

## Article

# Environment of European Last Mammoths: Reconstructing the Landcover of the Eastern Baltic Area at the Pleistocene/Holocene Transition

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**Abstract:** The Eastern Baltic area stands out as a unique location due to the finds of Europe's youngest dated mammoth remains (12.6–11.2 ka cal BP). Our study explores the drastic climate and landcover changes during the extinction of these gigantic herbivores at the Pleistocene/Holocene boundary. We used macrofossil analysis to determine the major contemporary terrestrial plant genera present in the area and used corresponding pollen taxa for REVEALS model-based landcover reconstructions. Our results indicate that these last mammoths utilised the open landcover of the Eastern Baltic, which developed as the continental ice sheet retreated during the termination of the last glaciation. Due to climate warming during the initial stages of the Holocene interglacial, the Eastern Baltic became speedily populated by birch and pine forests. The abrupt disappearance of typical forb-dominated tundra indicators, such as *Dryas octopetala*, and the fast increase in tree birch marked a shift from an open, tundra-like landscape to a forested one, making the environment inhospitable for mammoths even in northernmost Estonia by the beginning of the Holocene. A comparison between the isotopic values of nitrogen ( $\delta^{15}\text{N}$ ) and carbon ( $\delta^{13}\text{C}$ ) obtained from mammoths' molars from 14.3 and 11.3 to 43.5 and 39.1 ka cal BP showed that mammoths experienced a decline in the nutritional value of their diet, resulting in their demise in the Eastern Baltic.



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**Keywords:** pollen; plant macrofossils; woolly mammoth; LRA REVEALS; Estonia; Latvia

## 1. Introduction

The Eastern Baltic stands out amongst other European locations because the youngest woolly mammoth (*Mammuthus primigenius* Blumenbach) tooth remains in Europe were discovered here, dating to 12.6–11.2 ka cal BP [1]. Despite the scarcity of evidence, these and several other mammoth fossil finds suggest that these animals were present in the area during the Pleistocene/Holocene transition [1–3]. These findings raise questions about the environment these last mammoths inhabited and whether it affected their eventual extinction.

The extinction of mammoths has drawn the attention of numerous researchers globally, as these animals inhabited vast areas in Europe and North America [2,4,5] ca 110,000–12,000 years ago [6]. Different factors have been proposed as potential contributors to the extinction: landscape acidification, mineral deficiency [7], nutrient deficiency [8], large skeletal size, genetic mutations and diseases [9], climatic changes [3], and human hunting [10]. The abrupt disappearance of mammoths from Europe approximately 12,000 years

ago has been attributed to the decline of open biomes during the latter part of the Last Glacial–interglacial cycle, specifically during the Allerød and Early Holocene warming [2]. In the context of our research, certain factors, such as skeletal size, osteoporosis, or mineral deficiency, are challenging to investigate due to the limited number of samples and poor preservation of some mammoth remains. Nevertheless, we can assess the potential role of landcover change in the extinction of mammoths in the Eastern Baltic area. In contrast to a few finds dated to the termination of the last glaciation, the Eastern Baltic has an abundance of mammoth remains dated to the period prior to the Last Glacial Maximum (LGM). According to NGRIP Greenland ice core stratigraphy, the Last Glacial Maximum covers a period of 27–23 ka cal BP [11].

We focused our study on two contrasting periods: post-LGM and pre-LGM. Special attention was given to the post-LGM time interval between 14.3 and 11.3 ka cal BP because this period is crucial for understanding the environment in which the last European mammoths lived. While offering valuable insights into the past existence of mammoths, it is underrepresented in terms of pollen and plant macrofossil studies [12]. We plan to fill this critical gap in vegetational data by using plant macrofossils to determine the major contemporary terrestrial plant genera present in the Eastern Baltic and exploiting corresponding pollen taxa to make REVEALS model-based landcover reconstructions.

To determine whether the climatic and landcover changes were indeed the driving factors behind the extinction of the last European mammoths, we have compiled a comprehensive dataset consisting of all available pollen and plant macrofossil records and mammoth finds from the Eastern Baltic and a new pollen and plant macrofossil record from Lake Kaatsjärv in central Estonia. We will support the investigation by comparing the landcover changes during the 14.3–11.3 ka cal BP period with the landcover changes during the pre-LGM period (50–27 ka cal BP) to assess whether environmental changes played a definitive role in the decline of mammoths in the Eastern Baltic during the Late Pleistocene.

Furthermore, we extracted stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopic values from the two Eastern Baltic's youngest molar samples found from Puurmani in central Estonia and compared the results with the published isotopic values of other mammoths that lived during the investigated time period including newly obtained isotopic values from two mammoth molar samples from the pre-LGM time period for comparison.

## 2. Materials and Methods

### 2.1. Study Area

The Eastern Baltic has a transitional climate ranging from maritime in the west to continental in the east. The area is characterised by flat terrain covered with mixed forests. In Estonia, July's mean temperature is 16–17 °C, and February's (coldest month) is –2.5 to –7 °C today [13]. In Latvia, July's mean temperature is 17.4 °C and February's mean temperature is –3.7 °C [14]. Mean annual precipitation is 550–700 mm.

The Eastern Baltic area was glaciated during the LGM. The ice retreat from the region started ~18 ka cal BP years ago [15]. The current area of Latvia became ice-free at ~15 ka cal BP [16] and Estonia at ~13 ka cal BP [17]. The Eastern Baltic geomorphology is mostly characterised by undulating low-lying glacial moraine plains, insular heights not higher than 300 m a.s.l., and drumlins and eskers consisting of deposits left by the last ice sheet [18,19].

### 2.2. Materials

We use data from 27 pollen and 8 plant macrofossil records across the region to investigate the vegetation changes and reconstruct the living environment of Europe's last mammoths in Estonia and Latvia at the Pleistocene/Holocene boundary (Figure 1, Table 1). All selected sites are radiocarbon-dated and contain information about vegetation

development during the time interval between 14.3 and 11.3 ka cal BP. Lake Kaatsjärv in central Estonia was sampled for pollen and plant macrofossil analysis to fill a gap in available records. The well-dated pollen record from the Voka section (59.4144 N, 27.5981 E) [20,21] (Figure 1C) was used to reconstruct the pre-LGM landcover for 500-year time windows centred around 33, 34, 35, 36, and 37 ka cal BP.

**Table 1.** List of studied sites. EH—Early Holocene 11.7–11.3 ka cal BP, GS-1—Greenland stadial 1 12.85–11.7 ka cal BP (corresponding to Younger Dryas), GI-1—Greenland interstadial 1 14.6–12.85 ka cal BP [22].

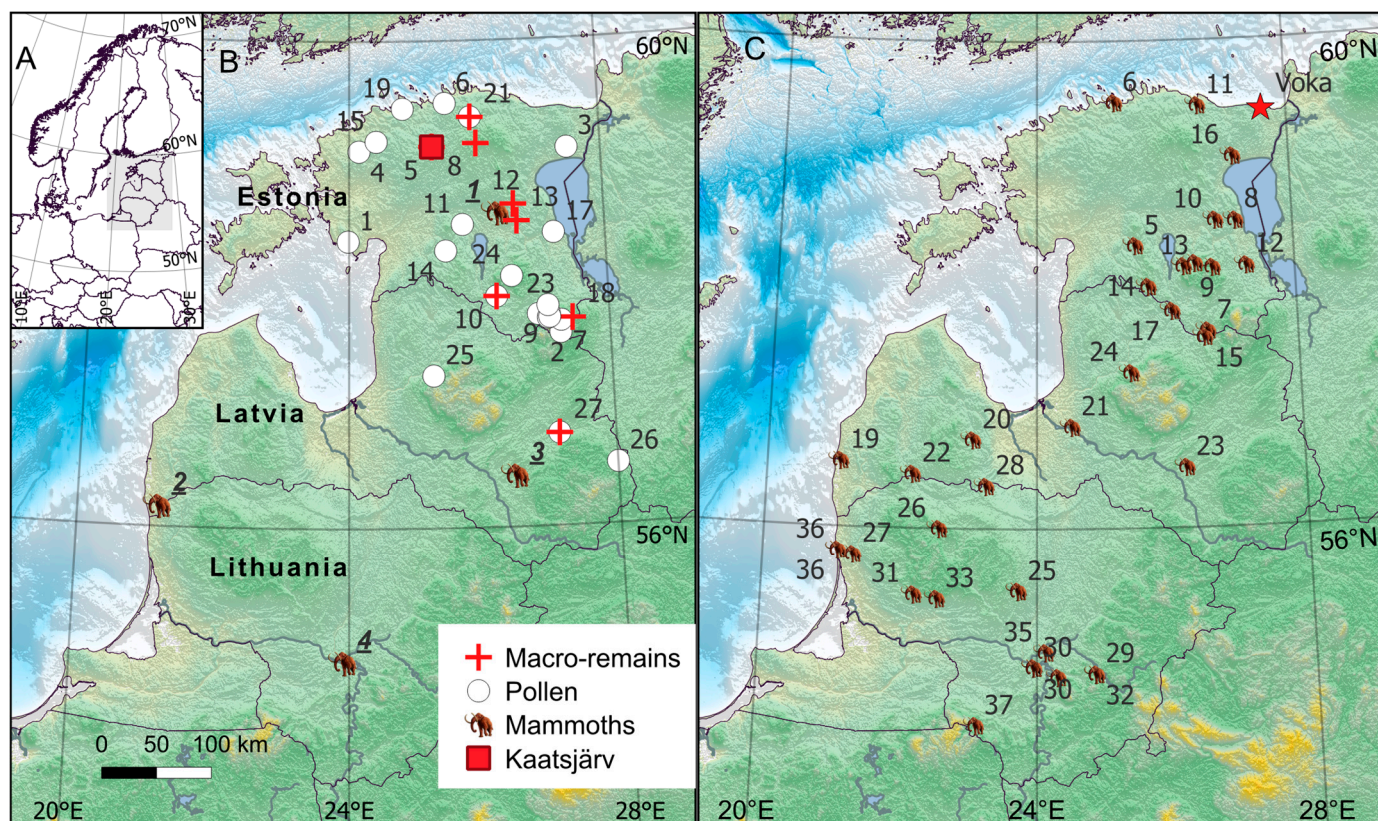
Site Number	Site	Longitude	Latitude	Analyses	Time Periods			Reference
					EH	GS-1	GI-1	
<b>Post-LGM sites</b>								
1	Ermistu	23.9829	58.3572	Pollen	+			[23]
2	Hino	27.2386	57.5831	Pollen		+		[24]
3	Imatu	27.4611	59.0997	Pollen	+			[25]
4	Järveotsa	24.1542	59.0956	Pollen	+	+		[26]
5	Kaatsjärv	25.3141	59.1318	Pollen, Macro	+	+	+	This study
6	Kahala	25.5315	59.4867	Pollen	+	+		[27]
7	Kirikumäe	27.2522	57.6830	Pollen	+	+		[28]
8	Kursi	26.0156	59.1558	Macro	+	+	+	[29]
9	Mäetilga	27.0719	57.7420	Pollen	+	+	+	[30]
10	Nakri	26.2731	57.8951	Pollen, Macro	+	+	+	[31]
11	Parika	25.7742	58.4903	Pollen		+		[32]
12	Prossa	26.5778	58.6492	Macro			+	[33]
13	Pupastvere	26.6239	58.5115	Macro	+		+	This study
14	Päidre	25.5033	58.2761	Pollen	+	+		[34]
15	Ruila	24.4297	59.1758	Pollen	+			[35]
16	Rõuge	26.905	57.7389	Pollen	+			[36]
17	Saviku	27.1940	58.4062	Pollen	+	+		[37]
18	Solova	27.4280	57.7004	Macro	+	+	+	[38]
19	Tondi	24.8533	59.4450	Pollen	+			[39]
20	Tuuljärv	27.0556	57.7056	Pollen	+	+		[40]
21	Udriku	25.9315	59.3719	Pollen, Macro	+	+	+	[41]
22	Vaskna	27.0783	57.7117	Pollen	+	+		[40]
23	Verijärv	27.0583	57.8083	Pollen	+			[42]
24	Väike_Juusa	26.5172	58.0592	Pollen		+		[43]
25	Äraiši	25.2828	57.2514	Pollen	+	+	+	[44]
26	Kurjanovas	28	56.5	Pollen	+	+	+	[45]
27	Lielais Svētiņu	27.1491	56.7591	Pollen, Macro	+	+	+	[12]

We used dates and locations of mammoth findings in the Eastern Baltic from previous publications to place these discoveries within the framework of landcover changes in the region (Table 2, Figure 1). The youngest mammoth finds in Europe come from the Puurmani site in Estonia (Table 2, Figure 1B), radiocarbon dated to  $11.8 \pm 0.36$  and  $11.9 \pm 0.25$  ka cal BP [1]. The youngest finds from Latvia are from the Rudzati and the Rucava sites (Table 2, Figure 1B) and are dated to  $12.2 \pm 0.18$  and  $15.4 \pm 0.11$  ka cal BP [3]. There is a ca 15,000-year gap in the mammoth records from the Eastern Baltic, as the area was covered in ice during the Last Glacial Maximum. This contemporaneous gap has been reported in unglaciated areas of Northern Europe as well [46]. Therefore, the second youngest

mammoth find in Estonia (Rõngu) is dated to 30.2–29.3 ka cal BP [3] and in Latvia (Veselava and Pļaviņas) from 32.8 to 29.7 ka cal BP [47] (Table 2, Figure 1C)

**Table 2.** C<sup>14</sup> dated mammoths remains in Eastern Baltic.

	Site	Longitude	Latitude	Lab Code	<sup>14</sup> C age ka BP	Calibrated Ages, ka cal BP		Description	Reference
						at 95%	Weighted Average		
<b>Post-LGM</b>									
<i>Estonia</i>									
1	Puurmani	26.2905	58.5758	Hela-423	10.1 ± 0.2	12.6–11.2	11.8 ± 0.36	Molar	[1]
1	Puurmani	26.2897	58.5788	Hela-425	10.2 ± 0.1	12.5–11.4	11.9 ± 0.25	Molar	[1]
<i>Latvia</i>									
2	Rucava	21.1603	56.1634	LuS 7538	12.88 ± 0.07	15.6–15.2	15.4 ± 0.11	Molar	[47]
3	Rudzati	26.453	56.4171	Hela-1316	10.31 ± 0.07	12.5–11.8	12.2 ± 0.18	Scapula	[47]
<i>Lithuania</i>									
4	Jiesia river	23.8963	54.8952	LuS 7529	13.8 ± 0.08	17–16.5	16.7 ± 0.14	Molar	[47]
<b>Pre-LGM</b>									
<i>Estonia</i>									
5	Heimtali	25.5002	58.3197	Hela-420	>37	42.1–41.7		Tusk	[1]
6	Ihasalu	25.202	59.4971	OxA 11563	46.5 ± 1	52.4–46.7	49.4 ± 1.52	Ivory	[48]
6	Ihasalu	25.202	59.4971	Hela-426	>41	44.4–43.5		Molar	[1]
7	Kallaste	26.5813	57.6105	Hela-421	>38	42.4–42.2		Molar	[1]
8	Koosa	27.0724	58.5116	OxA-12058	40.9 ± 0.6	44.8–43	43.9 ± 0.49	Tooth	[48]
9	Krüüdneri	26.6959	58.1284	Poz-118416	39.5 ± 1.3	45.5–41.9	43.5 ± 0.97	Tusk	This study
10	Kukemetsa	26.7619	58.5148	Poz-118415	34.6 ± 0.7	41.2–37.8	39.7 ± 0.84	Tusk	This study
11	Kunda	26.54	59.4613	Hela-424	>38	42.4–42.2		Tusk	[1]
12	Mooste	27.2209	58.1404	Hela-418	30.64 ± 0.83	37.1–33.4	35.2 ± 0.89	Molar	[1]
13	Rõngu	26.2442	58.1435	Poz-16733	25.63 ± 0.17	30.2–29.3	29.9 ± 0.22	Humerus	[3]
14	Taagepera	25.6921	57.982	OxA-11562	42.2 ± 0.65	46.1–44	45 ± 0.52	Molar	[3]
15	Tahkumägi	26.5375	57.5573	Hela-422	>38	42.4–42.2		Bone	[1]
16	Tudulinna	27.07	59.0377	OxA 11562	34.81 ± 0.34	40.7–39.3	40 ± 0.36	Ivory	[48]
16	Tudulinna	27.07	59.0377	Hela-414	>40	43.3–42.9		Tusk	[1]
17	Valga	26.05	57.78	OxA-11607	28.78 ± 0.16	33.8–32.3	33.2 ± 0.36	Tooth	[48]
18	Vitipalu	26.4154	58.1652	Poz-118499	38.3 ± 0.9	43.9–41.4	42.5 ± 0.56	Tooth	This study
<i>Latvia</i>									
19	Aizpute	21.0562	56.539	Hela-1315	>40	43.3–42.9		Tusk	[3]
20	Jaunpils	23.013	56.731	LuS 7537	40.7 ± 0.8	45–42.7	43.8 ± 0.6	Molar	[47]
21	Ikšķile	24.4976	56.8378	LuS 7535	40.85 ± 0.75	45–42.8	43.9 ± 0.58	Molar	[47]
22	Kalni, Nigrande	22.1266	56.4466	Hela-1314	30.42 ± 0.77	36.6–33.3	35 ± 0.8	Tusk	[3]
23	Plavinas	26.195	56.496	LuS 7536	27.85 ± 0.2	32.8–31.2	31.8 ± 0.31	Molar	[47]
24	Veselava	25.398	57.279	LuS 7539	25.8 ± 0.17	30.7–29.7	30.1 ± 0.17	Molar	[47]
<i>Lithuania</i>									
25	Ariogala	23.6999	55.4833	FTMC-FR-48-2	28.633 ± 0.1	33.3–32.2	32.9 ± 0.32	Incisivi	[49]
25	Ariogala	23.6999	55.4833	FTMC-FR-48-1	25.159 ± 0.09	29.8–29.2	29.4 ± 0.18	Incisivi	[49]
26	Sviraičiai	22.5315	55.9974	RICH-22970	35.415 ± 0.23	41.1–40	40.6 ± 0.27	Humerus fragment	[49]
27	Žemgrindžiai	21.29	55.77	FTMC-OZ78-1	26.579 ± 0.05	31.1–30.8	30.9 ± 0.08	Tibia	[49]
28	Žagare esker	23.2191	56.3511	KIA-55701	27.96 ± 0.23	32.9–31.4	32 ± 0.39	Incisivi	[49]
29	Kazokiškiai	24.8198	54.8076	OxA-10874	46.3 ± 1.1	52.4–46.2	49.3 ± 1.64	Incisivi	[3]
30	Jiesia	23.9282	54.858	LuS-7531	42.3 ± 1	47.1–43.2	45.2 ± 0.92	Molar	[47]
30	Jiesia	23.9282	54.858	LuS-7532	41.35 ± 0.8	45.6–43	44.3 ± 0.68	Molar	[47]
30	Jiesia	23.9282	54.858	OxA-10872	40.9 ± 0.65	44.9–42.9	43.9 ± 0.52	Incisivi	[3]
31	Jucaičiai	22.1791	55.4522	OxA-10870	40.6 ± 0.8	44.9–42.7	43.8 ± 0.59	Molar	[3]
32	Kazokiškiai	24.8198	54.8076	OxA-10875	38.05 ± 0.7	43–41.5	42.3 ± 0.36	Incisivi	[3]
32	Kazokiškiai	24.8198	54.8076	OxA-10873	33.74 ± 0.38	39.6–37.5	38.6 ± 0.59	Incisivi	[3]
33	Pilsudai	22.5133	55.4173	LuS-7533	33.65 ± 0.3	39.4–37.5	38.5 ± 0.52	Molar	[50]
34	Kruonis	24.2709	54.7805	OxA-10810	30.35 ± 0.25	35.3–34.4	34.8 ± 0.26	Incisivi	[3]
35	Turžėnai	24.0924	54.9838	LuS-7528	21.4 ± 0.12	26–25.4	25.7 ± 0.13	Molar	[50]
36	Olando kepure	21.0675	55.7977	Hela-3320	27.49 ± 0.25	31.9–31.1	31.5 ± 0.22	Molar	[49]
36	Olando kepure	21.0675	55.7977	LuS 7918	>43	45.8–45.1		Molar	[3]
37	Juodeliu	23.1044	54.3868	OxA-10844	>31.4	36.1–35.5		Tusk	[3]



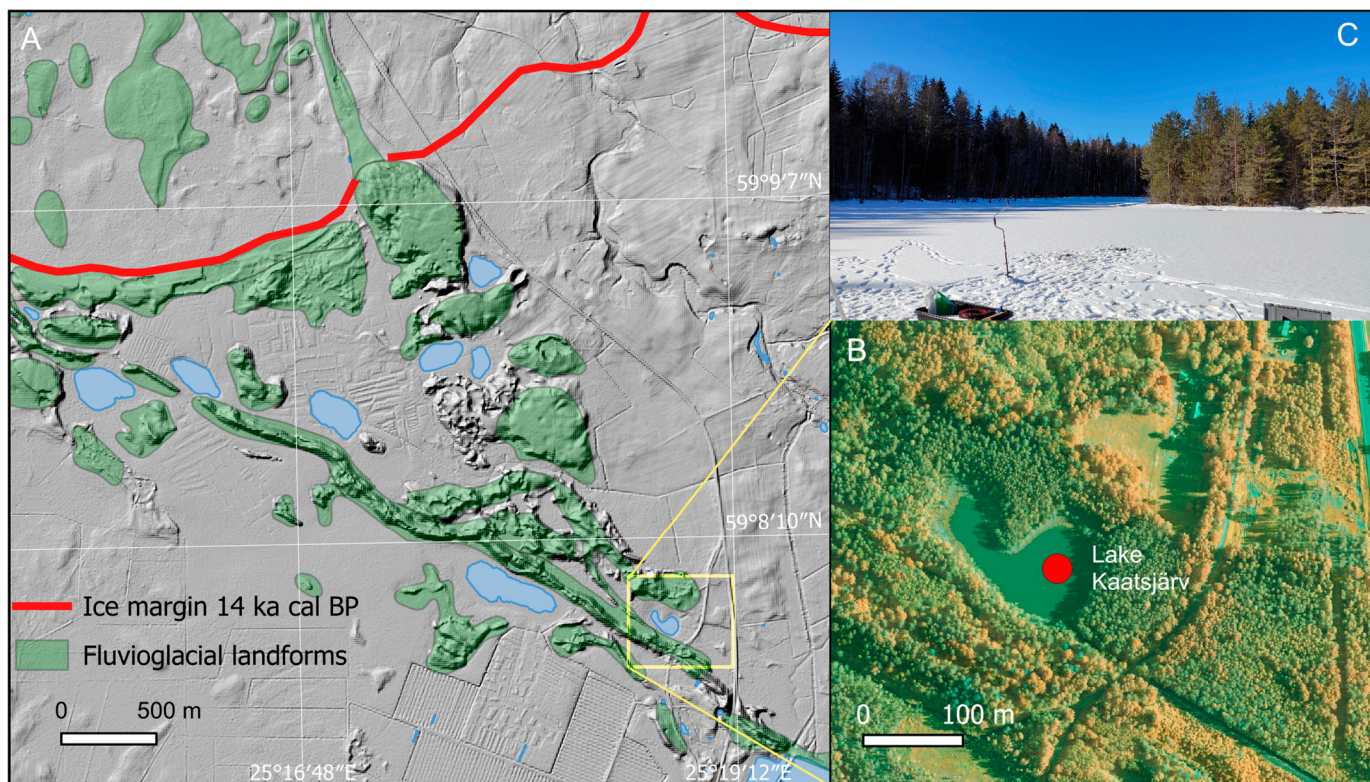
**Figure 1.** Overview map (A) and maps of the Eastern Baltic area showing post-LGM. (B) and pre-LGM. (C) known woolly mammoth finds and available plant macro remains and pollen records. Site descriptions and site numbers are given in Tables 1 and 2. Numbers in regular font refer to pollen and plant macrofossil site, underlined numbers in bold and italics refer to mammoth sites.

We have analysed two dentine samples from the youngest Estonian mammoth at Puurmani for stable carbon ( $\delta^{13}\text{C}$ ) and nitrogen ( $\delta^{15}\text{N}$ ) isotopes, which contain information about fauna's diet, contemporary plant cover, etc. [51,52]. In addition, we have analysed dentine samples from Krüüdneri (KRÜ) and Kukemetsa (KUK) sites (Table 2).

Possibility of abrupt changes in sedimentation rate and interruptions in sediment accumulation during the Late Glacial time [33] could impact the accuracy of the time determination and complicate establishing a chronological framework [53]. Keeping this in mind, we used only well-dated sequences to diminish possible inaccuracies and avoided interpolations beyond the dates.

### 2.3. Analysis of Lake Kaatsjärv Sediments

Lake Kaatsjärv (Figure 2) is a small lake in central Estonia (59.1318 N; 25.3141 E), surrounded by a mixed pine forest. The area of the lake is 1 ha, the elevation is 68.5 m above sea level (a.s.l.), and the maximum water depth is 6 m. The lake is located in front of the Pandivere (14.2 ka cal BP) ice marginal zone [17,54].



**Figure 2.** Shaded relief map with some geological landforms (A) and false colour forestry orthophoto CIR-NGR (B) of the Lake Kaatsjärv area [55]. (C) Lake Kaatsjärv view from the coring point.

The sediment core was taken from the ice using a 1 m long and 10 cm diameter Russian corer. The retrieved cores were photographed in the field, packed into plastic tubes, and transported to the laboratory, where they were stored in a cold room at 4 °C until sampled for  $^{14}\text{C}$  pollen and plant macrofossil analysis. The water depth at coring point was 400 cm. We analysed a 1.3 m long sediment sequence (980–1100 cm below lake water surface) covering the time period ca 11.5–13 ka cal BP. The organic matter (OM) and mineral matter (MM) content of the sediment was determined by loss on ignition (LOI) [56]. Carbonate matter content (CM) was calculated as the difference between LOI at 950 °C (for 2 h) and LOI at 550 °C, multiplied by 1.36 to express carbonates as  $\text{CO}_3^{2-}$  [56]. The noncarbonate mineral matter (MM) content was calculated by subtracting OM and CM from the total dry sample weight.

The age of the Lake Kaatsjärv sediments was determined using radiocarbon dating. Sediment samples for AMS  $^{14}\text{C}$  dating were wet sieved through a 0.2 mm mesh; afterwards, the terrestrial plant macrofossils were selected and analysed in the Poznan radiocarbon laboratory. The age–depth model was constructed using the Oxcal 4.4.4 deposition model [57,58] and the IntCal20 calibration curve [59]. All modelled ages used in this study are given as weighted averages in calibrated years before the present (ka cal BP), where 0 = 1950 CE.

For pollen analysis, 1 cm<sup>3</sup> of sediment was taken. Altogether, seven samples were analysed. One *Lycopodium* spore tablet (13,911 spores per tablet; Batch No. 710961) was added to each sample before the chemical treatment to estimate the concentration of microscopic objects per cm<sup>3</sup> [60]. Samples were treated with 10% HCl and 10% KOH, followed by the standard acetolysis method [61,62]. Mineral matter was removed with hot 40% hydrofluoric acid [63]. The pollen identification follows Fægri and Iversen [62] and Beug [64]. A minimum of 500 terrestrial pollen grains per sample was counted and identified to the lowest possible taxonomic level using pollen keys, the reference pollen

collection at the Department of Geology at Tallinn University of Technology, and other literature sources [64,65]. The percentages of terrestrial taxa were calculated based on arboreal and non-arboreal terrestrial pollen sum, excluding sporomorphs of aquatic and wetland plants. Aquatics, spores, and non-pollen palynomorph percentages were calculated in relation to the terrestrial pollen sum [66].

For plant macrofossils analyses, ~55 cm<sup>3</sup> of sediment at 2 cm intervals were taken from Lake Kaatsjärv. In total, 35 sediment samples were processed for plant macrofossil content. Samples for plant macrofossil analysis were prepared following [67]. Samples were wet sieved through the mesh of 0.125 mm. Plant macrofossils and other remaining materials were examined using a stereo and light microscope. We used plant macrofossils atlases, reference collections, and relevant literature during identification [68,69].

The results of plant macrofossil analysis (expressed as the number of plant macrofossils per 100 cm<sup>3</sup> of sediment, i.e., concentration) and pollen (expressed as pollen percentages) analysis are presented in a combined diagram generated using TILIA v.2.0.1 [70].

#### 2.4. Landcover Reconstructions

We have used pollen and plant macrofossil analysis results to reconstruct the composition of the terrestrial landcover, with special attention to the open versus forested conditions. Accordingly, we have included only terrestrial plant taxa and restricted the pollen records to the tree taxa and herb families represented in any of the plant macrofossil datasets confirming local presence of the taxon in order to reduce possible effects of redeposited and long-distance transported pollen (Table 3).

Plant macrofossil analysis from lake sediments represents an extra-local signal that could lead to an overrepresentation of aquatic plants and an underrepresentation of terrestrial plants. As a result, some important components of terrestrial vegetation could be missing from the records. We used presence/absence data rather than concentrations or percentages to diminish such effects to specify the terrestrial landcover type.

The cover fractions of the selected 21 tree, shrub, and herb taxa (Table 3), representing >90% of the total terrestrial pollen sum, were reconstructed from pollen data using the REVEALS (Regional Estimates of Vegetation Abundance from Large Sites) model [71]. We used the REVEALSinR function from the DISCOVER package in R [72]. The REVEALSinR parametrisation used the actual basin diameters, the Pollen Productivity Estimates (PPEs) relative to Poaceae, standard errors (SEs), and fall speeds of pollen, as shown in Table 3. The distance weighting method was set standard GPM (Gaussian Plume model) for stable conditions. The REVEALS model enables us to overcome the discrepancies between the proportions of pollen counts and vegetation cover derived from differences in pollen production and dispersal abilities of the taxa. The model is intended to estimate the vegetation proportions on a regional scale using pollen data derived from large basins. We have not strictly followed this assumption, as the data used here were derived from different-sized lakes. However, several previous investigations have shown the method's stability even when pollen records from variable-sized basins have been used [73,74]. Furthermore, the lake sizes were generally considerably larger than today during the Late Glacial period, and the contemporary landcover was sparse, suggesting that most of the recorded pollen was of regional origin regardless of the lake size.

Pollen Productivity Estimates (PPEs) and pollen fall speeds are necessary inputs for the REVEALS model. A large variety of PPE datasets is available from different locations in Northern Hemisphere [75]. Best results are usually achieved using the PPEs derived from environments like those attempted to reconstruct. We have therefore used the PPEs obtained from arctic and boreal environments of Northern Europe [76–78] and North

America [79,80] whenever available (Table 3). The PPEs for a few taxa missing from the above-mentioned sources were adopted from Europe-based sets [75].

The reconstructed cover proportions of terrestrial plant macrofossils and selected terrestrial pollen taxa (Table 3) were amalgamated into two major landcover types typical of the Late Glacial and Early Holocene environments in the Eastern Baltic area: (1) open landcover represented by different herbs, sedges (e.g., *Carex* spp., *Eriophorum* spp.), grasses (Poaceae), dwarf shrubs from heather (Ericaceae) family, and willow (*Salix* spp.); (2) forested landcover represented by typical boreal trees like birch (*Betula*), pine (*Pinus*), spruce (*Picea*), and aspen (*Populus*) (Table 3).

Many researchers do not differentiate between different birch pollen types. Therefore, it must be kept in mind that the birch pollen type used here includes pollen grains produced by both tree (*Betula pendula* and *B. pubescens*) and shrub (*B. nana* and *B. humilis*) forms of birch as the dataset was harmonised to a level obtainable for all exploited records. As birch is included here as a forest indicator, the possible addition of smaller or larger amounts of shrub-derived birch pollen could lead to an overestimation of forestation degree by reconstructions.

The pollen-based landcover reconstructions are presented as cover proportions, and macrofossils are shown based on the presence/absence of the determined landcover type indicator species. The results of landcover reconstructions are presented using QGIS 3.34 [81].

**Table 3.** The Pollen Productivity Estimates (PPEs) relative to Poaceae, standard errors (SE), and fall speeds of pollen grains used for calculations derived from <sup>1</sup> [82]; <sup>2</sup> [76]; <sup>3</sup> [80]; <sup>4</sup> [77]; <sup>5</sup> [78]; <sup>6</sup> [75].

Landcover Type	Taxon	PPE (SE)	Fall Speed
Open	<sup>2</sup> Apiaceae	0.21 (0.03)	0.042
	<sup>6</sup> <i>Artemisia</i>	4.33 (1.592)	0.014
	<sup>2</sup> Asteraceae sect. <i>Cichorioideae</i>	0.07 (0.02)	0.029
	<sup>6</sup> Brassicaceae	0.07 (0.04)	0.021
	<sup>5</sup> <i>Calluna</i>	0.3 (0.03)	0.038
	<sup>1</sup> Caryophyllaceae	0.6 (0.05)	0.032
	<sup>6</sup> Chenopodiaceae	4.28 (0.27)	0.019
	<sup>2</sup> Cyperaceae	0.13 (0.03)	0.035
	<sup>1</sup> <i>Equisetum</i>	0.09 (0.02)	0.021
	<sup>5</sup> Ericaceae (incl. <i>Empetrum nigrum</i> and <i>Vaccinium t.</i> )	0.09 (0.035)	0.032
	<sup>1</sup> <i>Juniperus</i>	1.4 (0.05)	0.016
	Poaceae	1 (0)	0.035
	<sup>2</sup> Ranunculaceae (incl. <i>R. acris t.</i> )	0.08 (0.02)	0.02
	<sup>2</sup> Rosaceae (incl. <i>Filipendula</i> and <i>Dryas octopetala</i> )	0.18 (0.04)	0.022
	<sup>2</sup> Rumex (incl. <i>R. acetosa</i> and <i>R. acetosella t.</i> )	0.04 (0.02)	0.018
	<sup>5</sup> <i>Salix</i>	0.09 (0.03)	0.022
<sup>6</sup> <i>Urtica</i>	10.52 (0.31)	0.01	
Forested	<sup>4</sup> <i>Betula</i> (incl. <i>B. humilis</i> and <i>B. nana</i> )	2.24 (0.2)	0.024
	<sup>5</sup> <i>Picea</i>	2.8 (0.21)	0.056
	<sup>4</sup> <i>Pinus</i>	8.4 (1.34)	0.031
	<sup>3</sup> <i>Populus</i>	0.11 (0.09)	0.026

## 2.5. Isotopic Analysis

Two mammoth molars found at Puurmani manor TAM G441:47 and TAM G441:48 were collected from the Estonian Museum of Natural History and sampled using a Dremel 300 drill. Two mammoth molars from Krüüdneri (KRÜ) and Kukemetsa (KUK) were sampled from the collection of the Museum of Tartu University. Collagen extraction for carbon

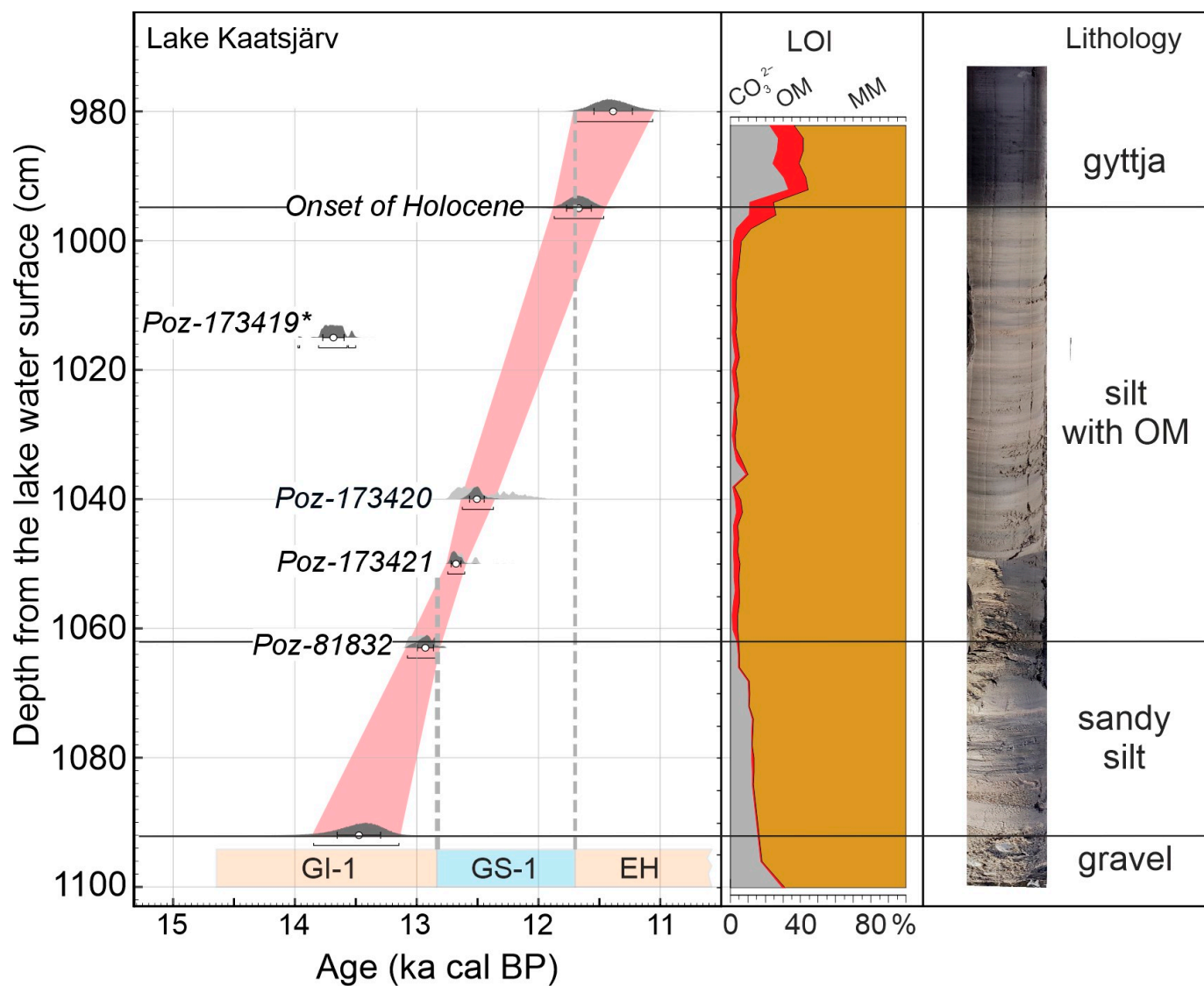


and nitrogen isotope analysis was conducted using Protocol F by Cersoy et al. [83] and analysed in a Thermo-Finnigan Delta V Plus mass spectrometer paired with an elemental analyser (Thermo Flash 1112) at Tartu University. The samples were analysed in duplicates, and the average of two was used.

### 3. Results

#### 3.1. Lithology and Chronology of Kaatsjärv

The lithology of Kaatsjärv is presented in Figure 3. Radiocarbon dating results are given in Table 4 and Figure 3. Radiocarbon date Poz-173419 is considered to be an outlier.



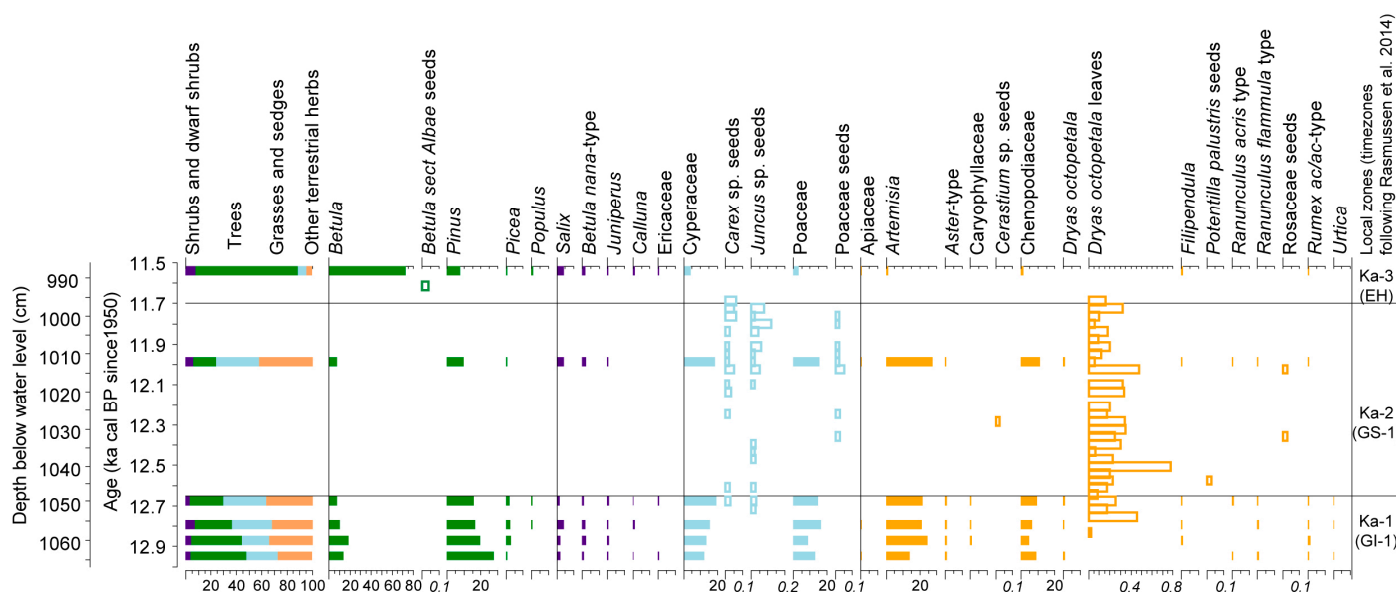
**Figure 3.** Lake Kaatsjärv sediment sequence age–depth model, loss on ignition (LOI) results and lithology. The modelled ages are shown at a 95.4% probability range. The graphs on the age–depth curve show the likelihood (grey) and posterior (black) probability distribution of the calibrated radiocarbon dates. The weighted average ages are shown by white circles with associated standard errors (black lines), and an asterisk marks the outlier not used in the model. OM: organic matter, MM: mineral matter. GI-1 and GS-1: Greenland interstadial and stadial, respectively [22], EH: part of the Early Holocene.

**Table 4.** <sup>14</sup>C dates from Lake Kaatsjärv. OxCal deposition model results are given as modelled ages at a 95.4% probability range and corresponding weighted averages. Poz-173419 is marked with an asterisk because this date is an outlier that was not used in the age model.

Depth, from the Lake Water Surface, cm	Lab Code	<sup>14</sup> C age ka BP	Modelled Ages ka cal BP		Remark	Dated Material
			At 95.4% Probability Range	Weighted Average		
1015	Poz-173419 *	11.8 ± 0.07	14.0–13.5	13.7 ± 0.09	0.3 mgC	<i>Dryas octopetala</i> leaves unidentified stems and leaves
1040	Poz-173420	10.5 ± 0.120	12.6–12.4	12.5 ± 0.06	0.08 mgC	<i>Dryas octopetala</i> leaves unidentified stems and leaves
1050	Poz-173421	10.6 ± 0.07	12.8–12.6	12.7 ± 0.04	0.18 mgC	<i>Dryas octopetala</i> leaves unidentified stems and leaves
1058–1068	Poz-81832	11 ± 0.06	13.1–12.8	12.9 ± 0.07		Bulk sediment

### 3.2. Kaatsjärv Plant Macrofossils and Pollen Diagram Description

The biostratigraphical material from Lake Kaatsjärv (Figure 4) was divided into three zones determined following the Greenland Ice Core Chronology (GIGC05modelext) [22].



**Figure 4.** Combined diagram of selected taxa showing pollen percentages (filled bars) and terrestrial plant macrofossils concentrations expressed as the number of plant macrofossils per 100 cm<sup>3</sup> of sediment (outlined with a thick stroke).

Ka-1 (GI-1; 13.5–12.85 ka cal BP). This zone is characterised by *Pinus* domination in the pollen spectrum among tree taxa, but its part decreases by the end of the zone. *Picea* is not as prominent as *Pinus* but also increases by the end of the zone. At the same time, *Cyperaceae* and *Poaceae* increase noticeably, as does *Artemisia* and *Chenopodiaceae* pollen. There is a peak in Non-Arboreal Pollen (NAP) taxa at 12.8 ka cal BP. Plant macrofossil finds were very rare in this zone, mainly consisting of rare *Tomentopnum nitens* leaves.

The lowermost pollen samples from sandy silt sediments of Lake Kaatsjärv, below 1068 cm, >13.0 ka cal BP, contain redeposited pollen, making it unsuitable for our analysis. The presence of tree taxa like *Alnus*, *Ulmus*, and *Corylus* in this sequence is inconsistent with the vegetation and climate information for that period and was excluded from further analysis. The issue of redeposited pollen in the periglacial sediments is a common problem for the Eastern Baltic [12]. In addition, these samples have lower pollen concentrations and contain a high amount of corroded pollen grains.

Ka-2 (GS-1; 12.85–11.7 ka cal BP). This is the only zone where the plant macrofossils become prominent. In this zone, *Pinus* gradually decreases amongst tree pollen taxa, and *Betula* continues to decrease. *Quercus* decreases by the end of the zone. *Salix*, in contrast, increases throughout the zone. Poaceae, Cyperaceae, Chenopodiaceae, and *Artemisia* continue to increase. Plant macrofossils of KA-2 are represented by *Potentilla palustris*, *Carex*, and *Juncus* seeds. *Dryas octopetala* peaks at the depth of 12.5 ka cal BP.

The zone demonstrates a noticeable change in the vegetation composition as *Cerastium*, Rosaceae, and Poaceae seeds are present. By the end of the zone, however, Rosaceae, Poaceae, *Carex*, and *Juncus* seeds decline; *Dryas octopetala* also decreases and abruptly disappears at 11.7 ka cal BP.

Ka-3 (EH; 11.7–11.3 ka cal BP). *Pinus* increases in the pollen spectrum, but *Betula* becomes dominant in the zone among tree taxa, surpassing *Pinus*. Herbs like Poaceae, Cyperaceae, *Artemisia*, and Chenopodiaceae are decreasing. There is very little to no herb-derived macrofossil material in this zone. However, the seeds belonging to tree-type birch, *Betula* sect. *Albae* appear in this zone for the first time. The plant macrofossil assemblage instantly changes to *Betula* sect. *Albae* and *Potamogeton* dominated (Supplementary Materials Data).

### 3.3. Landcover Reconstruction

Maps encompassing Estonia and Latvia representing pollen-based landcover proportions and plant macrofossil-based presence/absence evidence of open (represented by herbs and shrubs) and forested (represented by tree taxa) landcover were generated for three time periods: GI-1 (14.6–12.85 ka cal BP), GS-1 (12.85–11.7 ka cal BP), EH (11.7–11.3 ka cal BP) (Figure 4).

GI-1 (14.6–12.85 ka cal BP). Half of Estonia's current territory was submerged by the Baltic Ice Lake and delimited by the glacier in the north [54,84]. Sparse vegetation dominated by herbaceous plants indicates a cold, open environment with limited tree cover. According to pollen data, trees were present in northern and southern Estonia and central Latvia during this period. However, plant macrofossil evidence shows open landscapes with no tree cover in central and northern Estonia and a mixture of open and forested landscapes in southern Estonia and central Latvia.

GS-1 (12.85–11.7 ka cal BP) (Younger Dryas). Pollen evidence shows that central Estonia was an open landscape, with a marked decline in forest cover, but northern and southern Estonia kept some tree cover. However, according to plant macrofossils, open landscapes dominated Estonia, and trees were present only in central Latvia.

EH (11.7–11.3 ka cal BP). Pollen evidence shows the predominantly open landscape in eastern Estonia, whereas the northern and western parts of Estonia and the south of Estonia and Latvia were predominantly occupied by forests. Plant macrofossils indicate that the trees established their presence in northern Estonia and kept their presence in central Latvia, whereas the trees in central and southern parts of Estonia only started to establish their presence.

### 3.4. Isotopic Results

Isotopic results are summarised in Table 5. We used the C:N atomic ratio to evaluate the extent of bone decomposition and its potential impact on the results. Following the criteria outlined by [85], C:N ratio values should fall within a range of 2.9–3.6. The acceptable nitrogen (N%) and carbon (C%) values should be higher than 1% and 3% [86]. TAM G441:47 and TAM G441:48 displayed nitrogen values of 0.5% and 0.9%, carbon values of 2.3 and 2.5, and C:N ratios of 4.1 and 2.7, respectively, outside of the ranges that are considered acceptable. KRÜ and KUK displayed acceptable C:N ratios of 3.1 and 3.3, respectively. Stricter criteria for the C:N ratio of 3.1–3.3 range suggested by Guiry and Szpak (2021) [87] also show that C:N ratios of TAM G441:47 and TAM G441:48 fall outside of the acceptable range, whereas KRÜ and KUK show acceptable C:N ratios.

**Table 5.** Summary of the isotopic results of four mammoth molars from three different Estonian sites.

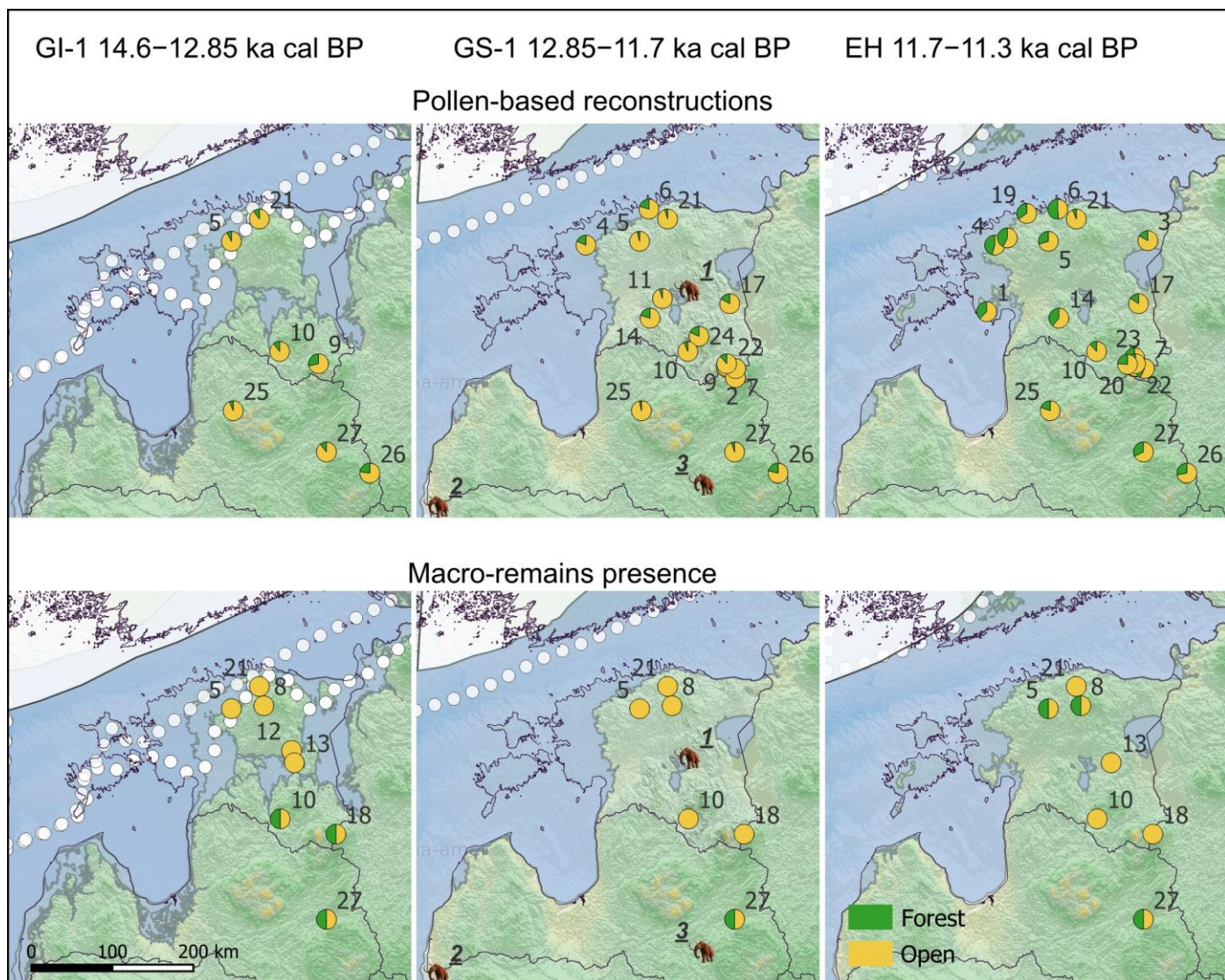
Sample ID	Material	$\delta^{15}\text{N}$ (‰) $\pm$ SD	$\delta^{13}\text{C}$ (‰) $\pm$ SD	N	C	C:N
KRÜ	Mammoth molar	+9.8	−21.1	1.1	3.6	3.1
KUK	Mammoth molar	+10.1 $\pm$ 0.02	−20.6 $\pm$ 0.05	1.0	3.6	3.3
TAM G441:47	Mammoth molar	+7.4 $\pm$ 0.09	−20.2 $\pm$ 0.4	0.5	2.3	4.1
TAM G441:48	Mammoth molar	+6.5 $\pm$ 0.9	−21.2 $\pm$ 0.9	0.9	2.5	2.7

## 4. Discussion

### 4.1. Landcover Reconstructions

The combined effect of climate cooling and warming and changes in the extent of major water bodies and dry land created a highly variable landscape with a dynamically changing landcover for three millennia (14.6–11.3 ka cal BP) at the end of Pleistocene and the beginning of Holocene. The drastic water level changes in the Baltic basin caused by the combined effect of glacial meltwater input and glacioisostatic land uplift considerably changed the shoreline of the Eastern Baltic (Figure 5) [84]. The landscape emerged as a barren periglacial wasteland behind the retreating ice front, with continental ice cover persisting in northern Estonia until 14 ka cal BP and in southern Finland up to 11.7 ka cal BP [15]. The soil in the deglaciated region can develop in 100–1000 years [88], and shrubs and grasses can appear relatively shortly after glacier retreat according to modelling studies from Greenland [89], which shows that after the ice retreat in the Eastern Baltic, the landscape could become attractive for herbivores in a relatively short time period.

According to our pollen-based reconstructions, the area of present Estonia and Latvia was covered with sparse open landcover during a two millennia-long warmer period (GI-1, 14.6–12.85 ka cal BP) at the end of the last glaciation (Figure 5). Open dry tundra-like communities with grasses, sedges, mugworts (*Artemisia*), and members of the amaranth family (Chenopodiaceae) dominate the herb pollen assemblage at Lake Kaatsjärv (Figure 4). While such herbal vegetation composition is typical for most of the Late Glacial pollen sequences from the Eastern Baltic [12], there is no contemporary plant macrofossil evidence of mugworts or amaranth family members in the region. However, it must be kept in mind that both *Artemisia* and Chenopodiaceae are wind-pollinated taxa and therefore prone to be overrepresented in pollen spectra. Most pollen-based reconstructions show low (10–20%) but steady tree cover in Estonia and Latvia. However, our results of plant macrofossil analysis suggest that at least boreal trees (birch and pine, spruce, and aspen) were present in Latvia. Furthermore, there is evidence of tree birch (*Betula sect. Albae*) presence in Lithuania already around 18.7 ka cal BP, directly after ice retreat from the region [49].



**Figure 5.** Palaeo-geographic maps showing pie charts representing pollen-based reconstructions of open (yellow) and forested (green) landcover proportions and the presence of herb (yellow) and tree (green) macrofossil evidence. The extent of major water bodies is shown according to [54]. Contemporary for presented time slice continental ice margin is shown with a white overlay and tentative maximum extent with dotted white lines [15,54]. Numbers in regular font refer to pollen and plant macrofossil site, underlined numbers in bold and italics refer to mammoth sites.

Our findings agree with those of earlier studies by [29,90] and indicate that the late Pleistocene mammoth populations in the Eastern Baltic area could have been trapped between the quickly developing forests in the south and the receding ice edge and meltwater lakes in the north. The contemporary plant macrofossil evidence supports the above-described pattern of vegetation cover closely following the climate changes more clearly than the pollen-based reconstructions (Figure 5). While considering pollen-based results, it should be noted that the REVEALS model cannot estimate the part of the non-vegetated ground and could, therefore, lead to gross overestimation of plant cover proportions for both open and forested landcover types for mostly barren landscapes [91]. On the other hand, the sparse vegetation cover producing low amounts of pollen could cause an overrepresentation of long-distance-derived pollen grains in pollen samples. The study on the modern forest–tundra ecotone in Scandinavia shows that the arboreal component dominates the background pollen and can contribute ca 60% of the total pollen loading in

samples from open tundra [78]. The aerobiological observations have shown that pollen produced by members of the birch and pine family can travel >1000 km distances [92,93]. The plant macrofossil-based evidence shows that the first tree-type birch (*Betula sect. alba*) and pine trees immigrated into eastern Latvia (Lake Lielais Svetinu) ca 13.5 ka cal BP [94]. First, trees, the tree-type birch, reached the shores of Lake Nakri in southern Estonia, which was also already during GI-1 (Figure 5) [31].

The last climate cooling episode, GS-1 (12.85–11.7 ka cal BP), corresponding to the Younger Dryas climatostratigraphic episode before the current interglacial, caused considerable climate cooling, especially in the northern part of the Eastern Baltic [95,96]. Both pollen- and plant macrofossil-based evidence show a clear decrease in tree cover in Estonia and Latvia (Figure 5). Furthermore, the results of the biostratigraphic analysis from Lake Kaatsjärv, situated in the border zone between the retreating glacier and immigrating vegetation with abundant finds of *Dryas octopetala* leaves accompanied by diminishing amount of tree pollen and dominance of typical dry tundra elements as grasses, mugworts, and members of amaranth family among herb pollen, show clear evidence of prevailing open forb-dominated tundra conditions (Figure 4). However, the tree macrofossil finds from Latvia suggest that at least some tree populations, probably established already during the previous warmer period, survived the climate cooling (Figure 5). Amon et al. [94] have reported continuous finds of birch seeds, pine and spruce needles, and stomata from Lake Lielais Svetinu, Latvia.

Subsequently, by 11.7 ka cal BP, the GS-1 stadial ended abruptly with rapid climate warming [97]. The disappearance of *Dryas octopetala* and the emergence of herbs such as *Cerastium* and Rosaceae family members, along with the discovery of tree macrofossils in Lake Kaatsjärv, appear concurrently with climate warming. According to Birks and Birks [98], the annual mean temperature in northern Norway steeply rose to around 6 °C during the first 500 years of the Holocene. The formerly dominating Chenopodiaceae diminished drastically in pollen records and were replaced by a high amount of birch pollen (Figure 4). This signified a rapid transformation from a dry steppe tundra into a forested landscape, considerably reducing the shrub and herb layers.

During 11.7–11.3 ka cal BP, the pollen and plant macrofossils recorded from Lake Kaatsjärv and other parts of Estonia show the establishment of more widespread tree cover and abrupt shrinkage of the open landscapes (Figures 4 and 5). While forests were speedily advancing in Latvia and southern Estonia, northern and western Estonia was submerged by the Baltic Ice Lake [54], with the glacier front situated in southern Finland [15,99].

#### 4.2. Mammoths and Environment

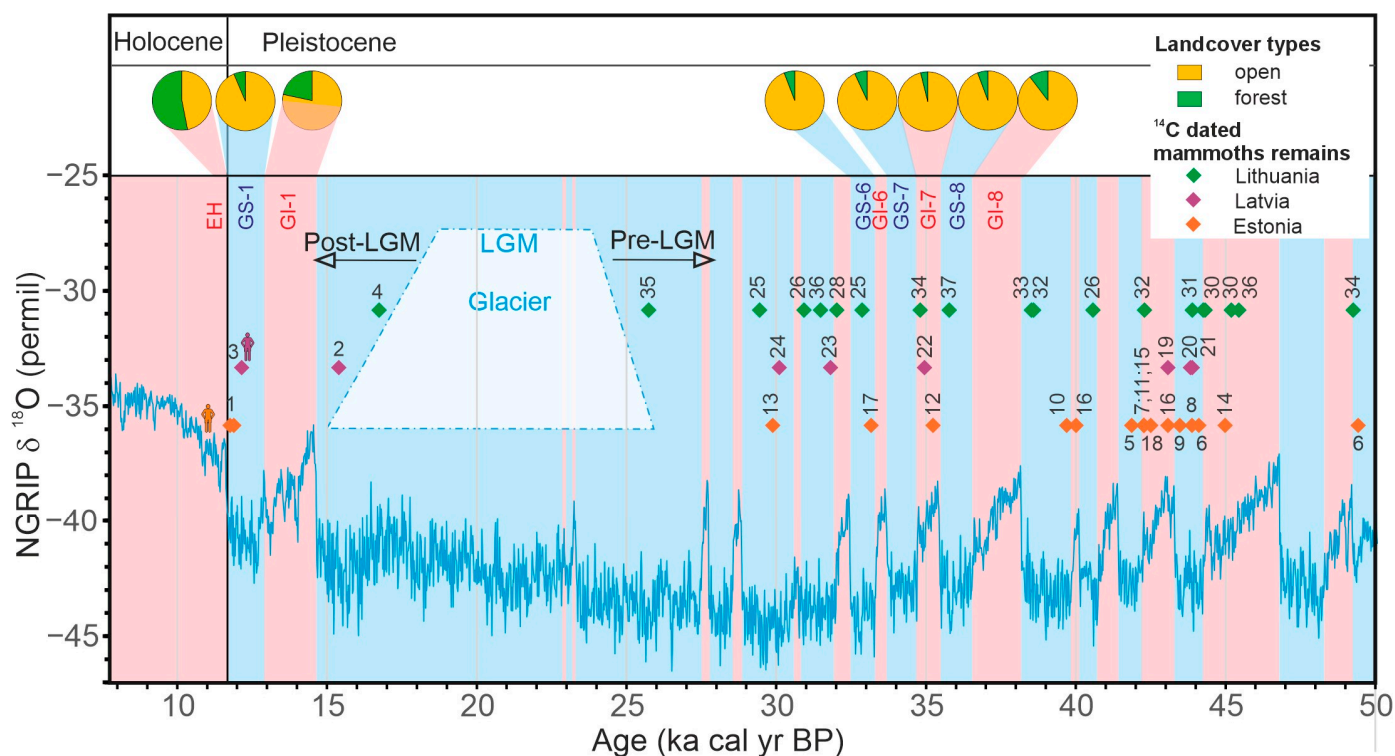
Rapid landcover change and afforestation in connection with rapid climate warming have been suggested to be one of the major factors leading to the extinction of herbivorous megafauna in Northern Europe at the end of the Pleistocene [3]. Furthermore, Ukkonen et al. [3] noted that a higher abundance of mammoth remains in Northern Europe is primarily associated with colder periods of the post-LGM, such as the GS-2 and GS-1 stadials, and are absent during warmer intervals, like GI-1 interstadial. This observation fully agrees with our results and raises the question of whether a similar pattern could be observed during the earlier time periods [96]. The pre-LGM warmer period during the last glaciation, ca 60–27 ka cal BP, led to ice-free conditions in the Eastern Baltic region (Figure 6). However, these climate oscillations were less pronounced, and the environmental conditions were more stable than those at the Late Pleistocene/Early Holocene boundary [22].

While only four mammoth molar samples have been found in Estonia and Latvia from the post-LGM period and dated between 15.4 and 11.8 ka cal BP, many more are known from the pre-LGM period, dated 50–27 ka cal BP (Figure 6, Table 2) [3]. Furthermore, it is

important to consider that the true extent of mammoth presence during this time may be heavily underrepresented due to the erosive effects of subsequent glacial advances [17]. Much of the material, including potential mammoth remains, could have been buried, eroded, or displaced, limiting our ability to capture the actual abundance and distribution of mammoth populations during the pre-LGM [1,22,100]. Due to the scarcity of the  $^{14}\text{C}$  dated remains, it is difficult to make firm conclusions about whether a long-term coherent pattern of climate-dependent distribution of woolly mammoth exists in the Eastern Baltic region. However, the available data suggests the tendency of the mammoth appearance in connection to colder periods both during the pre- and post-LGM (Figure 6).

In contrast to the numerous pre-LGM mammoth finds known from the Eastern Baltic area, the finds of contemporary (50–27 ka cal BP) well-dated sediment sequences suitable for biostratigraphic analysis are much less frequent. To the authors' knowledge, only one site from the study area—the Voka site (Figure 1) in the northeastern part of Estonia covering 38–32 ka cal BP—is rigorously dated to this period (Figure 6) [20,21].

The Pleistocene herbivorous megafauna depended on fodder of high nutritional value [101]. Based on the mammoths' stomach content analysis, Cyperaceae and *Artemisia* were the key components of mammoths' diet [102]. Our reconstructions from the pre-LGM Voka site and our post-LGM reconstructions representing the cooler GS-1 stadial indicate an environment dominated by dry steppe-tundra communities, which are rich in forbs, graminoids, shrubs, including abundant finds of *Dryas octopetala* leaves, and pollen from Cyperaceae, *Artemisia*, and Chenopodiaceae. As steppe animals that thrived in vast, open landscapes [99], such landcover composition suggests an abundant subsistence basis with plentiful food sources for mammoths to graze on. An examination of the Voka pollen-based landcover reconstructions reveals that the landcover was notably stable during many millennia of the pre-LGM, exhibiting only minor differences between vegetation composition of cold and warm phases. The post-LGM landcover was much more dynamic, and even though the open tundra-like environment prevalent during GS-1 seems to have been suitable for mammoths, the animals may have struggled to adapt to the rapid climate change-induced shifts in landcover characteristic to the end of the last glaciation and the beginning of the Holocene (Figure 4). The volatile nature of the environmental conditions could also explain a considerably lower number of mammoth finds belonging to the post-LGM compared with the pre-LGM (Figure 6). The vegetation changes from forb-dominated, dry steppe-tundra to landcover dominated by woody plants and graminoids were shown to be concurrent with large-scale megafaunal extinction in eastern Siberia during the early Holocene [103,104]. Our results show a similar pattern for Northern Europe, with a clear connection between the rapid afforestation combined with the decline of the dry forb steppe-tundra elements coinciding with the last finds of woolly mammoth remains, leading to the ultimate extinction at the transition to the Holocene. Human activities, hunting, and the associated impacts on mammoth habitats are often considered to be among the primary factors contributing to the mammoths' demise [9,105]. However, in the Eastern Baltic, the evidence of the coexistence of woolly mammoths with local prehistoric hunter-gatherers is ambiguous. Meanwhile, the evidence from the oldest known settlement in Latvia, the Mellupite settlement ( $12.3 \pm 0.14$  ka cal BP) [106], predates the last mammoth find by 200 years, suggesting short-term co-existence and possible hunting. However, the last mammoth in Estonia predates the first known settlement, the Pulli settlement ( $11 \pm 0.17$  ka cal BP), by ca 800 years, making hunting as a course for extinction unlikely [107–109].



**Figure 6.** Radiocarbon-dated mammoth remains, NGRIP  $\delta^{18}\text{O}$  curve, and pollen-based landcover reconstructions from Voka and Lake Kaatsjärv. Blue colour corresponds to the stadials (colder periods) and pink to the interstadials (warmer periods) [22]. Numbers correspond to the site numbers in Table 2.

#### 4.3. Isotopic Evidence

Comparing palaeobotanical reconstructions based on pollen and plant macrofossil data and isotopic composition of herbivorous faunal remains has been shown to provide a deeper insight into vegetation changes in the investigated region and the diet of the tested animals, e.g., [110]. Similar to pollen data, stable isotopic records from mammoths offer a broad regional signal, with nitrogen and carbon isotope values representing an integrated summary of the dietary intake over the final years of the analysed specimen because bone collagen in adult proboscideans remodels over years and even decades, e.g., [111,112]. Isotopic data derived from dentine remains the only available tool for dietary reconstruction in this context because we do not have access to soft tissues such as blood, muscle, or hair, which would enable more precise dietary reconstructions [113]. While pollen data shows general changes in the vegetation composition, isotopic analysis provides complementary information about trophic interactions and dietary habits of the animals that inhabited the landscape. While the isotopic results from only four dentine samples are insufficient for a full-scope reconstruction, the isotopic data are still valuable for comparative purposes and to support our landcover reconstruction-based interpretation. According to [114,115], animals consuming 100% C3 plants have their collagen  $\delta^{13}\text{C}$  values close to  $-21.5\text{‰}$ . Carbon ( $\delta^{13}\text{C}$ ) isotopic values ( $-20.2\text{‰}$  and  $-21.2\text{‰}$ ) from Puurmani samples indicate a diet based on predominantly C3 plants. It has been shown that the depletion in  $\delta^{13}\text{C}$  can be characteristic of plants in heavily forested areas (e.g., [116]). Occasionally, mammoths could supplement their diet with woody vegetation, resulting in lower carbon isotope values [103]. We did not observe this trend in our samples. Nevertheless, the rapid forestation of the landscape in Estonia at the end of the studied period offers the possibility that mammoths in this region may have consumed woody vegetation at certain times to compensate for the



decreased amount of suitable vegetation. Future research on mammoth dietary habits in the Eastern Baltic could explore this potential relationship in more detail.

The  $\delta^{15}\text{N}$  values from Puurmani (+6.5‰ and +7.4‰) point to a low-protein, high-fibre diet and align with nitrogen values reported for other European mammoth sites, e.g., [103], who reported lower average  $\delta^{15}\text{N}$  values of 5.6‰ from the Eliseevichi site (14.47 ± 0.4 ka cal BP) and 6.1‰ from Yudinovo (15.7–14.4 ka cal BP) for the European plain, both lower than the values from Puurmani. This suggests that mammoths in the European Plain were not necessarily faring better in their diet than their Estonian counterparts. In contrast, the  $\delta^{15}\text{N}$  values from the Krüüdneri (9.8‰) and Kukemetsa (10.1‰) are higher and resemble isotopic values for older periods in the European plain, where [103] reported average  $\delta^{15}\text{N}$  values of 9.4‰ from Khotylovo (24.9 ka cal BP) and 6.6‰ from Avdeevo (22.7 ka cal BP), indicating some regional variation in the isotopic values. Multiple studies have shown that climatic conditions, like aridity and temperature, can impact the  $\delta^{15}\text{N}$  values of plants (e.g., [117]) and, as a result, impact the  $\delta^{15}\text{N}$  values from mammoths' collagen. The nitrogen isotope values decrease from the environmentally more favourable pre-LGM period to the less favourable period during the post-LGM. This trend corresponds well with our landcover reconstructions. Lowered nitrogen values from the Puurmani site align with an observed general decline in  $\delta^{15}\text{N}$  values around 16.0 ka cal BP noted across south-central Siberia, the European Plain [103], and Central and Western Europe [104].

More stable environmental conditions and a diet abundant in forbs (*Dryas octopetala* being one of them), sedges, and mugworts may explain the potentially larger mammoth populations in the Eastern Baltic during 38–32 ka cal BP in contrast to 14.3–11.3 ka cal BP. The presence of a thriving megafauna population could have led to significant trampling effects [118], which could, in turn, promote gap-based recruitment in vegetation [119]. This process could have favoured the proliferation of forbs as suggested by [120]. Forbs are notably more nutrient-rich than grasses [121] and more easily digestible [122], making them an optimal food source for sustaining large herbivores. Michelsen et al. [123] demonstrated that graminoids, abundant in open tundra ecosystems, typically exhibit higher  $\delta^{15}\text{N}$  values than trees and shrubs. Similarly, herbs and subshrubs are more common in open environments and more isotopically enriched than vegetation associated with forested areas. Thus, the higher  $\delta^{15}\text{N}$  values during interglacial periods likely reflect a grass-dominated diet, consistent with the open steppe-tundra landscapes of the time. In contrast, postglacial landscapes were characterised by the increasing dominance of forests and larger vegetation, such as trees and shrubs, leading to a dietary shift towards tree leaves and needles. This dietary change resulted in more depleted  $\delta^{15}\text{N}$  values in mammoth tissues, reflecting the transition in their ecological environment.

This interpretation supports the hypothesis that a shifting environment impacted mammoth survival and dietary habits. Based on the limited isotopic records, the conditions in central Estonia at the onset of the Holocene were probably no longer as favourable for mammoths as in earlier periods: forests dominated the northern and southern regions of Estonia and central Latvia, which did not satisfy their dietary needs.  $\delta^{15}\text{N}$  values from the pre-LGM Krüüdneri and Kukemetsa sites are higher than those from Puurmani, which can indicate a significant change in their diet and possibly the loss of the specialised ecological niche of these animals over time. Our observations agree with the findings of [124], who also discovered that the extinction of mammoths in the central East European plains during the Late Pleistocene was likely driven by the loss of their optimal habitat.

The C% and %N values and the C:N ratio of the samples from both Puurmani mammoth samples indicated that the samples are likely to have been altered by post-depositional processes. However, it is challenging to establish the factor that caused this alteration due to the lack of information about the burial context and the small selection of samples.

The poor preservation of the two mammoth molar samples from Puurmani has posed significant challenges to our research, as the samples' condition raises concerns about the reliability of the nitrogen and carbon isotopic values. Additional mammoth discoveries from this period and isotopic analysis of these findings may provide more crucial insights into the trophic position of the mammoths in the Eastern Baltic. Additionally, Figure 5 shows that the mammoth population in the Eastern Baltic declined since 50–33 ka cal BP. Our landcover reconstructions and isotopic results show that the rapid forestation and the limited availability of suitable nutrients significantly contributed to the decline of mammoth populations in Estonia during the Late Pleistocene.

## 5. Conclusions

Our analysis demonstrates considerable differences in the pre- and post-LGM landcover response to climate changes. While moderate climate changes during the pre-LGM period did not lead to considerable changes in the landcover composition, the larger climate fluctuations post-LGM led to rapid changes. The landcover reaction to intermittent colder and warmer periods was vigorous, resulting in a series of tree cover expansion and shrinkage, ending with abrupt afforestation and the disappearance of dry steppe with tundra-like open herb communities suitable for mammoths brought by rapid climate warming at the beginning of Holocene. Plant macrofossils show the progression of the tree colonisation more clearly than pollen-based reconstructions. During 11.7–11.3 ka cal BP, pollen and plant macrofossil data from Kaatsjärv show the establishment of tree cover and the abrupt disappearance of *Dryas octopetala*, a key component of forb tundra, indicating that central Estonia became inhospitable for mammoths.

We analysed four mammoth dentine samples belonging to the youngest mammoth finds in Europe (14.3–11.3 ka cal BP, 43.5 ka cal BP, and 39.1 cal BP). Although the isotopic results for carbon and nitrogen isotopic values from the Puurmani samples are not highly reliable due to the poor preservation state, and only two measured values are insufficient to draw wider conclusions about the diet of the last European mammoths, the depleted  $\delta^{15}\text{N}$  isotopic values align well with those observed in other European mammoth populations from the end of the Pleistocene. Consequently, the isotopic data suggest that the investigated post-LGM mammoths probably had a suboptimal, nitrogen-depleted diet, in contrast to the mammoth that inhabited the Eastern Baltic during the pre-LGM. This aligns well with the concurrent decline in nutrient-rich, herb-dominated communities and the overall expansion of less suitable tree communities for herbivore consumption.

**Supplementary Materials:** The following supporting information can be downloaded at <https://www.mdpi.com/article/10.3390/land14010178/s1>.

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