



Late Saalian–early Eemian vegetation patterns on the Polish Lowland: A detrended correspondence analysis (DCA) approach

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ABSTRACT

This study of Late Saalian and early Eemian Interglacial vegetation on the Polish Lowland enabled a reconstruction of the transition from glacial to interglacial conditions and of early Eemian Interglacial succession characteristics.

A total of 536 pollen spectra from 25 sites covering the Polish Lowland from west to east were analysed for selected cryophilous and thermophilous taxa, including pollen classified as redeposited; the relationships among them were examined using Detrended Correspondence Analysis (DCA).

The results suggest that the Late Saalian vegetation was a mosaic-like pattern of tundra and steppe with fragmented thickets of shrubs and pioneer trees. The onset of warming after ice sheet retreat was marked by the presence of Poaceae and Cyperaceae and redeposited thermophilous pollen, which indicates dynamic erosion processes in conditions of increased environmental humidity. The progressive warming (Zeifen Interstadial) favoured the expansion of shrubs thickets (*Hippophaë rhamnoides*, *Juniperus*, *Ephedra*) and fragmented birch-pine forests. Records from sites in the central Polish Lowland indicate that the transition from glacial to interglacial conditions was not smooth (i.e., a disturbed ecological gradient), which supports the hypothesis of a cold oscillation, correlating with the Kattegat Stadial, just before the Interglacial. The beginning of Eemian Interglacial is characterised by a predominance of birch or/and pine dense forest communities, sub-synchronous species encroachment, depending on local habitat conditions.

Spatial analysis reveals a clear east–west climatic gradient, with greater habitat patchiness in the west and traces of a short cold oscillation (the Kattegat Stadial) in the central Polish Lowland, while the eastern sites show a stable succession. The DCA results confirm that the glacial–interglacial transition was spatially diverse, shaped by local substrate properties, humidity and climatic factors. The reconstructed vegetation model allows us to understand the patch-mosaic structure of Late Saalian habitats and regional palaeoenvironmental gradients.

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1. Introduction

The Late Saalian (the lateglacial of the Saalian Glaciation) spans approximately several thousand years within the established Quaternary chronostratigraphic framework, corresponding broadly to the MIS 6a-5e interval (Lisiecki and Raymo, 2005; Gibbard et al., 2010; Gibbard and Hughes, 2021). It is not a formally defined chronostratigraphic unit, and the duration of this transition is difficult to constrain precisely. The difficulty in clear definition stems from the fact that estimates depend on three factors: the definition of the lower boundary of the Eemian, the proxies used to identify the onset of interglacial conditions, and the temporal resolution and completeness of the sedimentary record. Marine and terrestrial records indicate that this transition involved distinct climatic and environmental changes associated with ice-sheet retreat and the subsequent development of interglacial ecosystems (e.g., Lisiecki and Raymo, 2005; Beets et al., 2006; Hodell and Curtis, 2008; Margari et al., 2010; Tzedakis et al., 2018). Palaeoclimate studies document the period using various data (mainly $\delta^{18}\text{O}$, pollen) primarily gathered in the northern hemisphere. The period also exhibits a biodiversity that indicates that the transition to interglacial conditions was not smooth but proceeded in a two-stage climatic oscillation (Fig. 1). These data are presented in the collective work of Seidenkrantz et al. (1996) and recently for the Polish Lowland by Majecka et al. (2026). Marine, lacustrine and terrestrial pollen records from dozens of sites suggest the existence of a “Younger Dryas”-type climate oscillation just prior to the Marine Isotope Stage 6/5e boundary. The Western European terrestrial sedimentary record of this period shows traces of relatively warm conditions following the deglaciation of the Saalian ice sheet. It also indicates that this warming (called the Zeifen Interstadial) was interrupted by a sudden cold and arid interval (the Kattegat Stadial) spanning between marine isotope events 6.01 and 6.0; Seidenkrantz et al. (1996). This climate deterioration has been associated with a weakening of the AMOC during Heinrich Event 11 (Heinrich, 1988), as it was documented by Beets et al. (2006) in the Amsterdam Basin. One of the first records of climate oscillations at the end of the Saalian Glaciation was found in the Brokenlande profile from northern Germany (Menke and Ross, 1967). It contained the first traces of gradual vegetation development after the ice retreat in a mosaic pattern of tundra and cold steppe communities rich in reworked pollen material (pollen zone

SS A indicated as Stadial 1, according to Menke and Ross, 1967). The following climate change, though with reworked pollen grains persisting, began with the spread of shrub communities, dominated first by *Hippophaë rhamnoides*, *Juniperus*, *Betula nana* and herbaceous plants (NAP), followed by birch forest (pollen zone SS B corresponding to the Zeifen Interstadial). The subsequent cooling corresponding to the Kattegat stadial (pollen zone SS C in Brokenlande) was seen in the increased share of herbaceous plant pollen (NAP) and pine (*Pinus*) alongside a decrease in birch (*Betula*) pollen, while juniper (*Juniperus*) pollen peaked. The subsequent decline in juniper and sharp proportional increase in birch pollen are linked to the beginning of the Eemian interglacial (Menke and Ross, 1967; Menke and Tynni, 1984).

Climatic oscillations preceding the onset of the LIG (Last Interglacial) have also been documented in multiproxy palaeoclimate records from southern Europe, including Monticchio (pollen; Allen and Huntley, 2009), the Iberian Margin and Corchia Cave in central Italy (pollen, benthic $\delta^{18}\text{O}$, and speleothems; Tzedakis et al., 2018), Tana che Urla in central Italy (speleothems; Regattieri et al., 2016), the eastern Adriatic (pollen; Novellino et al., 2025), and Lake Ohrid, Albania (pollen; Donders et al., 2021). These records provide a broader context for interpreting environmental changes during the Late Saalian–Eemian transition. In particular, multiproxy records integrating vegetation, hydrological, and temperature indicators offer an opportunity to assess whether the shifts between cooler and warmer conditions observed at different European sites either represent a regionally coherent climatic signal or reflect geographically variable and local ecosystem responses.

In the Polish Lowland, 50 Eemian profiles have been documented that contain pollen recording lateglacial Saalian vegetation at their base (Majecka et al., 2026). These sites are primarily located in the area between the maximum extent of the Warta Stadial (the Warthanian) of the Odranian Glaciation (the Saalian) in the south and the boundary of the Vistulian (Weichselian) glaciation in the north (Marks, 2023). The Late Saalian vegetation was first presented in the work *Eemian History of Vegetation in Poland Based on Isopollen Maps* (Kupryjanowicz et al. (eds.), 2018). Using the isopollen map method, changes in vegetation cover in Poland just before and during the Eemian Interglacial were reconstructed based on percentage data.

Based on the pollen database collected at that time, we conducted a comprehensive vegetation assessment for the Late Saalian. A recent

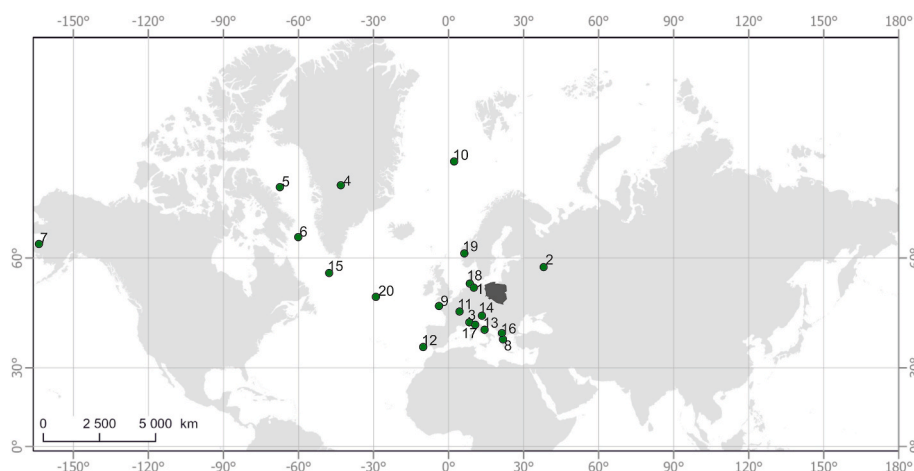


Fig. 1. Locations of the selected sites with documented Zeifen–Kattegat oscillations in various proxy records. In alphabetic order: 1 - Brokenlande (Menke and Ross, 1967) - pollen; 2 - Cheremoshnik-5 (Novenko et al., 2005) - pollen; 3 - Corchia (Tzedakis et al., 2018) - speleothems; 4 - GRIP (Dansgaard et al., 1993) - $\delta^{18}\text{O}$ (ice); 5 - HU76-029-040 (Aksu, 1985) - $\delta^{18}\text{O}$ (planktic); 6 - HU75-58 (Fillon, 1985) - $\delta^{18}\text{O}$ (planktic); 7 - Imuruk Lake (Shackleton, 1979) - pollen; 8 - Ioannina basin (Tzedakis et al., 2003) - pollen, $\delta^{18}\text{O}$, $\delta^{13}\text{C}$; 9 - Jersey (Keen et al., 1996) - pedostratigraphy; 10 - K-11 (Imbrie et al., 1993) - $\delta^{18}\text{O}$ (planktic); 11 - La Grande Pile (e.g., Woillard, 1979) - pollen; 12 - MD01-2444 (Margari et al., 2010; Tzedakis et al., 2018) - pollen, $\delta^{18}\text{O}$ (benthic); 13 - Monticchio (Allen and Huntley, 2009) - pollen; 14 - MIR1/Istrian coast (Novellino et al., 2025) - pollen; 15 - ODP Site 646/HU90-013-013P (Aksu et al., 1989; Hillaire-Marcel et al., 1994; Stoner et al., 1995) - $\delta^{18}\text{O}$ (planktic), rock magnetism; 16 - Orhid Lake (Donders et al., 2021) - pollen; 17 - Tana che Urla (Regattieri et al., 2016) - speleothems; 18 - Rederstall (Menke and Tynni, 1984) - pollen; 19 - Stordalsgrotta (Lauritzen, 1991, 1995) - speleothems; 20 - V30-97/DSDP Site 607 (Ruddiman et al., 1987) - $\delta^{18}\text{O}$ (benthic). Poland's location in Europe is marked grey.

revision of pollen data indicated that the pollen data for the Polish Lowlands are highly variable. Geographic trends recorded in the percentage shares of heliophilous taxa from western, central and eastern Poland exhibit a pre-interglacial climatic gradient across the Polish Lowlands, most likely resulting from combined effects of Atlantic circulation from the west and continental influences from the east (e.g., Zagwijn, 1992; Frenzel et al. (eds.), 1992; Guiot et al., 1993). There has also been discussion of the inhomogeneous features of Eemian succession onset in the Polish Lowlands, which led to the lower Eemian boundary being revised for key Polish sites (Majecka et al., 2026).

The complexity of datasets and multiplicity of sites make it difficult to extract information suitable for summaries. Pollen data therefore need standardising. Numerical methods have facilitated ecological interpretation of palynological data (Nalepka, 2005). Ecological assessment has principally been supported by CONISS analysis (CONstrained Incremental Sum of Squares), a multivariate statistical method for quantitatively partitioning stratigraphic data (Walanus, 1997; Walanus and Nalepka, 2007).

The main aims of this work are:

- 1) to characterise Late Saalian vegetation patterns;
- 2) to determine the Saalian/Eemian transition based on vegetation shift;

- 3) to examine the geographic gradient (from west to east), i.e. the axis of changes in palaeoenvironmental features from the Late Saalian to the beginning of the Eemian Interglacial;
- 4) to determine whether interstadial-stadial climatic oscillations are visible in the Late Saalian.

2. Materials

2.1. Pollen database

The database provided by the Polish Academy of Sciences in Kraków and the University of Białystok, as well as the authors' databases, constitute the set of raw data used to compare vegetation succession characteristics among the selected sites (Fig. 2, Table 1). The data have previously been published (list of references in Table 1).

The analysis was performed for 30 selected spectral sequences of pollen (i.e., pollen percentage data) from 25 locations. A spectral sequence is defined as a stratigraphically ordered succession of consecutive pollen spectra, each representing the percentage composition of identified pollen taxa in successive samples collected from a sediment profile. Each pollen spectrum reflects the vegetation composition at a particular stage of sediment deposition, while the entire spectral sequence records temporal changes in vegetation and climate. Three sequences of pollen spectra come from the Wola Starogrodzka site

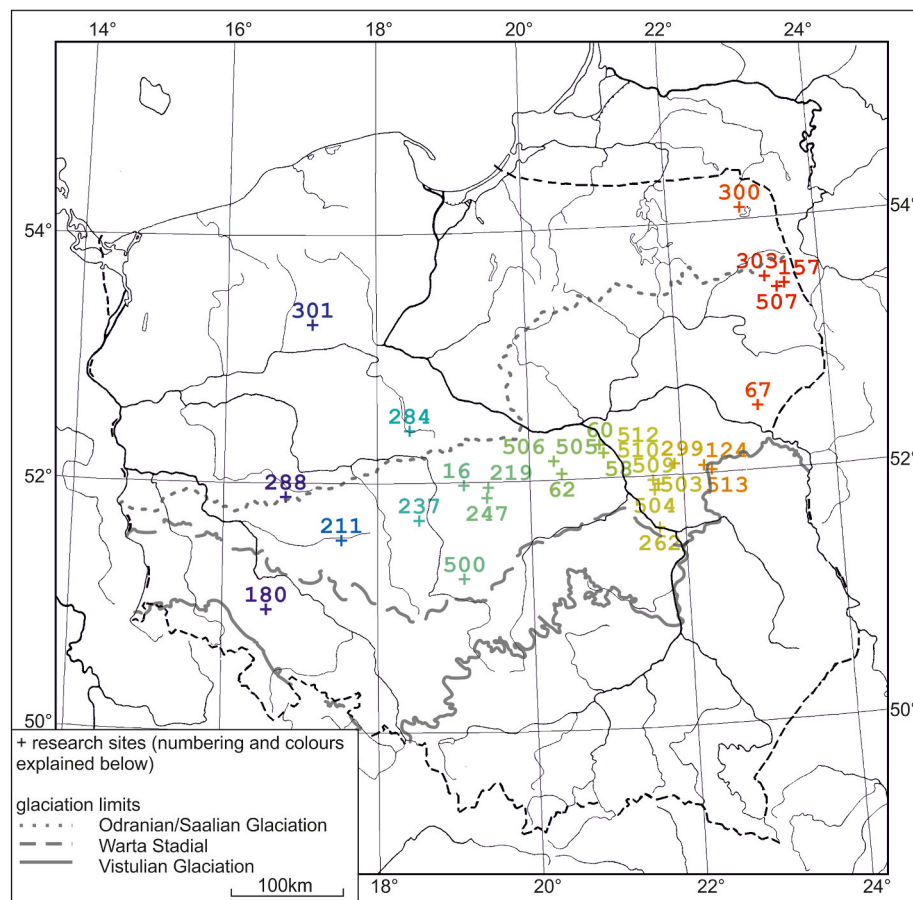


Fig. 2. Geographical distribution of selected sites with Late Saalian pollen records (original references in Table 1) used for DCA estimations (glaciation limits after Marks, 2023). Site ID number (identification number in the Eemian isopollen database) in geographical order from west to east: 288 - Zbytki 2; 180 - Imbramowice; 301 - Buntowo; 211 - Szklarka 13; 284 - Ruszków; 237 - Raczków; 16 - Powodów Stary W-2/52; 500 - Parchliny 2016; 13 - Modlna 5; 247 - Zgierz Rudunki II; 219 - Besiekierz 1/88; 506 - Struga g-120; 505 - Struga WH-15; 62 - Żyrardów 2/69; 60 - Warszawa-Wawrzyszew XV; 58 - Warszawa Kasprzaka; 510 - Wola Starogrodzka G-122; 509 - Wola Starogrodzka G-70; 512 - Wola Starogrodzka WH-122; 504 - Żabieniec 0; 262 - Kletnia Stara; 503 - Kozłów; 299 - Porzeźnica; 124 - Wiśniew; 513 - Dziewule; 300 - Szwajcaria 1; 67 - Choroszczewo; 303 - Jąłówka; 507 - Starowlany; 157 - Ludomirowo; Colours indicate geographic longitude of sites, consistent with DCA scatterplots. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Table 1

List of sites/profiles used in estimations (in geographical order from west to east) with references.

Site/profile	No izo ^a	Coordinates	References
Zbytki 2	288	51°52'N; 16°49'E	Kuszell (1997)
Imbramowice	180	50°58'N; 16°34'E	Mamakowa (1989)
Buntowo	301	53°15'N; 17°07'E	Kuszell and Malkiewicz (2008); Chmal (2009); Malkiewicz (2018)
Szklarka 13	211	51°31'N; 17°33'E	Kuszell (1998)
Ruszków	284	52°25'N; 18°26'E	Kozyra and Skompski, 1995; Janczyk-Kopikowa (1997); Mirosław-Grabowska et al. (2009)
Raczków	237	51°41'N; 18°33'E	Zaloba and Jastrzębska-Mamełka (1990)
Powodów Stary W-2/52	16	51°58'N; 19°08'E	Balwierz (1989); Dutkiewicz (1992a), b
Parchliny 2016	500	51°14'N; 19°09'E	Majecka et al. (2022)
Modlna 5	13	51°58'N; 19°23'E	Klatkova and Balwierz (1990)
Zgierz Rudunki II	247	51°52'N; 19°26'E	Jastrzębska-Mamełka (1985)
Besiekierz 1/88	219	51°57'N; 19°27'E	Janczyk-Kopikowa, 1991
Struga g-120	506	52°09'N; 20°20'E	Zalat et al. (2021); Bober et al. (2023)
Struga WH-15	505	52°09'N; 20°20'E	Bober et al. (2018)
Żyrdów 2/69	62	52°03'N; 20°26'E	Krupiński (1978)
Warszawa- Wawrzyszew XV	60	52°17'N; 20°56'E	Krupiński and Morawski (1993)
Warszawa Kasprzaka	58	52°13'N; 20°59'E	Krupiński (1988)
Wola Starogrodzka G-122	510	52°00'N; 21°37'E	Kupryjanowicz et al. (2021), 2023
Wola Starogrodzka G-70	509	52°00'N; 21°37'E	Kupryjanowicz et al. (2023)
Wola Starogrodzka WH-122	512	52°00'N; 21°37'E	Kupryjanowicz et al. (2023)
Żabieniec 0	504	51°56'N; 21°38'E	Pidek et al. (2022)
Kletnia Stara	262	51°38'N; 21°41'E	Janczyk-Kopikowa (1987); Żarski (1990)
Kozłów	503	51°59'N; 21°41'E	Suchora et al. (2022)
Porzewnica	299	52°08'N; 21°54'E	Krupiński (1998); Bruj and Krupiński (2006)
Wiśniew	124	52°04'N; 22°17'E	Pidek and Terpilowski (1993)
Dziewule	513	52°02'N; 22°23'E	Bińka and Nitychoruk (2003)
Szwajcaria 1	300	54°08'N; 22°58'E	Borówko-Dłużakowa and Halicki (1957)
Choroszczewo	67	52°33'N; 23°02'E	Kupryjanowicz (2008)
Jałówka	303	53°35'N; 23°14'E	Rychel et al. (2014)
Starowlany	507	53°30'N; 23°23'E	Kupryjanowicz (2008)
Ludomirowo	157	53°32'N; 23°29'E	Bitner (1957)

^a Site/profile identification number in the Eemian isopollen database and in Fig. 2. Numbers above 500 indicate sites added to the database after 2018 (Kupryjanowicz et al. (eds.), 2018).

(Kupryjanowicz et al., 2021, 2023) and two from the Struga site (Zalat et al., 2021; Bober et al., 2018, 2023). A total of 536 spectra were used for estimation. Selected spectra, according to the authors' studies, document the Late Saalian and Eemian Interglacial pollen vegetation, corresponding to E1 and E2 R PAZ in the Polish palynostratigraphy (Mamakowa, 1989; Kupryjanowicz et al. (eds.), 2018). Spectra related to the Late Saalian were analysed to identify the main vegetation pattern in the Late Saalian; early Eemian Interglacial spectra were analysed to capture the Saalian/Eemian vegetation shift.

The criteria for including sites in the estimation were.

- at least spectra sequences cover the Late Saalian and maintain continuity until the beginning of the Eemian Interglacial corresponding to E1-E2 R PAZ;
- geographical locations range from west to east (to capture the geographic gradient of palaeoenvironmental features).

2.2. Taxa

Vegetation was characterised in terms of taxa identified through pollen analysis in the spectra from the analysed tables. Numerical analyses were performed for the selected taxa sets, but not for all taxa contained in the tables. Sets were selected by choosing taxa that have been qualitatively recognised as climatic indicators with significant value in ecological interpretations. The ecological characteristics of the analysed taxa are presented in detail according to Ralska-Jasiewiczowa et al. (eds.), (2004) and Kupryjanowicz et al. (eds.), (2018). The 24 taxa we selected for analysis were those that best represent habitats in cold climatic conditions: *Pinus* undiff., *Betula* undiff., *Picea abies* t., *Abies alba*, *Juniperus*, *Hippophaë rhamnoides*, *Salix* undiff., *Betula nana*, *Artemisia*, *Poaceae* undiff., *Cyperaceae*, *Chenopodiaceae*, *Ephedra*, *Ericaceae*, *Helianthemum* undiff., *Selaginella selaginoides* and Indeterminate undiff. *Chenopodiaceae* is no longer recognised as a separate family but is currently treated as the subfamily *Chenopodioideae* within *Amaranthaceae* (Chase et al., 2016). However, as the present study draws upon archival sources and cites records dating from a period when *Chenopodiaceae* was recognised as a distinct family, the historical family-level classification is retained in accordance with the original sources. Most of the selected taxa correspond to glacial plants distributed during the early Lateglacial in the northern Alpine foreland (Lang et al. (eds.), 2023). Indeterminate undiff. comprises pollen grains that could not be assigned to a specific taxon due to, for example, poor preservation, damage, deformation, or insufficient diagnostic features. We consider it possible that this category in the original source data may also include reworked (rebedded) pollen, including pollen of Neogene taxa. Such pollen may provide valuable information on the nature and dynamics of geomorphological processes under cold climatic conditions. Thermophilous tree taxa characteristic of interglacial periods were considered separately: *Alnus* undiff., *Carpinus*, *Corylus avellana*, *Fraxinus*, *Quercus*, *Tilia cordata* t., and *Ulmus*. Some of these taxa occurred frequently in the pollen spectra, whereas others were sparsely represented and recorded at only a few sites. To illustrate the variation in the percentage contribution of individual taxa, the mean percentage values for individual sites were grouped into ranges (Table 2).

3. Methods: detrended correspondence analysis (DCA)

Following Hill and Gauch (1980), detrended correspondence analysis (DCA) was used to examine vegetation data with the aim of visualising relationships among species and among sites. A data matrix was compiled that comprised the percentage shares of pollen grains and spores representing selected terrestrial plant taxa. The data represented many sequences of pollen spectra selected stratigraphically to span the Late Saalian, the Eemian, and the transition between the two. The data matrix was then analysed using R (v. 4.2.2., “vegan” package, “decorana” function).

Table 2

Ranges of mean percentage value of taxa (abbreviations used in the scatterplots) in the studied sites/profiles: +: 0.1–3%; ++: 3–30%; +++: >30%. Taxa used in the second set of taxa (cryophilous taxa only) are marked in grey.

* Site/profile identification number in the Eemian isopollen database and on Fig. 2. Numbers above 500 indicate sites added to the database after Kupryjanowicz et al. (eds.) (2018)

** Chenopodiaceae is currently treated as the subfamily Chenopodioideae within Amaranthaceae (Chase et al., 2016). In this study historical family-level classification is retained in accordance with the original sources.

No izo*	T	r	e	e	s	a	n	d	s	h	r	u	b	s	H	e	r	b	s					
	<i>Pinus</i> undiff. (Pi)	<i>Betula</i> undiff. (Be)	<i>Picea abies</i> t. (Pic)	<i>Abies alba</i> (Ab)	<i>Ulmus</i> (Ul)	<i>Fraxinus</i> (Fra)	<i>Quercus</i> (Qu)	<i>Tilia cordata</i> t. (Ti)	<i>Corylus avellana</i> (Cor)	<i>Carpinus</i> (Car)	<i>Alnus</i> undiff. (Al)	<i>Juniperus</i> (Ju)	<i>Hippophae rhamnoides</i> (Hip)	<i>Salix</i> undiff. (Sal)	<i>Betula nana</i> (B n)	<i>Ephedra</i> (Eph)	<i>Ericaceae</i> undiff. (Er)	<i>Artemisia</i> (Ar)	<i>Poaceae</i> undiff. (Po)	<i>Cyperaceae</i> undiff. (Cyp)	<i>Chenopodiaceae</i> (Che)**	<i>Helianthemum</i> undiff. (Hel)	<i>Selaginella selaginoides</i> (Sel)	Indeterminate undiff. (Undet)
288	+++	+++																						
180	+++	++	+	+	+	+	+	+		+	+		+	+		+	+	++	++	++	+	+	+	+
301	+++	+++	+	+	+	+	+	+			+		+	+		+	+	++	++	++	+	+	+	+
211	++	++	++	+	+	+					++	+	+	+		+	+	++	++	++	+	+	+	+
284	+++	+++	+	+	+	+		+				+				+		+	+	+	+			+
237	+++	++	++		+	+		+			+							++	++	+				
16	+++	++	++	+	+	+		+			++	+				+		++	++	++	+	+		
500	+++	+++	+	+	+	+					+		+			+		++	++	++	+			++
13	+++	++	++	+	+	+	+		+		++	+		+		+		++	++	++	+	+	+	++
247	+++	++	++	+	+	+		+			+	++	++	+		+		++	++	++	+	+	+	++
219	+++	++	+	+	+	+						+		+		+	+	++	++	++	+	+	+	+
506	+++	++	+	+	+	+		+				+				+		++	++	+	+	+	+	+
505	+++	+++	+	+	+	+	+		+		+	+		+	+	+		++	++	++	+	+	+	+
62	+++	++	+	+	+	+					+	+		+		+		++	++	++	+	+	+	+
60	+++	++	++	+	+	+	+	+		+	+	+		++		+		++	++	++	+	+	+	++
58	+++	++	++	+	+	+	+	+	+		+	+		+		+		++	++	++	+	+	+	+
510	+++	++	+	++	+	+	+	+	+	+	+	+	+	+		+		++	++	++	+	+	+	+
509	+++	++	++	+	+	+	+	+			+	+		+	+	+		++	++	++	+	+	+	+
512	+++	+++	+	+	++	+	+	+	+	++	+	+	+		+	+		++	++	++	+	+	+	+
504	+++	+++	++	+	+	+		+	+		+	+		+	+			++	++	++	+		+	+
262	+++	++	++	+	+	+	+	+			+	+		+		+	+	++	++	++	+			+
503	++	++	++	+	++	+	+	+	+	++	+	+	+	+				++	++	++	+	+	+	+
299	+++	++	++	+	+	+		+			+	+				+		++	++	++	+			+
124	+++	++	++	+	++	+		+	+		+	+				+		++	++	++	+	+	+	+
513	+++	++		+								++				+	+	++	++	++	+	+	+	+
300	++	++	++	+	+	+	+	+	+	+	+	+				++		++	++	++	+			+
67	+++	++	+	++	+	+					+	+		+		+		++	++	++	+	+	+	+
303	+++	++	+	++		+					+	+				+		++	++	++	+	+	+	+
507	+++	++	+	+	+	+			+		+	+	+		+			++	++	++	+	+	+	+
157	+++	++	+	+	+	+								+		+		++	++	++	+	+	+	++

Detrended correspondence analysis facilitates the visual representation of complex phenomena by reducing the dimensionality of multi-dimensional data. This process, called “ordination” involves identifying (as a rule) the two-dimensional representation that groups similar spectra and most clearly distinguishes spectra that differ in composition. Each spectrum is then assigned a value along each of these new dimensions identified as the two best, allowing the various spectra to be plotted on a two-dimensional scatterplot. The spectra representing each period of particular climatic conditions will typically appear in its own rough grouping on the scatterplot, revealing progressive changes in assemblage structures that correlate with changes in environmental factors over time. In this case, the environmental factors are climate warming and cooling, which are reflected in changes in the shares of thermophilous and cryophilous taxa. All data values (percentages of pollen) were square-root (SQRT) transformed prior to DCA. This transformation reduces the over-influence of highly represented taxa (*Pinus* undiff., *Betula* undiff., etc.). Were a particular spectrum to contain 64% *Pinus* undiff. and 1% *Hippophae rhamnoides*, taking the square root would leave us comparing 8 with 1 (which are no longer percentages, but this is inconsequential). This “flattening” prevents the analysis from being overly sensitive to changes in the small number of taxa that are proportionally most abundant in a given profile.

One DCA ordination was performed for cryophilous and thermophilous taxa together, and another for cryophilous taxa only (see: Materials chapter). The purpose of selecting the first taxa set (cryophilous and thermophilous taxa) was to distinguish plant communities in the transition zone from glacial to interglacial shift and to determine the

moment of onset of Eemian Interglacial vegetation as well. This was intended to indirectly confirm the correctness of the palynostratigraphic divisions of the spectra at the analysed sites, which were based on ecological knowledge (Figs. 3 and 5A).

The DCA using only cryophilic taxa was intended to demonstrate the relationships and characteristics of vegetation variability within the Late Saalian. The results are presented in scatter diagrams and DCA correlation loadings (Figs. 4 and 5B). In Fig. 5, the blue line shows the spectral sequence – a stratigraphically ordered sequence of consecutive pollen spectra, and the red arrow shows its stratigraphic direction.

The colours used on the scatter diagrams are intended to highlight the diversity in the geographic location of the sites. Each spectrum is assigned (according to source interpretation based on ecological knowledge) one of three symbols ordering it to the Late Saalian (+symbol), the first spectrum from the Eemian Interglacial (o symbol) and subsequent spectra for the beginning of the Eemian Interglacial (-symbol) (Figs. 3–5). The colours of the spectra symbols in the scatter diagram are consistent with those used for individual sites in Fig. 2.

4. Results

4.1. DCA: taxa set 1: cryophilous and thermophilous taxa

The first principal component DCA1 explains 22% of the data variance. The results of the DCA analysis on the examined taxa set show two primary groups of distinct taxa (Fig. 3). The group of taxa characterised by negative DCA1 values comprises principally the herbaceous plants

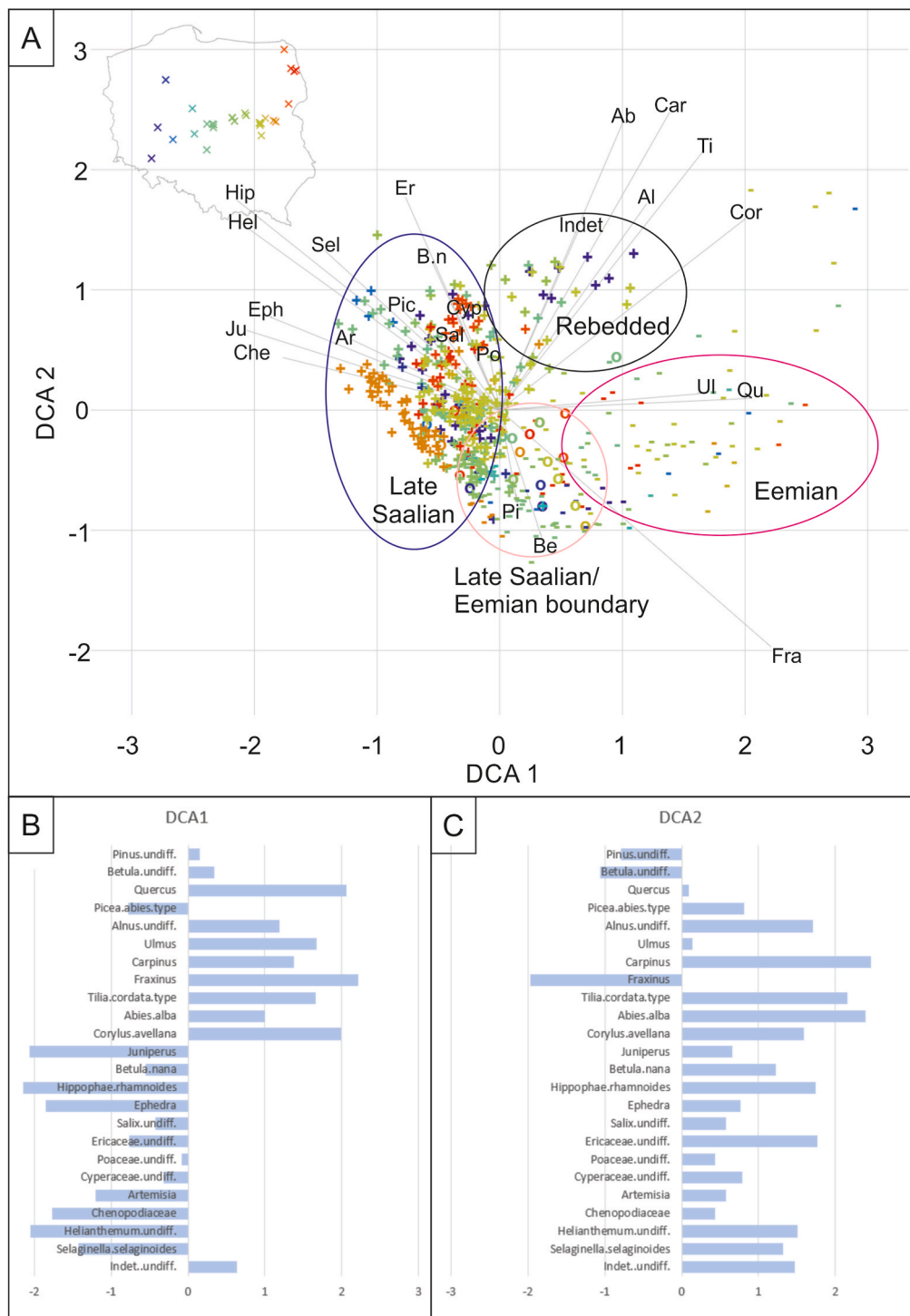


Fig. 3. Detrended correspondence analysis (DCA) from the first taxa set (cryophilous and thermophilous taxa). Analysis was performed using R software (v4.2.2; [R Core Team, 2022](#)). DCA1 explains 22% of the data variance and DCA2 - 13%. Interpreted DCA groups are shown (see text for explanation).

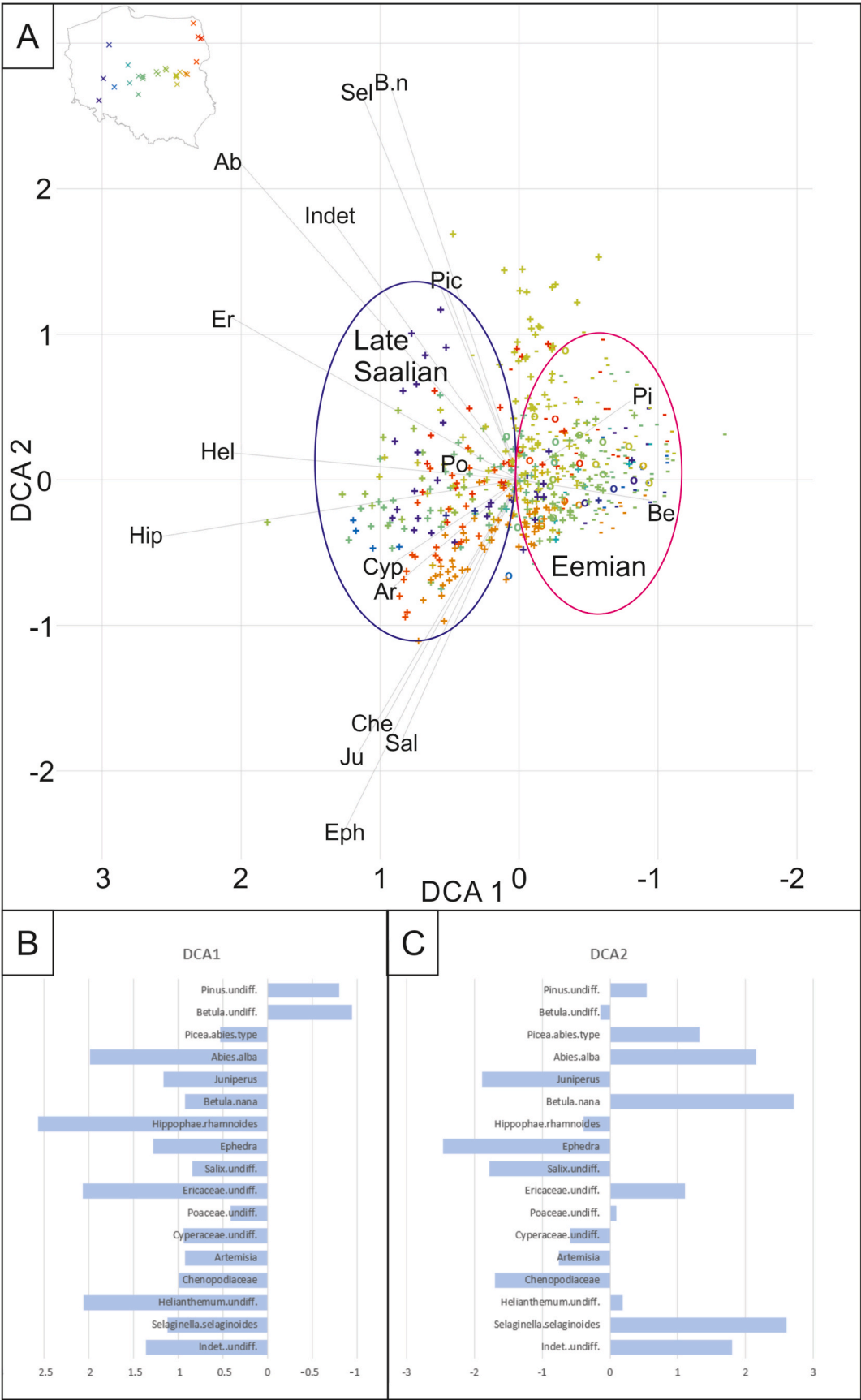
A: scatterplot;

+: point symbol of the spectrum classified as Late Saalian; o: point symbol of the first Eemian Interglacial spectrum; -: point symbol of the spectrum classified as Eemian Interglacial. Individual spectra were classified into palynostratigraphic units according to the authors, respectively (see [Table 1](#)). Individual spectra in the Imbramowice profile were classified according to [Majecka et al. \(2026\)](#).

Spectrum symbols on the scatterplot are shown in colours consistent with those used for individual sites in [Fig. 2](#).

Abbreviations of taxon names: Pi - *Pinus* undiff., Be - *Betula* undiff., Pic - *Picea abies* t., Ab - *Abies alba*, Ul - *Ulmus*, Fra - *Fraxinus*, Qu - *Quercus*, Ti - *Tilia cordata* t., Cor - *Corylus avellana*, Car - *Carpinus*, Al - *Alnus* undiff., Ju - *Juniperus*, Hip - *Hippophae rhamnoides*, Sal - *Salix* undiff., B.n - *Betula nana*, Eph - *Ephedra*, Er - *Ericaceae* undiff., Ar - *Artemisia*, Po - *Poaceae* undiff., Cyp - *Cyperaceae* undiff., Che - *Chenopodiaceae*, Hel - *Helianthemum* undiff., Sel - *Selaginella selaginoides*, Indet - Indeterminate undiff.

B, C: DCA correlation loadings (to component 1 and 2). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)



(caption on next page)

Fig. 4. Detrended correspondence analysis (DCA) from the second set taxa (cryophilous taxa only). Analysis performed in R software (R Core Team, 2022). DCA1 explains 19% of the data variance and DCA2 – 13%. Interpreted DCA groups are shown (see text for explanation).

A: scatterplot;

+: point symbol of the spectra classified as Late Saalian; o: point symbol of the first Eemian Interglacial spectrum; -: point symbol of the spectra classified as Eemian Interglacial. Individual spectra were classified into palynostratigraphic units according to the authors, respectively (see references in Table 1). Individual spectra in the Imbramowice profile were classified according to Majecka et al. (2026).

Spectrum symbols on the scatterplot are shown in colours consistent with those used for individual sites in Fig. 2.

B, C: DCA correlation loadings (to component 1 and 2).

Abbreviations of taxon names: Pi - *Pinus* undiff., Be - *Betula* undiff., Pic - *Picea abies* t., Ab - *Abies alba*, Ju - *Juniperus*, Hip - *Hippophaë rhamnoides*, Sal - *Salix* undiff., B.n - *Betula nana*, Eph - *Ephedra*, Er - *Ericaceae* undiff., Ar - *Artemisia*, Po - *Poaceae* undiff., Cyp - *Cyperaceae* undiff., Che - *Chenopodiaceae*, Hel - *Helianthemum* undiff., Sel - *Selaginella selaginoides*, Indet - Indeterminate undiff. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Artemisia, *Chenopodiaceae*, *Helianthemum* undiff., *Selaginella selaginoides* (DCA1 < -1, down to ≈ -2); but also the shrubs *Hippophaë rhamnoides*, *Juniperus* (DCA1 < -2), *Ephedra* (DCA1 < -1); and the tree *Picea abies* t. is characterised by negative DCA1 value (DCA1 < -1). The second group of taxa exhibits significantly positive DCA1 values and contains the tree taxa *Fraxinus*, *Quercus*, *Corylus avellana* (DCA1 ≥ 2), *Ulmus*, *Tilia cordata* t., *Carpinus*, *Alnus* undiff., *Abies alba* (DCA1 ≥ 1). These more thermophilic taxa are typical of deciduous and mixed forest communities. Some taxa are obviously irrelevant to DCA1 – namely, *Ericaceae* undiff., *Betula nana*, *Salix* undiff., *Cyperaceae* undiff., *Poaceae*, undiff., *Pinus* undiff., *Betula* undiff and Indeterminate undiff. This group of taxa accounts for the least variance in the spectra. DCA2 explains 13% of the variance and predominantly comprises taxa with a positive DCA value, with only three taxa exhibiting negative values. The taxa with significantly positive DCA2 values comprise the trees *Carpinus*, *Abies alba*, *Tilia cordata* t. (DCA2 ≥ 2), *Alnus* undiff.; the shrubs *Ericaceae* undiff., *Hippophaë rhamnoides* (DCA2 ≥ 1); the herbaceous plants *Helianthemum* undiff. (DCA2 ≥ 1); and the spore plants *Selaginella selaginoides*, as well as Indeterminate undiff. (DCA2 ≥ 1). Only *Fraxinus* (DCA2 ≈ -2), *Betula* undiff., *Pinus* undiff. (DCA2 ≤ -1) exhibit negative DCA2 values.

4.2. DCA: taxa set 2: cryophilous taxa only

DCA1 explains 19% of the variance and predominantly comprises taxa with positive DCA values (Fig. 4). Those taxa with significantly positive DCA2 values are *Hippophaë rhamnoides* (DCA1 > 2.5), *Ericaceae* undiff., *Helianthemum* undiff. (DCA1 > 2), *Abies alba* (DCA1 ≈ 2), *Ephedra*, Indeterminate undiff., *Juniperus*, *Selaginella selaginoides*, *Chenopodiaceae* (DCA1 > 1). The taxa *Pinus* undiff. and *Betula* undiff. exhibit negative DCA1 values. DCA2 explains 13% of the variance and comprises two groups of taxa. The group exhibiting negative DCA2 values comprises *Ephedra* (DCA2 < -2), *Juniperus*, *Salix* undiff., *Chenopodiaceae* (DCA2 < -1) and accounts for most of the variability. The group with significantly positive DCA2 values contains *Betula nana*, *Selaginella selaginoides*, *Abies alba* (DCA2 > 2), Indeterminate undiff., *Picea abies* t., and *Ericaceae* undiff.

5. Vegetation differentiation inferred from DCA analysis

Detrended correlation analysis revealed that spectra concentrate around taxon groups. Four groups of spectra were distinguished based on differences in vegetation characteristics, enabling a palaeoclimatic interpretation; this differentiation is reflected in the DCA results for the first set of taxa (cryophilous and thermophilous taxa), which show a higher degree of variation between the spectra groups (Fig. 3). The DCA results were less clear for the second set of taxa (cryophilous taxa only): this was the analysis that was designed to demonstrate the concentration of spectra in relation to the variability of taxa associated with cold climatic conditions (Fig. 4). Nevertheless, regardless of the DCA results, the analysis for both taxa groups confirmed the appropriateness of marking the spectra with the symbols applied (i.e., +: Late Saalian spectra; o: first spectrum of the Eemian Interglacial; -: younger spectra of the Eemian Interglacial). The concentration of spectra identified around specific

taxon groups confirms the high accuracy of the palynostratigraphic divisions at the study sites, which are based largely on classical ecological knowledge (sometimes supported by CONISS analysis).

5.1. Late Saalian vegetation

The spectra indicated as Late Saalian (+ point signature on Fig. 3 – taxa set 1) are mostly grouped in the scatterplot zone that represents a mosaic pattern of open-landscape steppe-tundra and open-landscape tundra communities, i.e.: *Poaceae* undiff., *Cyperaceae* undiff., *Artemisia*, *Chenopodiaceae*, *Helianthemum* undiff., *Salix* undiff., *Juniperus*, *Ephedra*, *Hippophaë rhamnoides*, *Ericaceae* undiff., *Betula nana*, *Selaginella selaginoides*, Indeterminate undiff. This group also included the tree taxa *Abies alba* and *Picea abies* t. This vegetation complex typifies cool, dry climates (Walter, 1984). The analysis showed the spectra from this period to be similar to each other. Most spectra are dominated by *Poaceae* undiff., *Cyperaceae* undiff., *Helianthemum*, *Artemisia*, indicating a predominance of open habitats, arid and moderately arid conditions, and alkaline, often poor, mineral substrate. Taller thickets occurred in patches on sandy-gravelly shallow soils. They consisted of communities of *Chenopodiaceae*, *Ephedra* and *Juniperus* and may have occurred in more well-drained areas. Places with sunny exposures were overgrown with *Hippophaë rhamnoides*, and areas with fluctuating humidity were overgrown with *Selaginella selaginoides*. Such places may have been lakeshores (Ralska-Jasiewiczowa et al. (eds.), 2004).

5.2. Ecological gradient in the Late Saalian

The flora of sites varies according to geographical location. Sites in the west show a large dispersion of spectra, indicating inhomogeneous plant community structures (Figs. 3–5).

Similarly, central and central-eastern sites are concentrated around the centre of the DCA scatterplot, which indicates they are similar to one another in terms of exhibiting inhomogeneous plant structures. This may indicate a very high patchiness of habitats in this period that depended on local abiotic factors, such as the morphology and physical properties of the substrate and differences in humidity (e.g., due to the proximity or absence of watercourses). The large influence of inter-site differences in local factors is seen in the relatively low percentage of DCA1 (~22–19% for both taxa sets). This indicates that there is no single main environmental gradient.

5.3. The onset of warming

Sites in the western (Imbramowice) and central Polish Lowland (e.g., Modlna 5, Warszawa-Wawrzyszew XV) show a grouping of spectra belonging to the Late Saalian period in the zone of the thermophilous taxa: *Carpinus*, *Abies alba*, *Tilia cordata*, *Alnus* undiff., *Corylus avellana*, and Indeterminate undiff. These often include indeterminate spores, which may have originated from Neogene redeposition. For example, at the Żabieniec Południowy site in central Poland, both Neogene taxa and dinoflagellates were identified, together with thermophilic taxa. (Majecka, 2014). Therefore, in our interpretation, the cluster of taxa

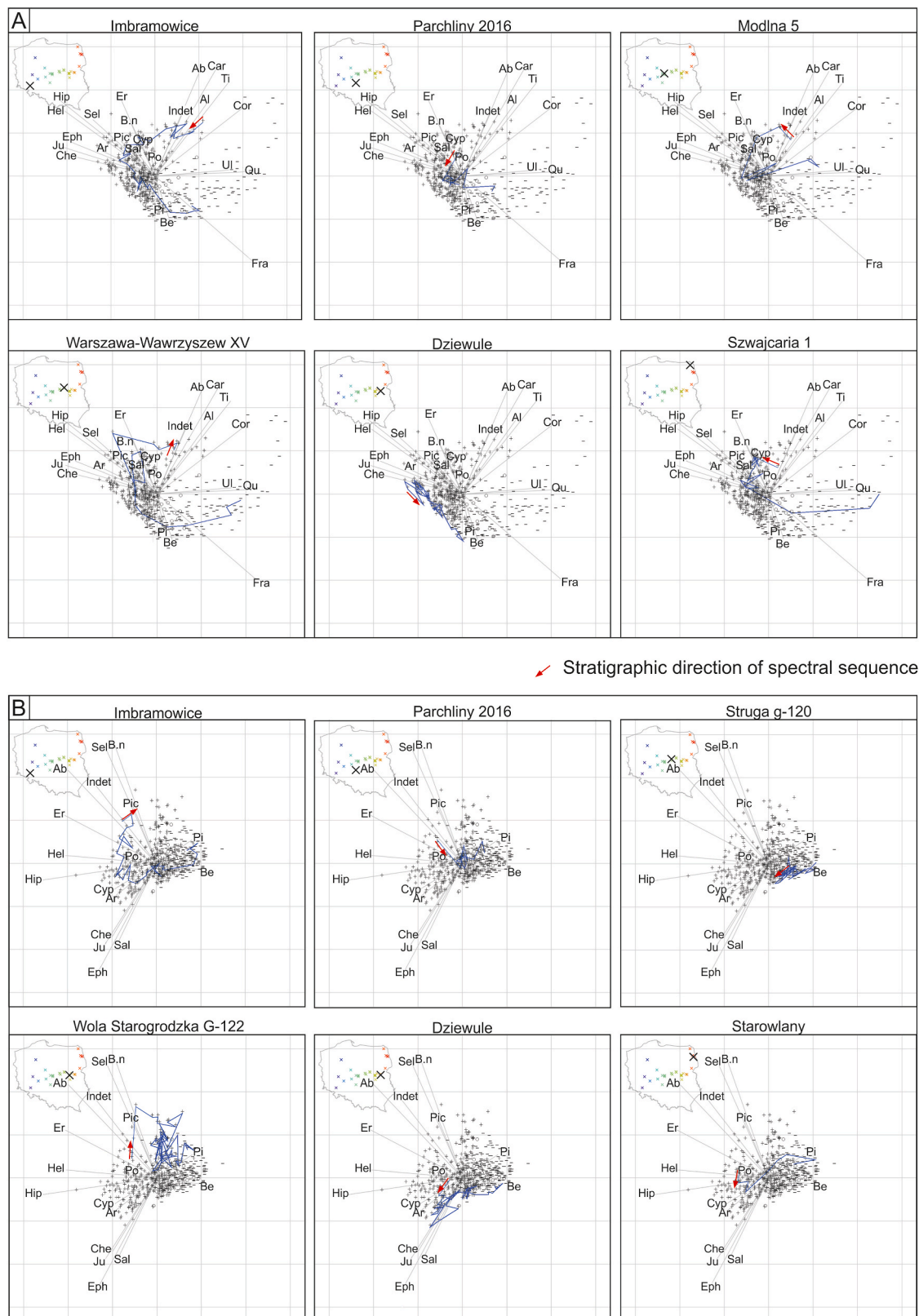


Fig. 5. DCA charts for selected sites separately. A: first taxa set (cryophilous and thermophilous taxa); B: second taxa set (cryophilous taxa only). Abbreviations of taxon names: Pi - *Pinus* undiff., Be - *Betula* undiff., Pic - *Picea abies* t., Ab - *Abies alba*, Ul - *Ulmus*, Fra - *Fraxinus*, Qu - *Quercus*, Ti - *Tilia cordata* t., Cor - *Corylus avellana*, Car - *Carpinus*, Al - *Alnus* undiff., Ju - *Juniperus*, Hip - *Hippophae rhamnoides*, Sal - *Salix* undiff., B.n - *Betula nana*, Eph - *Ephedra*, Er - *Ericaceae* undiff., Ar - *Artemisia*, Po - *Poaceae* undiff., Cyp - *Cyperaceae* undiff., Che - *Chenopodiaceae*, Hel - *Helianthemum* undiff., Sel - *Selaginella selaginoides*, Indet - Indeterminate undiff.

Indeterminate (Indet) as well as thermophilous taxa belongs to a rebedded pollen group (Fig. 3). In sites such as Imbramowice, Parchliny 2016, Warszawa-Wawrzyszew XV, Modlna 5 and Wola Starogrodzka G-122 this clustering reflected initial deposition with the pollen redeposition typical of this period (Fig. 5A). The presence of redeposited pollen indicates a period of dynamic depositional and erosional processes that may have resulted from the thawing of surficial permafrost (the active layer) due to warming and increased environmental humidity (French, 2007). The lakes of the lowest parts of the catchment were filled with mineral or mineral-organic sediments (Majecka et al., 2026). This initial pollen record with a high percentage of redeposited pollen does not reflect the vegetation of this period. Fluctuations in active layer thickness depending on substrate properties (permeability, slope) increased or lessened meltwater saturation capacity. Depending on the morphological position of sedimentation basins and the season, pollen could have been supplied to lakes by being washed from the catchment area (during periods of seasonal warming) or by long-distance transport (during periods of seasonal cooling). The *in-situ* vegetation may have consisted of hydrophilous plants from the Cyperaceae family and, in more stable soil, Poaceae (Matuszkiewicz, 2006). At some sites, the oldest spectra (in Wola Starogrodzka G-122 and G-70) may correspond to the zone SS A in the Brokenlande profile distinguished in western Germany (according to Menke and Ross, 1967) and to Stadial 1 (according to Seidenkrantz et al., 1996), as indicated by the high proportion of Poaceae and Cyperaceae, which reflect grass and sedge communities. In our opinion, Stadial 1 should therefore be regarded as the onset of warming, reflected in evidence for the intensification of geomorphological processes under conditions of progressively increasing environmental moisture but no in evidence of the vegetation pattern.

5.4. Cold oscillation at the threshold of the Eemian Interglacial

Traces of redeposition may also reflect younger disturbances in succession resulting from climatic oscillations. The DCA scatterplots (taxa set 1) for individual sites show the specificity of their ecological gradients (Fig. 5A).

For some sites, the spectral sequences suggest that succession changed course just before the beginning of the Eemian Interglacial. Examples include Imbramowice, Parchliny 2016, Modlna 5, Warszawa-Wawrzyszew XV and Wola Starogrodzka G-122. The progression of the spectra only weakly reflects an ecological gradient, suggesting that the transition from glacial to interglacial conditions was not smooth and may have included a brief cold oscillation just before the onset of the interglacial. This is manifested by the grouping of spectra around redeposition-typical taxa, the irregular spectral sequence, and the absence of a single taxon strongly driving variability. In our view, these patterns indicate unstable and variable environmental conditions associated with significant erosional processes, which intensified during the cooling phase. This disturbance can be correlated with the Kattegat Stadial recognised in Western Europe and with SS C in Brokenlande (Menke and Ross, 1967).

The profiles from the eastern Polish Lowland record no clear disturbances, and their courses differ fundamentally from the more westerly profiles (Dziewule, Starowlany, Szajcaria 1). One example of a relatively smooth transition, though recorded within relatively few spectra, is seen in the Starowlany profile. Similarly in other profiles from the north-east of the study area, no oscillatory transition was found, leading us to conclude that the oscillatory nature of the changes diminishes eastwards (Fig. 5A).

5.5. Eemian Interglacial

The concentration of spectra indicated as being from the earliest of the Eemian Interglacial (o point signature in Figs. 3 and 4) show a similarity in their importance in both taxa *Pinus* undiff. and *Betula*

undiff. We interpret this grouping in which birch and pine dominate as a shift in the environmental threshold and the onset of a major gradient of changes in environmental factors that marks the beginning of the interglacial period. Macroremains analyses from the Parchliny 2016 site indicate that birch and pine were present in central Poland during the Late Saalian and, based on their pollen percentage shares, may have formed forest communities (Majecka et al., 2022). However, the DCA results provide a different interpretation, associating the occurrence of birch and pine with the onset of warming at the beginning of the Eemian Interglacial. Therefore, the DCA results do not confirm the presence of established birch and pine forests during the Late Saalian (Figs. 3 and 4).

Climate warming degraded the permafrost, affected the drainage of the substrate and allowed the germination of these pioneer tree species. This in turn accelerated the warming by decreasing albedo. The DCA scatterplots for the Polish Lowland sites (Fig. 5B) show, in some cases, a distinct concentration spectra near birch, indicating a pattern for the onset of the Eemian similar to that observed in Western Europe, for example at the model site of Bispingen (Müller, 1974; Lauterbach et al., 2024). However, the R PAZ E1a *Pinus* subhorizon distinguished in Polish palynostratigraphy deviates from this pattern (Mamakowa, 1989). At the same time, there are also sites where the shift in the environmental threshold is associated with the concentration of spectra near *Pinus*, which is consistent with the palynostratigraphic framework. We suggest that these two pioneer taxa may occur sub-synchronously, entering sites with a temporal lag, while their expansion is likely controlled by local morphology, hydrological conditions, and substrate properties. According to Aalbersberg and Litt (1998) for the protocratic phase of the Eemian Interglacial (time slice Eemian-Quercetum mixtum-Corylus), the minimum mean temperature of January may have ranged from 0 to -2°C (from west to east) and the minimum mean temperature of July may have ranged, likewise, from $+20$ to $+18^{\circ}\text{C}$. A temperature gradient may have run along a SE-NW line, for winter and summer alike.

The analysed Eemian Interglacial spectra (- point signature on Figs. 3 and 4) according to ecological divisions corresponded to E1 and E2 R PAZ (Mamakowa, 1989). They are mostly concentrated away from the centre of the DCA scatterplots, indicating an increase in their difference. They show a bias towards the *Quercus* and *Ulmus* taxa (Fig. 3). *Fraxinus* stands out from the group here, and its DCA1 value of >2 indicates its importance in explaining the variability – this may mean that its importance reflects a strong ecological gradient (a clear change in environmental conditions). *Quercus*, *Fraxinus* and *Ulmus* are, according to Mamakowa (1989), characteristic of the regional pollen assemblage zone E3 designated in Polish palynostratigraphy. It is believed that their abundance reflects the strong influence of an oceanic climate in the beginning of the mesocratic phase of interglacial (Zagwijn, 1996; Mamakowa, 2003). This interpretation is consistent with the climatic reconstruction of Klotz et al. (2003), who estimated that mean summer temperatures at the beginning of the mesocratic phase of the Eemian were approximately 2°C higher than those of the present day (“present day” used according to Klotz et al., 2003). Similar vegetation and climatic patterns have been recorded in the Fürmoos (Müller et al., 2003), Samerberg (Grüger, 1989), and Jammertal (Müller, 2000; Müller et al., 2005) profiles in southwestern Germany.

6. Landscape reconstruction in the Late Saalian and early Eemian Interglacial

The use of DCA analysis and knowledge of plant ecology allowed us to capture the relationship between the distribution of plant communities and an ecological gradient. An ecological gradient is a continuous change in one or more environmental factors over space (or time) that causes gradual changes in species composition and structure and in the ecosystem functioning (Odum and Barrett, 2007). During the Late Saalian, the determinants of differences in vegetation certainly included climate (i.e., changes in temperature and precipitation) and the resulting humidity of habitats, the type of sediment composing the substrate, and

light exposure (shading of the habitat). These factors together shaped the spatial and temporal variability of plant communities, accounting for the observed variability of the palynological record.

Tundra landscape exhibits a mosaic pattern structure of vegetation that results from environmental heterogeneity. This heterogeneity is caused by the presence of permafrost and the ability of plants to form dense carpets or scattered cushions (Matveyeva, 1988). The Quaternary geology of glacialic areas of the Polish Lowland exhibits high patchiness of sediments and substrate morphology resulting from short-term, variable and overlapping processes of erosion and deposition in glacial and fluvioglacial environments, all of which act spatially unevenly. Glacial landscapes are represented by moraine landforms, while fluvioglacial environments are associated with outwash plain surfaces. Limmoglacial settings, in turn, are reflected by depressions, often forming the floors of closed basins. This heterogeneous surface affects the distribution of vegetation. Consequently, the vegetation image obtained through pollen analysis attests to considerable differences of plant habitats within small distances. This is especially the case under unstable climatic conditions in communities of low species diversity (Pianka, 1981). Thus, information on regional-level climate characteristics can only be obtained through analysis of data from multiple locales.

Information on the plant communities distinguished in the DCA analysis and knowledge of plant ecology were used to propose a model of vegetation distribution in habitats typical of the Late Saalian and early Eemian (Fig. 6). This model illustrates the relationship between

community distributions and the ecological gradient (ecological factors). We believe that the lack of vegetation specificity in the Late Saalian is confirmed by the low percentage of variability explained by the principal components (DCA1, DCA2). Taking the SQRT of each species percentage share before performing DCA analysis reduced potential for the analysis to be overly influenced by a small number of highly abundant taxa, but brings it closer to representing the ecological truth. In the Late Saalian, another major factor differentiating vegetation was the clear geographical gradient reflecting an eastwards increase in climatic continentalism and decrease in influence of the Atlantic Ocean.

The presented model does not constitute a complete representation of the actual plant communities of the lateglacial; rather, it is based on taxa purposely selected for their qualitative importance. The occurrence of permafrost in central Poland were illustrated after Klatkova (1996) as generally representative for the Polish Lowlands.

The vegetation pattern reconstructed in this study was compared with the high-resolution marine and terrestrial records from the MD01-2444 sequence (Margari et al., 2010; Tzedakis et al., 2018) and the global benthic $\delta^{18}\text{O}$ stack LR04 (Lisiecki and Raymo, 2005). The reconstructed succession pattern shows a high degree of agreement with the vegetation and climate changes associated with the MIS 6–MIS 5e transition, while also revealing regional features characteristic of the Polish Lowland. All three records document a transition from the open steppe-tundra vegetation of late MIS 6, through an unstable deglacial phase, to the rapid expansion of pioneer woodland followed by temperate deciduous forests during MIS 5e. At the same time, the Polish

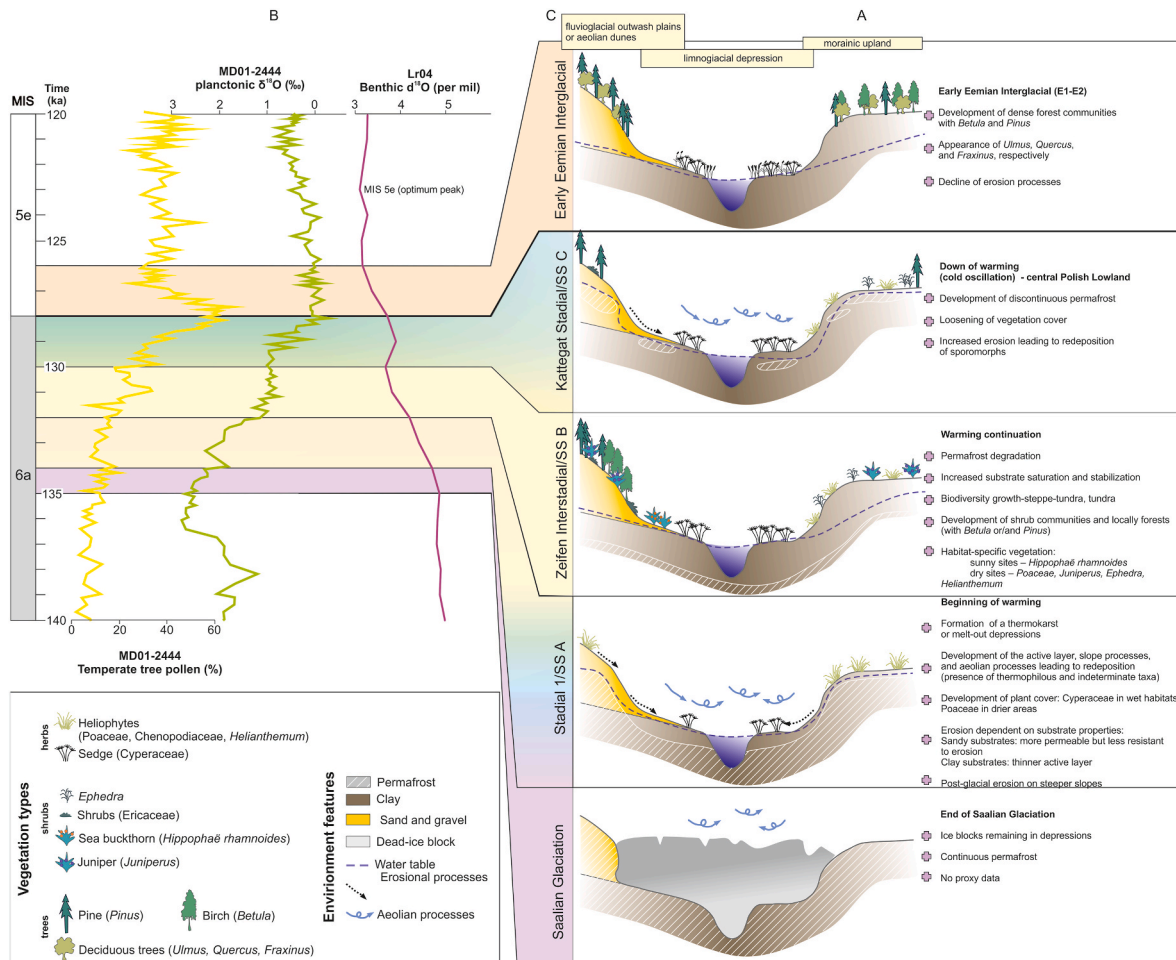


Fig. 6. A: Schematic model of vegetation distribution in habitats typical of the Late Saalian and early Eemian Interglacial; B: MD01-2444 sequence (Margari et al., 2010; Tzedakis et al., 2018) and the global benthic $\delta^{18}\text{O}$ stack LR04 (Lisiecki and Raymo, 2005); C: Climatic subdivision according to western Europe/Brokenlande (Menke and Ross, 1967; Seidenkrantz et al., 1996).

Lowland record provides additional evidence of regional characteristics of the pollen record, particularly the extensive redeposition of pollen resulting from periglacial processes during the initial phase of deglaciation. Furthermore, the short cooling oscillation, interpreted as the equivalent of the Kattegat Stadial, is clearly expressed in the local pollen records. It is more consistently reflected in the high-resolution MD01-2444 sequence than in the globally averaged and temporally smoothed LR04 benthic isotope stack.

7. Conclusions

The objective DCA analysis carried out allowed us to achieve the aims and to determine the vegetation pattern in the Late Saalian and the vegetation shift at the Saalian/Eemian transition.

- DCA analysis showed that the beginning of the warming process is recorded as pioneer vegetation representing Poaceae and Cyperaceae, but also in evidence of the redeposition of pollen of more thermophilous taxa. Redeposition may have been due to highly dynamic erosion processes in the active permafrost layer and perhaps to long-distance transport. This record not only reflects the vegetation growing in that period but is initial evidence of a successive warming.
- Further warming corresponding to the distinguished Zeifen Interstadial is expressed in the pollen record with a predominance of taxa from steppe-tundra and tundra communities, with a dominance of the heliophilous Poaceae, Cyperaceae, *Artemisia* and taxa indicating the occurrence of island shrub habitats, *Hippophaë rhamnoides* in sunny places, and *Juniperus* and *Ephedra* in higher, more well-drained locations. The DCA analysis did not indicate the presence of patchy forest communities of birch and pine during Late Saalian.
- A cool climate oscillation corresponding to the Kattegat Stadial was recorded at some of the sites in the central Polish Lowland. It manifests as the grouping of spectra around redeposition-typical taxa, the irregularity of the spectral sequence, and the domination of some taxa affecting variability, which combine to indicate unstable and variable environmental conditions associated with significant erosional processes, which would have intensified during the cooling phase.
- The early Eemian Interglacial was clearly recorded as spectral concentrations featuring *Pinus* and *Betula* assemblages. This indicates the onset of pioneer birch-pine forest succession and, at the same time, sub-synchronous species encroachment, depending on local habitat conditions.

The analysis of data from sites across the entire Polish Lowland allowed us to capture an east–west geographical gradient, i.e. the axis of changes in palaeoenvironmental features from the Late Saalian to early Eemian.

- The location-dependent vegetation diversity reflects the east–west climatic gradient resulting from eastwards decrease in influence of Atlantic circulation and increase in continentality. The eastern part of the Polish Lowland shows no noticeable cold oscillation (corresponding to the Kattegat Stadial). Changes in vegetation indicate successive warming, but the share of light-demanding plants indicates the warming was slow in the east and dynamic in the west.
- The similarity (between the western and central Polish Lowlands) in terms of the inhomogeneous plant structure of pollen spectra indicates a strong patchiness of habitats that depended on local morphology, substrate properties and humidity.
- Spectral sequences (from the central part of the Polish Lowland) showed that the transition from glacial to interglacial conditions was not smooth (a disturbed ecological gradient), which supports the hypothesis that a cold oscillation, correlating with the Kattegat Stadial, occurred just before the interglacial. The profiles from the

north-eastern Polish Lowland exhibited no oscillatory transition, leading us to conclude that the oscillatory nature of the changes diminished eastwards.

Analysis of the ecology of taxa from multiple sites combined with DCA resulted in the delineation of regional vegetation patterns and ecological gradients that are not visible in interpretations of individual pollen profiles. The presented vegetation models, based on qualitatively selected data, enabled the reconstruction of the distribution of communities in typical lateglacial habitats of the Saalian, although they certainly do not fully reflect the real-world mosaic-like pattern of the landscape.

CRediT authorship contribution statement

Aleksandra Majecka: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. Adam Walanus: Data curation, Methodology, Visualization, Formal analysis, Software. Dorota Nalepka: Data curation, Methodology, Resources, Software, Visualization, Writing – review & editing. Magdalena Filoc: Resources. Wojciech Granoszewski: Resources. Anna Hrynowiecka: Resources. Mirosława Kupryjanowicz: Resources. Małgorzata Malkiewicz: Resources. Małgorzata Nita: Resources. Bożena Noryśkiewicz: Resources. Irena Agnieszka Pidek: Resources. Hanna Winter: Resources. Łukasz Bujak: Software.

Declaration of competing interests

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.

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Data availability

All data and/or code is contained within the submission.

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