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Rare and relic plant species in the palynofloras of Allerød-Holocene sediments of the Lviv region in Ukraine: current botanic and palaeofloristic aspects

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Abstract. The successful solution of many aspects of palaeofloristic reconstruction is traditionally based on materials from palynomorphological and palaeopalynological studies. This paper summarizes an analysis of the palynofloral species composition from Allerød–Holocene deposits in 21 sections of the modern Lviv region. The analytical processing and generalization of the obtained palaeofloristic data enabled the identification of pollen and spores from 21 rare plant species in the fossil palynoflora. The species vary in conservation status within the extant flora. Currently, 15 of them occur in the plain part of the Lviv region. The remaining 6 are present only in the high mountains of the Ukrainian Eastern Carpathians.

Key words: Ukraine, Allerød-Holocene, Lviv region, relict species, palynoflora

1. Introduction

Ecological elements and processes in the past, present, and future are interconnected in a spatiotemporal continuum (Maguire *et al.* 2015; Nieto-Lugilde *et al.* 2021). Therefore, palaeobotany, palaeoecology, as well as modern botany, phytochorology, and ecology provide valuable information at different and complementary timescales that can improve predictions of biodiversity responses in the future (Willis *et al*. 2007; Blois *et al*. 2013; Jackson & Blois 2015; Maguire *et al.* 2015; Trondman *et al*. 2015; Wingard *et al*. 2017; Trindade *et al.* 2023).

The developmental patterns of the vegetation cover of the territory currently occupied by the Lviv region, during the Last Glacial Maximum (LGM, 21±2ka cal BP) to the Holocene (11 700 years BP to the present day) (Gibbard *et al*. 2020) are generally similar to the successions that are known for other regions of Central Europe (Wasylikowa *et al.* 1991; Goslar *et al*. 1999; Kalinovych 2000, 2009; Granoszewski 2003; Magri *et al.* 2006; Birks 2008; Kuneš *et al.* 2008; Filbrand-Czaja 2009; Marcysiak 2010; Bezusko *et al.* 2011; Petr & Novak 2014; Wanner et al. 2014; Vočadlová *et al.* 2015; Giesecke *et al*. 2017; Kuneš & Abraham 2017; Kalinovych *et al*. 2018).

The problem of preserving and protecting rare and relict plant species is multifaceted. One way to solve this problem successfully is to analyse complex retrospective and prognostic reconstructions of the distribution of these species in vegetation cover in the past. In Ukraine, the current stage of Upper Pleistocene and Holocene sediment palynological studies is characterized by the palaeofloristic substantiation of the individual history of distribution of some taxa in space and time (Bezusko *et al*. 2011, 2015, 2018, 2019a, 2019b; Bezusko & Tsymbalyuk 2019). Relevant and promising in this context is the use of results from comprehensive palaeofloristic and palynomorphological studies, forming a basis for spatiotemporal

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reconstructions of the distribution of some rare and relict species of the flora of Ukraine (Bezusko *et al*. 2013, 2020; Karpyuk *et al.* 2015; Tsymbalyuk & Bezusko 2017; etc.).

This work aims to summarize the currently available results on the identification of pollen and spores of rare and relict plant species in the palynoflora of Allerød-Holocene sediments in the Lviv region, and to reconstruct the spatial and temporal distribution histories of these taxa.

2. Materials and methods

Spatially, we considered in this study the modern Lviv region of Ukraine. Temporally, we took into account the last climatic rhythm of the Late Glacial (interstadial Allerød, AL; and stadial Late Dryas, DR-3) and the Holocene (Preboreal, PB; Boreal, BO; Atlantic, AT; Subboreal, SB; and Subatlantic, SA).

Using Small Polissia as a case study, we developed the first stratigraphic scheme in Ukraine for dividing Allerød to Late Glacial deposits based on palynological and radiocarbon data. Subsequently, new results from palynological and radiocarbon studies substantiated the division of Allerød-Holocene deposits across the plains of Ukraine (Bezusko *et al*. 2011). The primary stages of this scheme utilized a modified version of the classical Blytt-Sernander system (Khotinsky 1977). Reconstructions were expressed in uncalibrated years: DR-2/AL as 11 700 BP; AL/DR-3 as 11 000 BP; DR-3/PB as 10 300 BP (lower boundary of the Holocene); PB/BO as 9300 BP; BO/AT as 8000 BP; AT/SB as 4600 BP; and SB/SA as 2500 BP (Bezusko *et al.* 2011).

The palaeofloristic data obtained for the species composition of the Allerød-Holocene fossil palynoflora in 21 sections were used to analyse and summarize the participation of pollen and spores of rare and relict plant species (Fig. 1; Table 1).

Fig. 1. Map of palynological sites in the plain of the Lviv region (Western Ukraine), cited in the tables 1-7

Table 1. List of researched palynological sections in the Lviv region

No.	Open-casts/district	Age of sediments	Geographic coordinates	
			N	E
1	Varenzhanka/Sheptytskyi (former Sokalskyi)	BO, AT, SB, SA	50°34′53″	24°10′17″
2	Perespa/Sheptytskyi (former Sokalskyi)	DR-3, PB, BO, AT, SB, SA	50°24′06″	24°26′30″
3	Solokia/Sheptytskyi (former Sokalskyi)	PB, BO, AT, SB, SA	50°22′34″	23°44′15″
4	Kulychkivske/Sheptytskyi (former Sokalskyi)	BO, AT, SB, SA	50°18′19″	24°05′00″
5	Bolotnya/Sheptytskyi (former Sokalskyi)	PB, BO, AT, SB, SA	50°18′29″	23°55′32″
6	Stoyaniv I/Sheptytskyi (former Radekhivskyi)	PB, BO, AT, SB, SA	50°22′47″	24°39′46″
7	Stoyaniv II/Sheptytskyi (former Radekhivskyi)	BO, AT, SB, SA	50°22′47″	24°39′46″
8	Lopatyn/Sheptytskyi (former Radekhivskyi)	DR-3, PB, BO, AT, SB, SA	50°13′04″	24°50′30″
9	Radekhivske/Sheptytskyi (former Radekhivskyi)	PB, BO, AT, SB, SA	50°15′49″	24°45′35″
10	Lisne/Sheptytskyi (former Radekhivskyi)	PB, BO, AT, SB, SA	50°10′02″	24°46′06″
11	Polonychka/Sheptytskyi (Kamyanka-Buzka)	PB, BO, AT, SB, SA	50°08′36″	24°36′29″
12	Doroshiv/Lvivskyi (former Zhovkhivskyi, Nestorivhivskyi)	AL, DR-3, PB, BO, AT, SB, SA	49°56′15″	24°02′19″
13	Mali Pidlisky/Lvivskyi (former Zhovkhivskyi, Nestorivhivskyi)	BO, AT, SB, SA	49°55′15″	24°09′34″
14	Zvenyhorod-Kotsurivske/Lvivskyi (former Pustomytivskyi)	SB, SA	49°43′58″	24°14′49″
15	Rata/Novoyavorivskyi (former Yavorivskyi)	DR-3, PB, BO, AT, SB, SA	49°48′36″	23°05′16″
16	Tsetulya/Novoyavorivskyi (former Yavorivskyi)	SB, SA	49°57′50″	23°27′48″
17	Konyushkiv/Zolochivskyi	BO, AT, SB, SA	50°07′29″	25°02′50″
18	Pecheniya/Zolochivskyi	SB, SA	49°46′39″	24°22′10″
19	Zolochivske/Zolochivskyi	SB, SA	49°50′02″	24°51′20″
20	Well B-46/Zolochivskyi	SA	49°48′14″	24°55′31″
21	Medenychi/Drohobytskyi	SB, SA	49°25′37″	23°44′45″

To identify the Allerød-Holocene fossil palynoflora (spores and pollen grains of higher plants), standard determinants and keys commonly used in palynological analysis were employed (e.g., Erdtman 1952; Grychuk & Monoszon 1971; Kupriyanova & Aleshina 1972; Artyushenko & Romanova 1984; Moore *et al*. 1991; Nalepka & Walanus 2003; de Vernal 2014). Identifications were further supported by modern pollen slides of rare, relict, and endemic plants from the Palynotheca (KW-P) of the National Herbarium of Ukraine (KW) at the M.G. Kholodny Institute of Botany. Additionally, the recent palynomorphological data obtained via light and scanning electron microscopy by Z. M. Tsymbalyuk were utilized (Tsymbalyuk *et al*. 2008, 2018, 2019, 2021; Tsymbalyuk 2012; Tsymbalyuk & Mosyakin 2013; Tsymbalyuk & Bezusko 2017).

Taxa were identified to the lowest possible level. Access to the KW-P collection and the atlas by Artyushenko & Romanova (1984) specifically enabled the identification of Holocene sediment samples to the species level. Nomenclature follows the aforementioned keys and the "List of Vascular Plants of Ukraine" (Mosyakin

& Fedoronchuk 1999), with taxonomic validity verified using POWO (2025) and IPNI (2025).

3. Vegetation dynamics

During the LGM, a significant part of Europe – specifically its central and eastern regions – was dominated by periglacial steppe, desert-steppe, tundra, forest-steppe, and boreal-forest species (Starkel 1977a, 1977b; Novenko *et al*. 2005; Kołaczek 2007, 2011; Bezusko *et al*. 2011, 2018, 2019; Starkel *et al*. 2013; Magyari *et al*. 2014; Kuneš & Abraham 2017; Kobe *et al*. 2019). Large areas were covered with herbaceous vegetation dominated by species of the families Chenopodiaceae, Cyperaceae, Juncaceae, and Asteraceae, particularly in south-eastern Poland and in the bordering Lviv region (Bezusko *et al*. 2011; Starkel *et al.* 2017). A comparison of fossil pollen assemblages from the LGM vegetation of Eastern-Central Europe with surface pollen spectra from southern Siberia showed that this area shares many similarities with the LGM vegetation and is considered its best modern analogue (Magyari *et al*. 2014). Some alpine and arctic-alpine shrubs and subshrubs (e.g., *Alnus*, *Betula nana*-type, *Salix*, *Dryas octopetala*, *Juniperus*) occupied much smaller areas. Forests composed of dominant woody species *Pinus sylvestris*, *Betula pendula/pubescens*, *Larix*, *Pinus cembra*-type, *Pinus mugo*, *Picea abies*, *Hippophaë rhamnoides*, *Salix,* and *Populus*, developed in the region around 13 450 BP mainly in river valleys, on wet north-facing hillsides, replacing an open, steppe landscape (Kołaczek 2007, 2010, 2011; Kołaczek *et al*. 2010; Bezusko *et al*. 2011, 2015; Vočadlová *et al.* 2015; Kobe *et al.* 2019; Schwörer *et al*. 2022).

With the onset of interglacial warming (approximately 11 700 BP), significant changes occurred in plant communities of western Ukraine and south-eastern Poland. Light-loving arctic and alpine elements, as well as the low competitive *Pinus cembra*-type, disappeared from the vegetation cover of the plains. Woody vegetation became dominant. Along with boreal elements, *Pinus sylvestris, Betula*, and *Picea abies*, also broad-leaved components occurred, although they were not widely distributed (Szafer 1930, 1972; Środoń 1972; MacDonald *et al*. 2000; Kornaś & Medwecka-Kornaś 2002; Pokorný 2002; Kuneš *et al*. 2008; Kuneš & Abraham 2017; Kalinovych *et al*. 2018; Gerasimenko *et al.* 2019; Stančikaitė *et al*. 2022).

The first temperate trees detected in the deposits were *Ulmus* and *Corylus* between 11 700 and 10 250 BP. Roughly 1000 years later, they were followed by *Quercus*, *Fraxinus excelsior,* and *Tilia* (Ralska-Jasiewiczowa *et al.* 2004; Starkel *et al.* 2013; Schwörer *et al.* 2022). By the beginning of Starkel's chronozone AT1 (8 400 BP), landscapes dominated by mixed forests of *Ulmus, Quercus, Tilia, Fraxinus*, and *Corylus* were already established across Central and South-East Europe (Kołaczek 2007, 2011; Kołaczek *et al*. 2010; Bezusko *et al*. 2011; Starkel *et al*. 2013). Notably, on the plains of western Ukraine, *Tilia* forests expanded their area between 7 000 and 6 000 BP, preceding the expansion of *Quercus* forests, which occurred between 6 200 and 4 500 BP (Shelag-Sosonko & Gorochova 1972; Bezusko *et al*. 2011).

At the end of the Atlantic period (AT), the south-western lowlands of western Ukraine – much like adjacent territories in south-eastern Poland – showed low pollen values of *Carpinus*. This suggests the species was likely migrating from the south-east at that time (Ralska-Jasiewicz 1964; Gerasimenko 1997; Ralska-Jasiewiczowa *et al*. 2004; Bezusko *et al.* 2011).

At the boundary of AT and the beginning of the Subboreal phase (SB-1, 4 450±80-3 735±60 BP), the cooling climate led to a reduction in broad-leaved and coniferous-broad-leaved forest areas. During the subsequent phase of the Holocene, SB-2, warming contributed to the re-expansion of these forests, particularly involving *Ulmus*, *Tilia*, *Quercus*, *Betula,* and *Alnus*. At approximately the same time, other species entered the region – described by Prof. Starkel (Starkel *et al*. 2013) as "newcomer trees and late-migrants": *Picea*, *Fagus*, *Abies* (Magri *et al*. 2006; Magri 2008; Bezusko *et al.* 2011). The maximum presence of *Fagus* in the forest vegetation of the western Ukrainian plains occurred between 4 100 and 3 200 BP (Bezusko *et al.* 2011).

At the end of SB, a subsequent relative cooling led to a significant increase in boreal elements in the forests, particularly *Picea*. However, compared to the SB-1 phase, the scale of this phenomenon was much smaller.

During the SA phase of the Holocene (the last 2500 years BP), the most moisture-demanding components established themselves within tree communities: *Fagus* and *Abies* in the western part, and *Carpinus* in the eastern part of the region, as well as in Central Europe (Szafer 1972; MacDonald *et al*. 2000; Kalinovych 2000; Tinner & Lotter 2006; Bezusko *et al*. 2011; Ruddiman *et al*. 2016; Kalinovych *et al.* 2018). In that phase (SA), changes in Ukrainian vegetation cover occurred under the influence of both climatic and anthropogenic factors. In the palynological spectra formed during the last 1 000-800 BP, a significant concentration of pollen indicators of human activity is observed (Bezusko *et al*. 2011).

4. Study site

4.1. Vegetation

The presence of various landforms and the significant climatic differentiation in the Lviv region have formed the basis for diverse contemporary vegetation cover and considerable floristic richness. Forest communities (temperate broad-leaved deciduous forests, mixed, and small-leaved boreal remnants) are widespread in the region, whereas other plant communities represented in this region include extrazonal steppe coenoses, oligotrophic and eutrophic swamps, semi-natural post-forest meadows and pastures, as well as agro-phytocoenoses (Kalinovych *et al*. 2018; Seniv 2024).

On the hilly heights of north-western Podillya, where limestone and chalk deposits of the ancient Paratethys are on the surface, edaphic conditions do not contribute to the development of forests. Therefore, grassy xerotic coenoses have existed here since the glacial aridization of the climate (crioxerotic phase of LGM) (after Grychuk 1989) when the periglacial steppe vegetation stretched in a wide strip from the west to east of Europe (Grosset 1971; Kuneš *et al*. 2008, 2015; Magyari *et al*. 2014; Hurka *et al*. 2019). The latter are considered relicts of the Ice Age (Szafer 1923, 1930, 1935; Bezusko *et al*. 2011; Kalinovych *et al*. 2018). On the sandy substrates of Roztochchia and Small Polissia, patches of coniferous taiga with the participation of *Pinus sylvestris* and *Juniperus communis* are widespread; their formation was also caused by phytohistorical and edaphic conditions (Szafer 1935; Bezusko *et al*. 1985; Soroka 2008).

4.2. Flora

The flora of the plain of the Lviv region includes 1725 species of vascular plants (253 of them synanthropic) (Zelenchuk 1991; Malinovsky 2001; Sychak & Kahalo 2010), which form almost one-third of the species composition of the Ukrainian flora (Zaverukha 1985; Mosyakin & Fedoronchuk 1999). Such floristic richness is explained by environmental factors, the diversity of habitats, and the intersection of migration flows from past geological eras and the present in the region. Such circumstances have led to the presence of both common, widespread, and many rare and relict plant species in its flora. Among the 148 rare and relict species of the regional flora, listed in the Red Book of Ukraine (Didukh 2009), 142 taxa occur in the plain part of the Lviv region (Tasenkevich *et al.* 2015).

There is no simple relationship between the conditions of climate or soil and the areas of geographical distribution of relict plant sites, especially in the lowlands, because it must be remembered that "…the geographical image we have today is the result of a long and variable history, reaching back to the diluvial period" (Szafer 1930).

5. Results

The palynoflora species composition of 21 sections of Allerød-Holocene sediments located in the Lviv region of Ukraine was analysed. The palaeofloristic analysis revealed that spores and pollen of 21 species, which are classified in the flora of the region as rare and relict, occurred in the studied sediments. We found that 14 plant species listed in "Rare and Endangered Plant Species of Lviv Region" (Tasenkevich *et al*. 2015) were components of the studied fossil palynofloras. These species vary in conservation status: *Betula humilis* Schrank, *Botrychium lunaria* (L.) Sw., *B. multifidum* (S.G.Gmel.) Rupr. [according to POWO (2025) and IPNI (2025), syn. of *Sceptridium multifidum* (S.G.Gmel.) Nishida ex Tagawa], *Diphasiastrum complanatum* (L.) Holub, *Lycopodiella inundata* (L.) Holub, *Lycopodium annotinum* L., *Pinguicula vulgaris* L., *Scheuchzeria palustris* L., *Utricularia intermedia* Hayne, and *Utricularia minor* L. are classified as Vulnerable; *Diphasiastrum alpinum* (L.) Holub and *Staphylea pinnata* L. are Rare; while *Cystopteris sudetica* A.Braun & Milde and *Huperzia selago* (L.) Bernh. ex Schrank & C. Mart. are Not Evaluated. Seven plant species are listed in the Red Book of Ukraine (Didukh 2009) with the following conservation statuses: *Dryas octopetala* L. is classified as Rare; *Larix decidua* Mill. var. *polonica* (Racib. ex Wóycicki) Ostenf. & Syrach (according to POWO 2025, syn. *Larix polonica* Racib. ex Wóycicki), *Linnaea borealis* L., *Marsilea quadrifolia* L., and *Thalictrum foetidum* L. are Endangered; whereas *Pinus cembra* L. and *Selaginella selaginoides* (L.) P.Beauv. ex Schrank. & Mart. are Vulnerable. For each of these species, their distributions in the study area were reconstructed in both space and time (Table 2).

Table 2. Spatiotemporal differentiation of distribution patterns of some rare and relic species in the Lviv region during the Allerød-Holocene

Taxon name	Palynofloras of Allerød-Holocene sediments							District
	AL	DR-3	PB	BO	AT	SB	SA	
Betula humilis	–	+	+	+	–	–	–	Sheptytskyi
	+	+	+	+	+	+	–	Lvivskyi
	–	+	+	+	–	–	–	Novoyavorivskyi
	–	–	–	+	–	–	–	Zolochivskyi
Linnaea borealis	–	–	+	+	–	+	–	Sheptytskyi
	–	–	–	+	–	+	+	Lvivskyi
	–	–	–	–	+	–	–	Novoyavorivskyi
	–	–	–	+	–	–	+	Zolochivskyi

Larix sp. (*Larix decidua* var. *polonica*)	+	–	–	–	–	–	–	Lvivskyi
Pinus cembra type	–	+	+	–	–	–	–	Sheptytskyi
	+	+	+	+	–	–	–	Lvivskyi
	–	+	+	–	–	–	–	Novoyavorivskyi
Thalictrum foetidum	–	–	–	+	–	+	–	Sheptytskyi
	+	+	–	–	–	+	–	Lvivskyi
	–	–	–	–	–	–	+	Zolochivskyi
Dryas octopetala	–	+	+	+	–	–	–	Sheptytskyi
	+	+	+	+	–	–	–	Lvivskyi
	–	+	–	+	–	–	–	Novoyavorivskyi
	–	–	–	+	–	–	–	Zolochivskyi
Scheuchzeria palustris	–	–	–	–	+	+	–	Lvivskyi
	–	–	–	–	+	+	–	Novoyavorivskyi
	–	–	–	–	+	–	–	Zolochivskyi
Staphylea pinnata	–	–	–	–	+	–	–	Novoyavorivskyi
	–	–	–	–	+	–	+	Zolochivskyi
Pinguicula vulgaris	–	+	+	+	+	–	–	Sheptytskyi
	–	+	+	+	+	+	–	Novoyavorivskyi
Utricularia intermedia	–	+	+	+	+	–	–	Sheptytskyi
	–	+	–	+	–	–	–	Novoyavorivskyi
Utricularia minor	–	+	+	+	+	+	+	Sheptytskyi
	–	–	–	+	–	–	–	Novoyavorivskyi
	–	–	–	–	–	–	+	Zolochivskyi
Diphasiastrum alpinum	–	+	–	–	–	–	–	Sheptytskyi
	+	+	–	+	–	–	–	Lvivskyi
	–	+	–	–	–	–	–	Novoyavorivskyi
Diphasiastrum complanatum	–	+	+	+	+	+	+	Sheptytskyi
	+	+	+	–	+	+	–	Lvivskyi
	–	–	+	+	–	+	–	Novoyavorivskyi
	–	–	–	+	+	+	–	Zolochivskyi
Huperzia selago	–	–	+	+	+	+	+	Sheptytskyi
	+	+	+	–	+	–	+	Lvivskyi
	–	–	–	–	–	+	–	Novoyavorivskyi
	–	–	–	–	+	–	+	Zolochivskyi
Lycopodium annotinum	–	–	+	+	+	+	+	Sheptytskyi
	+	–	–	+	+	+		Lvivskyi
	–	–	–	–	+	–	–	Novoyavorivskyi
	–	–	–	–	+	+	+	Zolochivskyi
	–	–	–	–	–	+	+	Drohobytskyi
Lycopodiella inundata	–	–	+	+	+	+	+	Sheptytskyi
	+	+	–	–	+	+	–	Lvivskyi
	–	–	–	–	–	–	+	Novoyavorivskyi
	–	–	–	–	+	+	+	Zolochivskyi
	–	–	–	–	–	–	+	Drohobytskyi
Botrychium multifidum (*Sceptridium multifidum*)	+	+	–	–	–	–	–	Lvivskyi
Botrychium lunaria	–	–	–	–	+	+	–	Sheptytskyi
	+	+	–	+	–	+	–	Lvivskyi
	–	–	–	–	+	–	–	Novoyavorivskyi
	–	–	–	–	+	+	+	Zolochivskyi
Selaginella selaginoides	–	+	–	–	–	–	–	Sheptytskyi
	+	+	+	–	–	–	–	Lvivskyi
	–	+	–	–	–	–	–	Novoyavorivskyi
Marsilea quadrifolia	–	–	–	–	+	–	–	Sheptytskyi
	–	–	–	–	–	+	+	Lvivskyi
	–	–	–	–	–	+	–	Novoyavorivskyi
	–	–		–	–	+	+	Zolochivskyi
Cystopteris sudetica	–	+	–	–	–	–	–	Lvivskyi
	–	–	+	–	–	–	–	Novoyavorivskyi

6. Discussion

The results summarized in Table 2 indicate that each of the 21 species of rare and relict plants had its particular distributional history during the Allerød-Holocene. The palynological characteristics of deposits in sections located within the modern Lviv region were also examined (Kalinovych 2000, 2009; Andreeva 2010, 2011). Our results indicate that pollen and spores were identified to the genus level in 5 sections of north-western Podillya (Zolochivskyi district): *Botrychium* sp., *Diphasiastrum* sp., *Larix* sp., *Lycopodium* sp., *Marsilea* sp., *Thalictrum* sp., *Utricularia* sp., etc. (Andreeva 2010).

In the collective palynoflora of the Middle Holocene sediments (Atlantic and Subboreal times), pollen grains of *Lonicera caerulea* L. were identified (Andreeva 2011). This species has a conservation status of Rare, and its distribution in Ukraine is limited to Mount Petros (in the Chornohora massif of the Ukrainian Carpathians, 2020 m a.s.l.) (Didukh 2009; Tasenkevich *et al.* 2022). The palynoflora of the Allerød sediments of the Zarichia 2A section (Sambir district) included pollen of *Pinus cembra*-type and *Larix* sp. (Kalinovych 2009). Importantly, in the Late Dryas sediments of the Ozerne-3 section (Sambir district), pollen of *Taxus* sp., *Pinus cembra*-type, and *Larix* sp. was identified (Kalinovych 2000). *Taxus baccata* is a relict species and is listed as Vulnerable in the Red Book of Ukraine (Didukh 2009).

At present, Allerød-Holocene deposits are best studied in the Lviv, Sheptytskyi, and Novoyavorivskyi districts, compared to other areas.

Tables 3-7 summarize the spatiotemporal distribution and present the upper temporal limits for each

Table 3. Spatiotemporal differentiation of the distribution of rare and relic species in the Sheptytskyi district during the Late Dryas-Holocene

Taxon name	Palynofloras of Late Holocene sediments					
	DR-3	PB	BO	AT	SB	SA
Betula humilis	+	+	+	–	–	–
Linnaea borealis	–	+	+	–	+	–
Pinus cembra type	+	+	–	–	–	–
Thalictrum foetidum	–	–	+	–	+	–
Dryas octopetala	+	+	+	–	–	–
Pinguicula vulgaris	+	+	+	+	–	–
Utricularia intermedia	+	+	+	+	–	–
Utricularia minor	+	+	+	+	+	+
Diphasiastrum alpinum	+	–	–	–	–	–
Diphasiastrum complanatum	+	+	+	+	+	+
Huperzia selago	–	+	+	+	+	+
Lycopodium annotinum	–	+	+	+	+	+
Lycopodiella inundata	–	+	+	+	+	+
Botrychium lunaria	–	–	–	+	+	–
Selaginella selaginoides	+	–	–	–	–	–
Marsilea quadrifolia	–	–	–	+	–	–

Table 4. Spatiotemporal differentiation of the distribution of rare and relic species in the Lvivskyi district during the Allerød-Holocene

Taxon name	Palynofloras of the Allerød-Holocene sediments						
	AL	DR-3	PB	BO	AT	SB	SA
Betula humilis	+	+	+	+	+	+	–
Linnaea borealis.	–	–	–	+	–	+	+
Larix sp.	+	–	–	–	–	–	–
Pinus cembra	+	+	+	+	–	–	–
Thalictrum foetidum	+	+	–	–	–	+	–
Dryas octopetala	+	+	+	+	–	–	–
Scheuchzeria palustris	–	–	–	–	+	+	–
Diphasiastrum alpinum	+	+	–	+	–	–	–
Diphasiastrum complanatum	+	+	+	–	+	+	–
Huperzia selago	+	+	+	–	+	–	+
Lycopodium annotinum	+	–	–	+	+	+	
Lycopodiella inundata	+	+	–	–	+	+	–
Botrychium lunaria	+	+	–	+	–	+	–
Selaginella selaginoides	+	+	+	–	–	–	–
Marsilea quadrifolia	–	–	–	–	–	+	+
Cystopteris sudetica	–	–	–	–	–	+	–

Table 5. Spatiotemporal differentiation of the distribution of rare and relic species in the Novoyavorivskyi district during the Late Dryas-Holocene

Taxon name	Palynofloras of the Late Dryas-Holocene sediments					
	DR-3	PB	BO	AT	SB	SA
Betula humilis	–	+	+	–	–	–
Linnaea borealis	–	–	–	+	–	–
Pinus cembra type	–	+	–	–	–	–
Dryas octopetala	–	–	+	–	–	–
Scheuchzeria palustris	–	–	–	+	+	–
Staphylea pinnata	–	–	–	+	–	–
Pinguicula vulgaris	+	+	+	+	+	–
Utricularia intermedia	+	–	+	–	–	–
Utricularia minor	–	–	+	–	–	–
Diphasiastrum complanatum	–	+	+	–	+	–
Huperzia selago	–	–	–	–	+	–
Lycopodium annotinum	–	–	–	+	–	–
Lycopodiella inundata	–	–	–	–	–	+
Botrychium lunaria	–	–	–	+	–	–
Marsilea quadrifolia	–	–	–	–	+	–
Cystopteris sudetica	–	–	–	+	–	–

Table 6. Spatiotemporal differentiation of the distribution of rare and relic species in the Zolochivskyi district during the Holocene

Taxon name	Palynofloras of the Holocene sediments				
	PB	BO	AT	SB	SA
Betula humilis	–	+	–	–	–
Linnaea borealis	–	+	–	–	+
Thalictrum foetidum	–	–	–	–	+
Dryas octopetala	–	+	–	–	–
Scheuchzeria palustris	–	–	+	–	–
Staphylea pinnata	–	–	+	–	+
Utricularia minor	–	–	–	–	+
Diphasiastrum complanatum	–	+	+	+	–
Huperzia selago	–	–	+	–	+
Lycopodium annotinum	–	–	+	+	+
Lycopodiella inundata	–	–	+	+	+
Botrychium lunaria	–	–	+	+	+
Marsilea quadrifolia	–	–	–	+	+

Table 7. Spatiotemporal differentiation of the distribution of rare and relic species in the Drohobytskyi district during the Holocene

Taxon name	Palynofloras of the Holocene sediments				
	PB	BO	AT	SB	SA
Lycopodium annotinum	–	–	–	+	+
Lycopodiella inundata	–	–	–	–	+

species. For example, *Larix* pollen from the Allerød interstadial in the Lvivskyi district represented most probably *Larix decidua* Mill. var. *polonica.* In the Late Dryas, the upper temporal limit of *Selaginella selaginoides* was recorded in the Sheptytskyi district, while in the Lvivskyi district, it persisted into the first half of the Early Holocene (Preboreal). The upper temporal limit for *Dryas octopetala*, *Pinus cembra*-type, and *Diphasiastrum alpinum* is the first half of the Early Holocene (Boreal time).

Of the 21 rare species, whose spores and pollen were discovered in the sediments, most are currently found in the plain part of the area; only *Larix polonica, Pinus cembra, Dryas octopetala, Diphasiastrum alpinum,* and *Selaginella selaginoides* have survived since then in the mountains. *Larix polonica* was mentioned in herbarium collections for Roztochia and in the Eastern Bieszczady Mts in the early 20th century (Szafer 1972; Koporska 1929; Stoyko *et al.* 2004; Soroka 2008), but today survives only in 2 relict localities in the Gorgany massif (Stoyko *et al.* 2004).

Another Pleistocene autochthonous relict species, *Pinus cembra,* had a wider range in Europe during the last glaciation (Caudullo & de Rigo 2016). As temperatures rose, it was displaced by *Picea abies* to higher altitudes in the Alps and Carpathians (Caudullo & de Rigo 2016). *Dryas octopetala, Selaginella selaginoides,* and *Diphasiastrum alpinum* are arctic-alpine species occurring on high-altitude grasslands. As cold-resistant species, they primarily respond to global warming and are on the verge of extinction in the Ukrainian mid-altitude Carpathians (Kobiv 2018; Shiyan 2019; Tasenkevich *et al*. 2022; Walas *et al*. 2023).

7. Conclusions

The species composition of the palynoflora of Allerød-Holocene sediments of 21 open-casts in the Lviv region was analysed. Pollen grains of 21 rare and relict species were identified.

Generalized palaeofloristic materials have established, for the first time, the spatiotemporal differentiation of these species during the Allerød-Holocene in the Lviv region. Upper temporal limits and general regressive distribution trends were established for each species.

Comparative analysis of palaeofloristic and current floristic materials have expanded our understanding of vegetation cover formation in the region.

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References

Andreeva O.O. 2010. Palynological characteristics of the Holocene sediments of Northwestern Podillia. Scientific Bases of Preservation of Biotic Diversity 1(8), 1: 31-52.

Andreeva O.O. 2011. Holocene palynoflora of the northern part of Podillia (Ukraine). In: Problems of Modern Palynology, 2: 3-18. Syktyvkar: IG Komi National Center UrO RAS.

Artyushenko A.T. & Romanova L.S. 1984. Pollen morphology of relict, endemic, and rare species of Ukraine. 48 pp. Naukova Dumka Press, Kyiv.

Bezusko L.G., Karpiuk T.S. & Bezusko A.G. 2015. Paleochorology of *Alnus fruticosa* Rupr., *Betula nana* L., and *Botrychium boreale* Milde in lowland Ukraine in the Late Dryas. Ukr. Bot. J. 72(1): 3-7. https://doi/org/10.15407/ukrbotj72/01/003

Bezusko L.G., Karpiuk T.S., Mosyakin S.L. & Bezusko A.G. 2013. Paleochronological aspects of the distribution of *Taxus baccata* L. in the territory of lowland Ukraine in the optimum of the Riss-Würm interglacial. Ukr. Bot. J. 70(1): 35-41. https://doi/org/10.15407/ukrbotj70/01/035

Bezusko L.G., Klimanov V.A. & Shelag-Sosonko Yu.R. 1988. Climatic conditions of Ukraine in the Late Glacial and Holocene. In: Paleoclimates of the Holocene of the European territory of the USSR: 125-135. IG AN USSR, Moscow.

Bezusko L.G., Mosyakin S.L. & Bezusko A.G. 2011. Patterns and trends of development of the plant cover of Ukraine in the Late Pleistocene and Holocene. 447 pp. Alterpress, Kyiv.

Bezusko L.G., Mosyakin S.L. & Tsymbalyuk Z.M. 2019a. Spatio-temporal differentiation of distribution patterns of *Salicornia perennans*, *Halimione verrucifera*, and *Suaeda* cf. *prostrata* (Chenopodiaceae) in the plain part of Ukraine during the Allerød-Holocene. Journal of Geology, Geography and Geoecology 28(2): 221-229. https://doi:10.15421/111923

Bezusko L.G., Mosyakin S.L., Tsymbalyuk Z.M. & Nitsenko L.M. 2019b. Participation of *Ceratocarpus arenarius* (Chenopodiaceae) in Late Glacial and Holocene floras of the plain part of Ukraine. Ukr. Bot. J. 76(5): 418-426. https://doi/org/10.15407/ukrbotj76/05/418

Bezusko L.G., Mosyakin S.L. & Tsymbalyuk Z.M. 2020. Participation of some rare and relict plant species in the palynoflora of Allerød-Holocene deposits of the Forest Zone of Ukraine. In: Monitoring and protection of biodiversity in Ukraine: Plant Kingdom and Fungi. Ser. "Conservation Biology in Ukraine", 16(1): 90-120. Print Art, Kyiv-Chernivtsi.

Bezusko L.G., Tsymbalyuk Z.M. 2019. Distribution of *Origanum vulgare* (Lamiaceae) in the plain part of Ukraine in the Holocene. Chornomorski Bot. J. 15(2): 124-133. https://doi.org/10.32999/ksu1990-553X/2019-15-2-3

Bezusko L.G., Tsymbalyuk Z.M. & Mosyakin S.L. 2018. Distribution of *Kochia prostrata* (Chenopodiaceae) on the plain part of Ukraine over the Late Dryas-Holocene: paleofloristic and palynomorphological aspects. Visnyk of the Lviv University. Ser. Biol., 77: 39-46. https://doi.org/10.30970/vlubs.2018.77.04

Bezusko L.G., Vodopyan N.S. & Kayutkina T.M. 1985. The main stages of the development of vegetation and water bodies of Male Polissya in the Holocene. Ukr. Bot. J. 42(4): 30-35.

Birks H.H. 2008. The Late-Quaternary history of arctic and alpine plants. Plant Ecology & Diversity 1(2): 135-146. https://doi.org/10.1080/17550870802328652

Blois J.L., Williams J.W., Fitzpatrick M.C., Jackson S.T. & Ferrier S. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. Proc. Natl. Acad. Sci. U.S.A 110(23): 9374-9379. https://doi.org/10.1073/pnas.1220228110

Caudullo G. & de Rigo D. 2016. *Pinus cembra* in Europe: distribution, habitat, usage and threats. In: J. San-Miguel-Ayanz, D. de Rigo, G. Caudullo, T. Houston Durrant & A. Mauri (eds.). European Atlas of Forest Tree Species., pp. 120-121. Publication Office of the European Union, Luxembourg.

Didukh Y.P. (ed.). 2009. Red Book of Ukraine: Plant Kingdom. 912 pp. Globalkonsalting, Kyiv.

Erdtman G. 1952. Pollen morphology and plant taxonomy. Angiosperms. xii + 539 pp. Almqvist & Wiksell, Stockholm. https://doi.org/10.1080/11035895209453507

Filbrand-Czaja A. 2009. Studia nad historią szaty roślinnej i krajobrazu Borów Tucholskich. 131 pp. Wydawnictwo Naukowe Uniwersytetu Mikołaja Kopernika, Toruń.

Gerasimenko N.P. 1977. The natural environment of human habitat in southeastern Ukraine in the Late Ice Age and Holocene (based on the materials of the paleogeographical study of archeological monuments). Archeological Almanac (Donetsk) 6: 3-64.

Gerasimenko N., Ridush B. & Avdeyenko Y. 2019. Late Pleistocene and Holocene environmental changes recorded in deposits of the Bukovynka Cave (the East-Carpathian foreland, Ukraine). Quaternary International 504: 96-107. https://doi.org/10.1016/j.quaint.2018.03.028

Gibbard P.L. & Head M.J. 2020. Chapter 30 – The Quaternary Period. In: F.M. Gradstein, J.G. Ogg, M.D. Schmitz & G.M. Ogg (eds.). Geologic Time Scale 2: 1217-1255. https://doi.org/10.1016/B978-0-12-824360-2.00030-9

Giesecke T., Brewer S., Finsinger W., Leydet M. & Bradshaw R. 2017. Patterns and dynamics of European vegetation change over the last 15,000 years. Journal of Biogeography 44: 1441-1456. https://doi.org/10.1111/jbi.12974

Goslar T., Bałaga K., Arnold M., Tisnerat N., Starnawska E., Kuźniarski M., Chróst L., Walanus A. & Więckowski K. 1999. Climate-related variations in the composition of the Late Glacial and Early Holocene sediments of Lake Perespilno (eastern Poland). Quaternary Science Reviews 18: 899-911. https://doi.org/10.1016/S0277-3791(99)00004-9

Granoszewski W. 2003. Late Pleistocene vegetation history and climatic changes at Horoszki Duże, eastern Poland: a palaeobotanical study. Acta Palaeobotanica – Supplementum 4: 3-95.

Grosset G.E. 1971. The periglacial climate of the Upper Pleistocene, which caused the disappearance of the zone of broad-leaved forests on the territory of Europe, and the age of the relics of this formation // Bull. Moscow issled. prirody. Biol. 76(1): 18-36.

Grychuk V.P. & Monoszon M.Kh. 1971. Determinant of the monolete spores of ferns from the family Polypodiaceae R. Br., growing on the territory of the USSR. 126 pp. Nauka, Moscow.

Grychuk V.P. 1989. The history of the flora and vegetation of the Russian plain in the Pleistocene. 183 pp. Nauka, Moscow.

Hurka H., Friesen N., Bernhard K-G., Neuffer B. & Smirnov S. 2019. The Eurasian steppe belt: status quo, origin and evolutionary history. Turczaninowia 22(3): 5-71. https://doi.org/10.14258/turczaninowia22.3.1

IPNI. 2025. International Plant Names Index. Published on the Internet: https://www.ipni.org. [Retrieved 17 May 2025].

Jackson S.T. & Blois J. 2015. Community ecology in a changing environment: Perspectives from the Quaternary. Proc. Natl. Acad. Sci. U.S.A 112(16): 4915-4921. https://doi.org/10.1073/pnas.1403664111

Kalinovych N.O. 2000. Palynological study on the vegetation cover development of the Upper Dnister Plain in the Holocene. Scientific Bulletin of the Ukrainian State Forestry University 10(3): 69-74.

Kalinovych N. 2009. Vegetation cover of central Precarpathia at the end of the Pleistocene. Studia Biologica 3(2): 123-132. https://doi.org/10.30970/sbi.0302.042

Kalinovych N., Senchyna B. & Tasenkevich L. 2018. Plant cover. In: M. Nazaruk (ed.). Lviv region: natural conditions and resources, pp. 230-258. The Old Lev Publishing House, Lviv.

Karpyuk T.S., Bezusko L.G. & Bezusko A.G. 2015. Palaeochorology of *Selaginella selaginoides* (L.) P. Beauv. ex Mart. et Schrank and *Diphasiastrum alpinum* (L.) Holub in lowland Ukraine in the Late Dryas. Bull. Taras Shevchenko Kyiv National University, Biology 69(1): 16-19.

Khotinsky N.A. 1977. Holocene of Northern Eurasia. 198 pp. Nauka, Moscow.

Kobe F., Bittner M. K., Leipe Ch., Hoelzmann P., Long T., Wagner M., Zibulski R. & Tarasov P.E. 2019. Lateglacial and early Holocene environments and human occupation in Brandenburg, eastern Germany. Geography, Environment, Sustainability 12(2): 132-147. https://doi.org/10.24057/2071-9388-2018-50

Kobiv Yu. 2018. Trends in population size of rare plant species in the alpine habitats of the Ukrainian Carpathians under climate change. Diversity 10(30): 62. https://doi.org/10.3390/d10030062

Kołaczek P. 2007. Late Glacial and Holocene vegetation changes in the western part of Rzeszów foothills (Sandomierz basin) based on the pollen diagram from Krasne near Rzeszów. Acta Palaeobotanica 47(2): 455-467.

Kołaczek P. 2010. The development of Late Glacial and Holocene vegetation and human impact near Grodzisko Nowe in the Lower San Valley (Sandomierz Basin, south-eastern Poland. Acta Palaeobotanica 50(2): 101-117.

Kołaczek P. 2011. 12 millennia of climatic and human-induced vegetation changes in the Łower San valley near Jarosław (SE Poland) in the light of pollen analysis. Studia Quaternaria 28: 25-39.

Kołaczek P., Fiałkiewicz-Kozieł B., Karpińska-Kołaczek M. & Gałka M. 2010. The last two millennia of vegetation development and human activity in the Orawa-Nowy Targ Basin (south-eastern Poland). Acta Palaeobotanica 50(2): 133-148.

Koporska H. 1929. Spis roślin rzadziej spotykanych w okolicach Lublina i niektórych innych miejscowościach województwa lubelskiego. Acta Soc. Bot. Polon. 6(4): 350-366. https://doi.org/10.5586/asbp.1929.020

Kornaś J. & Medwecka-Kornaś A. 2002. Geografia roślin. 634 pp. Wydawnictwo Naukowe PWN, Warszawa.

Kuneš P. & Abraham V. 2017. History of Czech vegetation since the Late Pleistocene. In: Chytrý M., Danihelka J., Kaplan Z. & Pyšek P. (eds.). Flora and Vegetation of the Czech Republic, pp. 193-227. Springer, Cham. https://doi.org/10.1007/978-3-319-63181-3_6

Kuneš P., Svobodová-Svitavská H., Kolář J., Hajnalová M., Abraham V., Macek M., Tkáč P., & Szabó P. 2015. The origin of grasslands in the temperate forest zone of east-central Europe: Long-term legacy of climate and human impact. Quaternary Science Reviews 116: 15-27. https://doi.org/10.1016/j.quascirev.2015.03.014

Kuneš P., Pelánková B., Chytrý M., Jankovská V., Pokorný P. & Petr L. 2008. Interpretation of the last-glacial vegetation of eastern-central Europe using modern analogues from southern Siberia. Journal of Biogeography 35: 2223-2236. https://doi.org/10.1111/j.1365-2699.2008.01974.x

Kupriyanova L.A. & Aleshina L.A. 1972. Pollen and spores of the flora of the European part of the USSR. 171 pp. Nauka, Leningrad.

MacDonald G.M., Velichko A.A., Kremenetski C.V., Borisova O.K., Goleva A.A., Andreev A.A., Cwynar L.C., Riding R.T., Forman S.L., Edwards T.W.D., Aravena R., Hammarlund D., Szeicz J.M. & Gattaulin V.N. 2000. Holocene treeline history and climate change across northern Eurasia. Quaternary Research 53(3): 302-311. https://doi.org/10.1006/qres.1999.2123

Magri D. 2008. Patterns of post-glacial spread and the extent of glacial refugia of European beech (*Fagus sylvatica*). Journal of Biogeography 35: 450-463. https://doi.org/10.1111/j.1365-2699.2007.01803.x

Magri D., Vendramin G.G., Comps B., Dupanloup I., Geburek T., Gömöry D., Latałowa M., Litt T., Paule L., Roure J.M., Tantau I., Van Der Knaap W.O., Petit R.J. & De Beaulieu J.-L. 2006. A new scenario for the Quaternary history of European beech populations: palaeobotanical evidence and genetic consequences. New Phytologist 171: 199-221. https://doi.org/10.1111/j.1469-8137.2006.01740.x

Magyari E.K., Kuneš P., Jakab G., Sümegi P., Pelánková B., Schäbitz F., Braun M. & ChytrýM. 2014. Late Pleniglacial vegetation in eastern-central Europe: are there modern analogues in Siberia? Quat. Sci. Rev. 95: 60-79. https://doi.org/10.1016/j.quascirev.2014.04.020

Maguire K.C., Nieto-Lugilde D., Fitzpatrick M.C., Williams J.W. & Blois J.L. 2015. Modeling species and community responses to past, present, and future episodes of climatic and ecological change. Annual Review of Ecology, Evolution, and Systematics 12(4): 343-368. https://doi.org/10.1146/annurev-ecolsys-112-054441

Malinovsky K. 2001. Floristic diversity of the Lviv region. Proceedings of the Shevchenko Scientific Society. Ecological collection, VII: 135-143.

Marcysiak K. 2010. Arctic-alpine plants and climate change in Europe. Wiadomości Botaniczne 54(3/4): 21-29.

Moore P.D., Webb J.A. & Collinson M.E. 1991. Pollen Analysis. 216 pp. Blackwell, Oxford.

Mosyakin S.L. & Fedoronchuk M.M. 1999. Vascular plants of Ukraine. A nomenclatural checklist. 346 pp. Kyiv. https://doi.org/10.13140/2.1.2985.0409

Nalepka D. & Walanus A. 2003. Data processing in pollen analysis. Acta Palaeobotanica 43: 125-134.

Nieto-Lugilde D., Blois J.L., Francisco Bonet-García J., GieseckeT., Gil-Romera G. & Seddon A. 2021. Time to better integrate paleoecological research infrastructures with neoecology to improve understanding of biodiversity long-term dynamics and to inform future conservation. Environ. Res. Lett. 16, 095005. https://doi.org/10.1088/1748-9326/ac1b59

Novenko E.Yu., Velichko A.A., Suganova I.S., Junge F.W. & Boettger T. 2005. Dynamics of vegetation at the late Pleistocene glacial/interglacial transition (newdata from the center of the East European plain). Review of Palaeobotany and Palynology Polish Geological Institute Special Papers, Proceedings of the Workshop "Reconstruction of Quaternary palaeoclimate and palaeoenvironments and their abrupt changes" 16: 77-82.

Petr L. & Novak J. 2014. High vegetation and environmental diversity during the Late Glacial and Early Holocene on the example of lowlands in the Czech Republic. Biologia 69(7): 847-862. https://doi.org/10.2478/s11756-014-0381-9

Pokorný P. 2002. A high-resolution record of Late-Glacial and Early-Holocene climatic and environmental change in the Czech Republic. Quaternary International 91: 101-122. https://doi.org/10.1016/S1040-6182(01)00105-7

POWO. 2025. Plants of the World Online. Facilitated by the Royal Botanic Gardens, Kew. Published on the Internet. Available online at: https://powo.science.kew.org/ (Accessed Feb 09 2025).

Ralska-Jasiewicz M. 1964. Correlation between the Holocene history of the *Carpinus betulus* and Prehistoric Settlement in North Poland. Acta Soc. Bot. Polon. 33(2): 461-468. https://doi.org/10.5586/asbp.1964.032

Ralska-Jasiewiczowa M., Latalowa M., Wasylikowa K., Tobolski K., Madeyevska E., Wright H.E.Jr, Turner C., Nalepka D. & Walanus A. 2004. Late Glacial and Holocene History of vegetation in Poland based on isopollen maps. 444 pp. W. Szafer Institute of Botany, Kraków.

Ruddiman W.F., Fuller D.Q., Kutzbach J.E., Tzedakis P.C., Kaplan J.O., Ellis E.C., Vavrus S.J., Roberts C.N., Fyfe R., He F., Lemmen C. & Woodbridge J. 2016. Late Holocene climate: Natural or anthropogenic? Rev. Geophys. 54: 93-118. https://doi.org/doi:10.1002/2015RG000503

Seniv M.M. 2024. Phytodiversity of Male Opillya: analysis and transformation. – Abstract of PhD thesis in Biological Sciences: 03.00.05. 22 pp. Kyiv.

Shelag-Sosonko Yu.R. & Gorochova Z.N. 1972. Mixed forests with the participation of small-leaved lime (*Tilia cordata* Mill.) in the Pre-Carpathian region and their development in the Holocene. Ukr. Bot. J. 29(6): 737-743.

Schwörer C., Gobet E., van Leeuwen J.F.N., Bögli S., Imboden R., van der Knaap W.O., Kotova N., Makhortykh S. & Tinner W. 2022. Holocene vegetation, fire, and land use dynamics at Lake Svityaz, an agriculturally marginal site in northwestern Ukraine. Vegetation History and Archaeobotany 31: 155-170. https://doi.org/10.1007/s00334-021-00844-z

Shiyan N.M. 2019. Assessment of the state of distribution of *Diphasiastrum alpinum* (L.) Holub in Ukraine, for the determination of the status of its protection at the national level by IUCN categories. Current Issues of Biological Science pp. 4-10. Nizhyn.

Soroka M. 2008. Vegetation of the Ukrainian Roztochchia. 432 pp. Swit Publishing House, Lviv.

Środoń A. 1972. Roślinność Polski w czwartorzędzie. In: W. Szafer & K. Zarzycki (eds.). Szata roślinna Polski, 1, pp. 527-569. Państwowe Wydawnictwo Naukowe, Warszawa.

Stančikaitė M., Zernitskaya V., Kluczynska G., Valūnas D., Gedminienė L., Uogintas D., Skuratovič Ž., Vlasov B., Gastevičienė N., Ežerinskis Ž., Šapolaitė J. & Šeirienė V. 2022. The Lateglacial and Early Holocene vegetation dynamics: New multi-proxy data from central Belarus. Quaternary International 630: 121-136. https://doi.org/10.1016/j.quaint.2021.05.004

Starkel L. 1977a. Paleogeografia holocenu. 361 pp. Państwowe Wydawnictwo Naukowe, Warszawa.

Starkel L. 1977b. The palaeogeography of mid- and east Europe during the last cold stage, with west European comparisons. Philosophical Transactions of the Royal Society of London.B. Biological Sciences 280: 351-372. https://doi.org/10.1098/rstb.1977.0114

Starkel L., Michczyńska D.J. & Gębica P. 2017. Reflection of climatic changes during Interpleniglacial in the geoecosystems of South-Eastern Poland. Conference Proceedings of the 12th International Conference “Methods of Absolute Chronology” May 11-13th, 2016, Gliwice-Paniówki, Poland. Geochronometria, 44: 202-215. https://doi.org/10.1515/geochr-2015-0060

Starkel L., Michczyńska D.J., Krąpiec M., Margielewski W., Nalepka D. & Pazdur A. 2013. Progress in the Holocene chrono-climatostratigraphy of Polish territory. Geochronometria 40(1): 1-21. https://doi.org/10.2478/s13386-012-0024-2

Stoyko S.M., Milkina L.I., Tasenkevich L.O. & Kagalo O.O. 2004. Shrubs and trees. In: Protected vascular plants of Western regions of Ukraine, pp. 153-173. Liga-Press, Lviv.

Sychak N.M. & Kahalo O.O. 2010. Additions to the flora of the Lviv region (plain part). Scientific Foundations of Biodiversity Conservation 1(8), 1: 173-196.

Szafer W. 1923. Trzeciorzędowe rośliny górskie na wale scytyjskim w ostoi podolsko-wołyńskiej. Acta Soc. Bot. Pol. 1(1): 97-119. https://doi.org/10.5586/asbp.1923.011

Szafer W. 1930. Element górski we florze niżu polskiego. Rozpr. Wydz. Matem.-Przyrod., 69 (ser. III, t. 29) Dź. B, 3: 1-112.

Szafer W. 1935. Las i step na zachodniem Podolu. Rozpr. Wydź. Matem.-Przyrod., 71 (ser. III, t. 31) Dź. B: 1-123.

Szafer W. 1972. Szata roślinna Polski niżowej. In: W. Szafer & K. Zarzycki (eds.). Szata roślinna Polski, 2, pp. 17-188. Państwowe Wydawnictwo Naukowe, Warszawa.

Tasenkevich L., Kalinovich N., Soroka M., Borsukevich L., Danylyuk K., Khmil T., Prokopiv A., Dyka O., Zhuk O., Pirogov M., Senyk M., Skybitska M., Mamchur Z., Novikov A., Fostyak T., Honcharenko V., Romaniv M., Skrypets K. & Volosovych N. 2015. Rare and threatened plant species of the Lviv region. 2nd edition, corrected, supplemented. 167 pp. Lviv, ZUKC.

Tasenkevich L., Skrypec K., Seniv M., Khmil T., Walas Ł. & Boratyński A. 2022. Biodiversity of high-mountain woody plants in the East Carpathians in Ukraine. Dendrobiology 89: 1-19. https://doi.org/10.12657/denbio.089.001

Tinner W. & Lotter A.F. 2006. Holocene expansions of *Fagus silvatica* and *Abies alba* in Central Europe: where are we after eight decades of debate? Quaternary Science Reviews 25: 526-549. https://doi.org/10.1016/j.quascirev.2005.03.017

Trindade D.P.F., Carmona C.P., Reitalu T. & Pärtel M. 2023. Observed and dark diversity dynamics over millennial time scales: fast life-history traits linked to expansion lags of plants in northern Europe. Proceedings of the Royal Society B: Biological Sciences, 290(1990): 20221904. https://doi.org/10.1098/rspb.2022.1904

Trondman A.K., Gaillard M.J., Mazier F., Sugita S., Fyfe R., Nielsen A.B., Twiddle C., Barratt P., Birks H.J.B., Bjune A.E., Björkman L., Broström A., Caseldine C., David R., Dodson J., Dörfler W., Fischer E., van Geel B., Giesecke T., Hultberg T., Kalnina L., Kangur M., van der Knaap P., Koff T., Kuneš P., Lagerås P., Latałowa M., Lechterbeck J., Leroyer C., Leydet M., Lindbladh M., Marquer L., Mitchell F.J.G., Odgaard B.V., Peglar S.M., Persson T., Poska A., Rösch M., Seppä H., Veski S. &Wick L. 2015. Pollen-based quantitative reconstructions of Holocene regional vegetation cover (plant-functional types and land-cover types) in Europe suitable for climate modelling. Glob Change Biol 21: 676-697. https://doi.org/10.1111/gcb.12737

Tsymbalyuk Z.M. 2012. Palynomorphological characteristics of species of the genus *Pinguicula* L. in the flora of Ukraine. In: Plant Kingdom in the Red Book of Ukraine: Implementation of the Global Strategy for Plant Conservation, pp. 184-185. Palivoda A. V., Kyiv.

Tsymbalyuk Z.M. & Bezusko L.G. 2017. *Linnaea borealis* (Caprifoliaceae) in Ukraine: palynomorphological and paleofloristic aspects. Ukr. Bot. J. 74(6): 539-547. https://doi/org/10.15407/ukrbotj74/06/539

Tsymbalyuk Z.M., Bezusko L.G., Mosyakin S.L. & Nitsenko L.M. 2019. Palynomorphological features of species of the genus *Dipsacus* (Dipsacaceae): evaluation for purposes of systematics and spore-pollen analysis. Ukr. Bot. J. 76(1): 9-23. https://doi/org/10.15407/ukrbotj76/01/009

Tsymbalyuk Z.M., Bezusko L.G. & Nitsenko L.M. 2021. The Palynotheca (KW-P) of the M.G. Kholodny Institute of Botany of the National Academy of Sciences of Ukraine. In: Herbaria of the 21st century: achievements and challenges. Proceedings of International Scientific Conference dedicated to the 100th anniversary of the National Herbarium of Ukraine (KW) – the Herbarium of M.G. Kholodny Institute of Botany, NAS of Ukraine (1 October 2021, Kyiv), 38-41 pp. M.G. Kholodny Institute of Botany, NAS of Ukraine, Kyiv.

Tsymbalyuk Z.M., Bezusko L.G. & Nitsenko L.M. 2018. Palynomorphological features of species of the genus *Knautia* (Dipsacaceae): evaluation for purposes of systematics and spore-pollen analysis. Ukr. Bot. J. 75(3): 248-259. https://doi/org/10.15407/ukrbotj75/03/248

Tsymbalyuk Z.M. & Mosyakin S.L. 2013. Atlas of pollen grains of representatives of the families Plantaginaceae and Scrophulariaceae. 276 pp. "Nash Format" LLC, Kyiv. https://doi/org/10.15407/ukrbotj75/03/248

Tsymbalyuk Z. M., Mosyakin S. L. & Bezusko L. G. 2008. Comparative morphological characteristics of pollen grains of the genera *Pinguicula* L. And *Utricularia* L. of the flora of Ukraine. Ukr. Bot. J. 65(4): 520-534.

de Vernal A. 2014. Palynology (Pollen, Spores, etc.). In: J. Harff (ed.) Encyclopedia of Marine Geosciences, pp. 653-659. Springer. https://doi.org/10.1007/978-94-007-6644-0_87-1#

Vočadlová K., Petr L., Žáčková P., Křížek M., Křížová L., Hutchinson S.M. & Sobr M. 2015. The Lateglacial and Holocene in Central Europe: a multi-proxy environmental record from the Bohemian Forest, Czech Republic. Boreas 6(128): 1-6. Collegium Boreas. Published by John Wiley & Sons Ltd. https://doi.org/10.1111/bor.12126

Walas Ł., Pietras M., Mazur M., Romo Á., Tasenkevich L., Didukh Y. & Boratyński A. 2023. The perspective of Arctic-Alpine species in southernmost localities: the example of *Kalmia procumbens* in the Pyrenees and Carpathians. Plants 12(19): 2-19. https://doi:org/10.3390/plants12193399

Wanner H., Mercolli L., Grosjean M. & Ritz S. P. 2014. Holocene climate variability and change; a data-based review. Journal of the Geological Society 172 (2): 254-263. https://doi.org/10.1144/jgs2013-101

Wasylikova K., Cârciumaru M., Hartyanyi B., Paskevich G. & Yanushevich Z. 1991. East-Central Europe. In: W. van Zeist, K. Wasylikowa & K.-E. Behre (eds.). Progress in Old World Palaeoethnobotany, pp. 207-239. Balkema, Rotterdam.

Willis K.J., Araújo M.B., Bennett K.D., Figueroa-Rangel B., Froyd C.A. & Myers N. 2007. How can a knowledge of the past help to conserve the future? Biodiversity conservation and the relevance of long-term ecological studies. Phil. Trans. R. Soc. B 362: 175-186. https://doi.org/10.1098/rstb.2006.1977

Wingard G.L., Bernhardt Ch. & Wachnicka A. 2017. The Role of paleoecology in restoration and resource management – the past as a guide to future decision-making: review and example from the Greater Everglades ecosystem, U.S.A. Front. Ecol. Evol. 5: 1-24. https://doi.org/10.3389/fevo.2017.00011

Wodehouse R.P. 1935. *Pollen grains*. 574 pp. McGraw–Hill, New York.

Zaverukha B.V. 1985. Flora of higher and lower plants. In: Yu. Shelyag-Sosonko (ed.). Nature of the Ukrainian SSR, pp. 17-44. Naukova Dumka Press, Kyiv.

Zelenchuk A.T. 1991. Inventory list of vascular plants of Lviv region. Visn. Lviv. Un-ty. Ser. Biol. 21: 16-33.