and across Northern Europe [49]. Pollen studies from Northern Europe indicate that this cooling event may not be as apparent in records with lower ratios of broadleaved trees, potentially due to local geological and geographical factors [49–51].

Our findings indicate that tree biomass peaked during the Middle Holocene, aligning with a period of rising mean air temperatures (Figure 7). Supporting this, Matisons et al. [52] recently demonstrated that warmer climate conditions in the northeastern Baltic region enhanced the growth increment in Scots pine, bolstering its competitiveness and long-term sustainability in the area. A significant decline in tree biomass around Lake Lilaste was detected during the Late Holocene, coinciding with a period of reduced average temperatures (Figure 7). The findings demonstrate a clear correlation between dominant tree biomass and temperature, underscoring the influence of mean air temperature fluctuations on vegetation. This relationship is less apparent in the relative or percentage-based pollen data derived from Lake Lilaste sediments. Future climate projections indicate a potential increase in mean temperatures by at least 2 °C, suggesting that the region surrounding Lake Lilaste may experience a rapid rise in tree biomass, similar to conditions during the Middle Holocene. However, caution must be taken when interpreting biomass reconstructions. Modern pollen calibration to current tree biomass values in Latvia have shown relatively low correlations [29]. Therefore, further research is needed before drawing definitive conclusions about tree biomass trends around Lake Lilaste.

Land-use changes are most evident from the emergence of cultivated plant species during the Late Holocene. The anthropogenic influence around Lake Lilaste has been studied extensively, encompassing both vegetation changes and the presence of charcoal in sediment records. Evidence indicates that forest burning and deliberate human activities in the area date back to around CE 740. The increase in charcoal particles in the sediment layers aligns with a concurrent decline in pine populations [53,54]. Pollen analysis revealed cultivated plant species, such as rye and oat, appearing approximately 100 years after the earliest evidence of fire, suggesting a progressive increase in human impact over time. However, due to variations in the calibration of chronological data across different studies, this time lag may not be directly comparable. The findings indicate that the immediate surroundings of Lake Lilaste were not heavily utilized for agriculture, as evidenced by the relatively low representation of herbaceous, ruderal, and cultivated plant species in the local vegetation. Both afforestation and deforestation on sandy soils can have more pronounced effects than on forests growing on other soils, as they are relatively more sensitive to biodiversity variability [55,56]. This points to the importance of studying the sensitivity of sandy soils other than conventional farmland to environmental change, and of determining whether changes in climate and environmental conditions are relevant in the context of these areas.

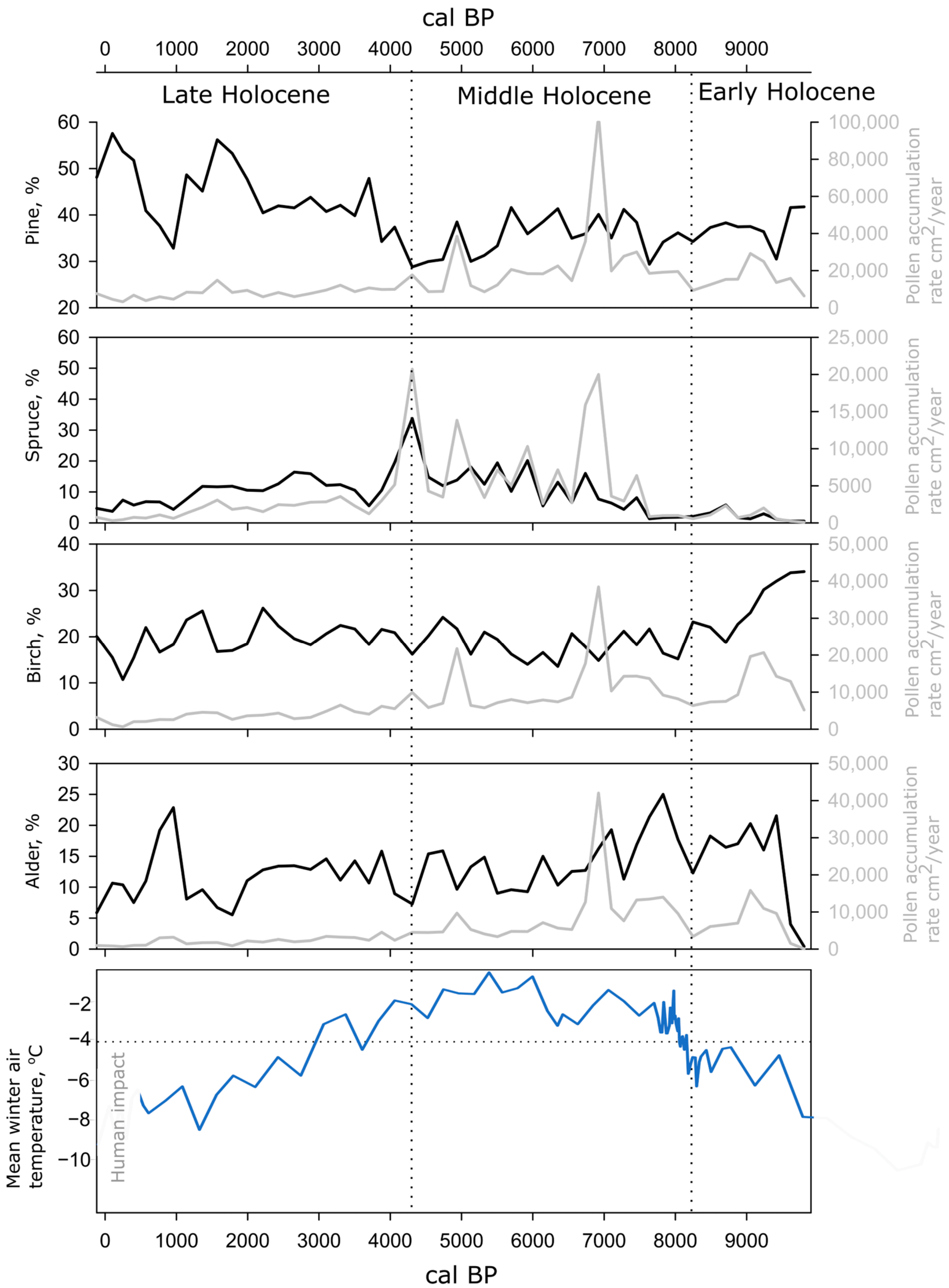

Figure 7. Reconstructions of dominant tree biomass around Lake Lilaste and mean winter air temperature for Latvia (dotted horizontal line denotes modern mean climate data; [46] Stivrins et al., 2015). Vertical dotted lines separate formal Holocene subdivisions: Early Holocene (11,700–8200 cal BP), Middle Holocene (8200–4200 cal BP), and Late Holocene (last 4200 years).

It is important to acknowledge that modern vegetation patterns are unlikely to be directly attributed solely to historical climatic conditions, as they have been shaped by a range of influencing factors. These factors include the interactions between Lake Lilaste and various stages of Baltic Sea development, episodes of extreme coastal weather, and the gradual rise in agriculture accompanied by diverse land management practices [30,31,57]. Consequently, drawing direct parallels between past and present conditions may lead to inaccuracies. However, the current landscape and forest structure are the outcomes of millennia of interactions among past climate variations, natural disturbances, and human activities. Therefore, evaluating historical trends in forest composition and biomass provides crucial insights into long-term forest dynamics. Integrating this understanding with interdisciplinary studies and diverse methodological approaches can enhance predictions of future ecological changes.

While our study shows general vegetation changes, it does not fully support the assumption that the composition of dominant trees will shift with climate change. In contrast, Dyderski et al. [18] quantified the projected range changes and threat levels of 12 European forest tree species by 2061–2080, considering three climate change scenarios. Their findings suggest that pine, spruce, and birch will be significantly affected by a warming climate. However, in the area around Lake Lilaste, pine trees have dominated throughout the Holocene, with no notable deviations in the composition of the dominant taxa. This may be due to pine's adaptation to grow on mineral-poor, sandy soils, whereas on richer soils, spruce and broadleaf species compete with pine [58]. The sandy soil along the Lake Lilaste shoreline provides ideal conditions for extensive pine populations, and their dominance is likely to persist under future warmer climatic conditions.

6. Conclusions

(1) The composition of dominant tree species in Central Latvia has remained relatively stable through the Holocene. This stability is attributed to the ecological adaptability of pine, birch, and alder to the sandy, nutrient-poor soils prevalent in the region.

(2) Despite warmer and drier conditions during the Middle Holocene, which favored the expansion of broadleaved trees across the Baltic region, their presence around Lake Lilaste remained limited. This reflects the restrictive nature of local geological and soil conditions on broadleaf growth and competition.

(3) While climate change may affect tree species, the dominant presence of pine, birch, and alder around Lake Lilaste is likely to continue due to its adaptation to the local soil conditions. This highlights the importance of considering site-specific ecological and geological factors when assessing future vegetation responses to climate change.

Author Contributions: Conceptualization, N.S; methodology, N.S.; software, N.S. and M.J.; validation, N.S.; formal analysis, N.S. and M.J.; investigation, N.S. and M.J.; data curation, N.S.; writing—original draft preparation, N.S.; writing—review and editing, M.J.; visualization, N.S. and M.J.; supervision, N.S. All authors have read and agreed to the published version of the manuscript.

Funding: This research was funded by the Estonian Research Council project grant PRG1993 and TK215, and the Latvian Science Council Project No. lzp-2021/1-0163. Additional funding was provided by the performance-based national basic research funding of the University of Latvia.

Data Availability Statement: The data are available upon request by contacting normunds.stivrins@lu.lv.

Acknowledgments: Gratitude to the Siim Veski, Merlin Liiv, Atko Heinsalu, Ieva Grudzinska-Elsberga and Bas van Geel.

Conflicts of Interest: The authors declare no conflict of interest.

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