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Research papers

Rare species in past pollen records and herbarium specimens: *Linnaea borealis* L. lived in north-eastern lowlands in Italy during the Neolithic

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ABSTRACT

This paper emphasises the role of detailed pollen identification in past records and the importance of historical herbaria in palaeoecological research on plant distribution over the last millennia. Palynological analyses of a sediment core, covering approximately the last 10,000 years, from the wetland surrounding the UNESCO archaeological site of Palù di Livenza, in the lowlands of Friuli-Venezia Giulia, revealed the unexpected presence of *Linnaea borealis* during the Mid-Holocene (about 8600–4200 cal yr BP) in north-eastern Italy. This species is a rare small suffruticose plant which grows among mosses in conifer and mixed forests, between 1200 and 2100 m a.s.l. In Italy, due to the restricted climatic requirements, its current distribution is limited to a few high-mountain stands and to four northern regions (Val d'Aosta, Piedmont, Trentino-Alto Adige, Lombardy). Pollen grains of *L. borealis* found in past samples from the Friuli-Venezia Giulia region raised interest because this species was not recorded so far in this region either at present or in the past. To confirm the identification, a morphological study was carried out on pollen from flowers collected from University Herbaria (Florence and Pisa). Dried pollen extracted from anthers was acetolysed and observed with a Digital Optical Microscope. Polar axis, equatorial axis, exine thickness, equatorial diameters, mesocolpium, and distance among apices of colpi were measured in current and past pollen grains. Morphological analysis confirms the presence of *L. borealis* in the sedimentary archive studied, adding an important insight into the knowledge of past and present biodiversity of the area.

1. Introduction

There is a general consensus that climate and environmental changes are increasingly shaping our world, both the environment and society (Feola, 2015; Harper and Snowden, 2017; Whitaker, 2023). In recent years, according to the commitment by European Union to an ambitious biodiversity recovery plan in its Biodiversity Strategy for 2030 and the Green Deal, several European projects have focused their attention to biodiversity, stressing its value and promoting the conservation (e.g., Hermoso et al., 2022; European Research Executive Agency, 2024). As a result, great interest is increasingly placed in the discovery, characterisation and analysis of rare or endemic plant species aiming at protecting and valorising endangered flora and habitats (e.g., Malhi et al., 2020). Palynology provides the direct evidence of past flora composition in the different regions, helps to identify the presence of rare taxa on a long-time scale, and often contributes the basic palaeoecological information that are required for understanding the dynamics of recent decline of plant species (Birks, 1993, 1996, 2012). The study of the past (palaeoecology, archaeology, history) is indeed of paramount importance to gain key information related to the biodiversity loss we are facing today (Boivin and Crowther, 2021) looking for cultural and technological practises and solutions (Mercuri et al., 2025a). Knowing the biodiversity of the past, however, requires a high level of identification, which is not always easy to achieve in pollen analyses and which sometimes requires in-depth studies of the pollen morphology of certain species.

This paper presents, for the first time to our knowledge, the discovery of pollen of *Linnaea borealis*-twinflower in a Holocene deposit in

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lowlands of Friuli-Venezia Giulia, a region of north-eastern Italy where the species does not currently live (Portal to the Flora of Italy, 2025; Acta Plantarum, 2025: Information on Linnaea borealis in Italy etc.). Thanks to a detailed morphological study, we show the discovery and significance of *L. borealis* in the Palù di Livenza basin. In this research, we assess the presence of this species in the palaeoecological record, proceed with a detailed morphological examination of herbaria specimens, and conclude by comparing these data to underline the significance of the occurrence of this rare species in the past.

L. borealis is a circumboreal species growing on uplands and is a typical plant of the acidophilic coniferous forests; it reaches its southern distribution limits in Poland and in scattered stations in more southern mountains (Welch, 2003). In Scandinavia the species is common but in other European countries, such as Poland, Germany and Slovenia, twinflower is endangered and protected as a glacial relict (Thiem and Buk-Berge, 2017). It is becoming quite rare in Scotland and is very uncommon in Italy. Recently, we identified its pollen in an off-site core c. 300 m south from the Neolithic site of Palù di Livenza (Zappa, 2025), but no evidence of it has never been found in previous pollen records from the area (e.g., Pini, 2004; Zappa et al., 2023). This paper does not intend to present all the data that emerged from the palynological/palaeoecological study but rather focuses on the novelty of the discovery of a species that is today absent from the study area. Therefore, only the main pollen data useful to discuss the record of *L. borealis* will be reported. The Palù pollen record documents on the presence of this rare species in the past, at a low elevation and as early as c. 8600 cal yr BP. This required a thorough morphological study of the pollen of *L. borealis* that, considering the rarity of the species today, was undertaken using reference specimens obtained from historical herbaria. This methodology is increasingly recommended in both systematic and applied palynology, as well as in studies of conservation biology focused on the conservation and protection of biodiversity (Greve et al., 2016; Nualart et al., 2017; Mandrioli, 2023), particularly with regard to endemic, endangered, or vulnerable species (e.g., Molano-Flores et al., 2023).

The present study on *L. borealis* has the following steps and aims (Fig. 1): (1) to support the identification of pollen in the palaeorecord by analysing specimens from the herbaria of Florence and Pisa, which are among the most prestigious institutions preserving *exsiccata* of this species in Italy; (2) to compare the pollen traits of the reference material with those observed in past records also discriminating them from similar pollen in the Caprifoliaceae family; (3) to highlight the uniqueness of the discovery of this species out of the current distribution area. This can be considered as an exemplar case study of how a detailed morphological analysis on the (unexpected) pollen of target species can open up cooperation between the more classically palaeoecological approach and the floristic aspects of palaeoenvironmental studies.

1.1. Some notes on Linnaea borealis L.

Linnaea borealis is a dwarf evergreen, stoloniferous shrub belonging to Caprifoliaceae, the Honeysuckle family (Angiosperm Phylogeny Group, 2016; Fig. 2). The English common name 'Twinflower' is due to its very distinctive inflorescence composed by two bell-shaped flowers on a forked Y-shaped stem. It blooms for about 7 days between June and August (most commonly June-beginning of July in Europe and Italy). After pollination, fruits (small, dry, one-seeded capsules) are kept for about 36 days. Seeds are dispersed through epizoochory, mainly by birds or other small animals, thanks to small hair bracts that stick on animal's fur (Thiem and Buk-Berge, 2017; Christenhusz, 2013). This plant grows among mosses on sandy, poor and acidic soils, under conifer or mixed forest canopies at high elevations. As it is a shallow-rooted species, *L. borealis* is susceptible to drought. Demographic fluctuations in its populations are seen according to humidity conditions, decreasing in dry years, while thriving in wetter stands (Piękoś-Mirkowa and Mirek, 2003).

A high number of stands of this species are disappearing in the world due to habitat unfavourable changes, such as the Wolin National Park in USA, and in Wisełka region in Poland (Piotrowska, 1966). Another issue concerns the light availability (Niva, 2003; Niva et al., 2006; Scobie and Wilcock, 2009) as the twinflower thrives in moderate sunlight but not in full sun; the growth of shrub layer in forest management successions (of species such as *Vaccinium myrtillus* and *V. vitis-idaea*) limits the twinflower populations competing for the same spaces (Thiem and Buk-Berge, 2017).

The current distribution of *L. borealis* is restricted to circumboreal areas of the northern Hemisphere (from Scotland to northern Europe through Russia to Siberia, northern Asia, Kamchatka, Japan, northern China and Mongolia, and from Alaska to Canada to Greenland; IPNI, 2025 and POWO, 2025). In Italy, the presence of the species is reported only on the mountains (1300–2000 m a.s.l) of four administrative regions: Val d'Aosta, Piedmont, Lombardy, three regions where *L. borealis* is listed as protected species (Absolute Regional Protection; Acta

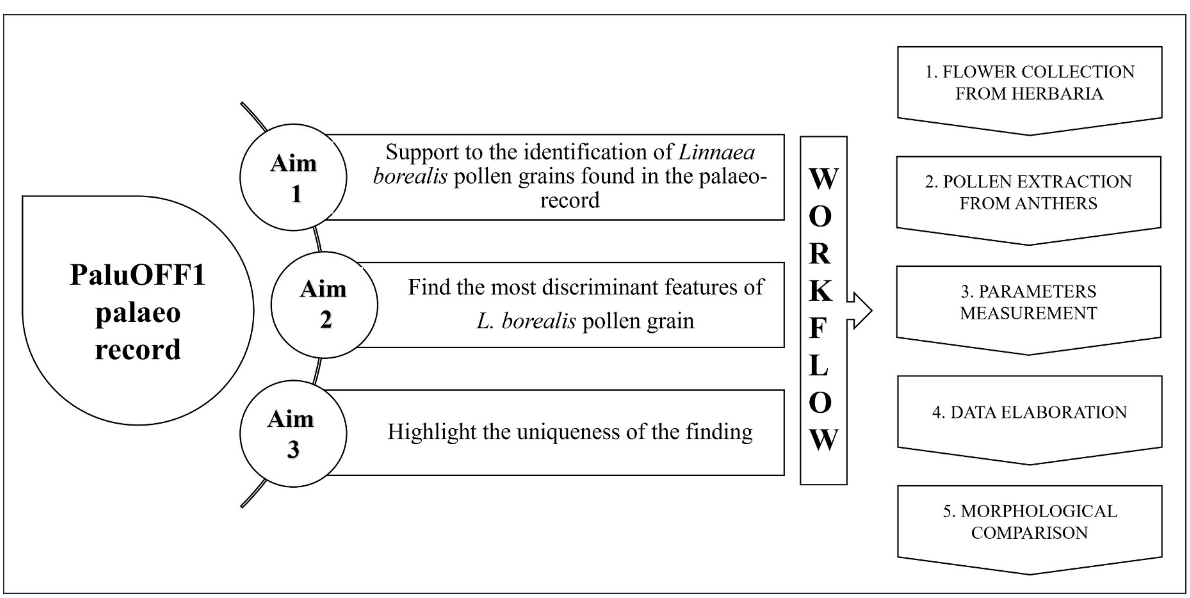

Fig. 1. Aims and workflow of the morphological study stimulated by palynological analyses of an off-site record and the finding of *Linnaea borealis* pollen in the Palù basin, north-eastern Italy.

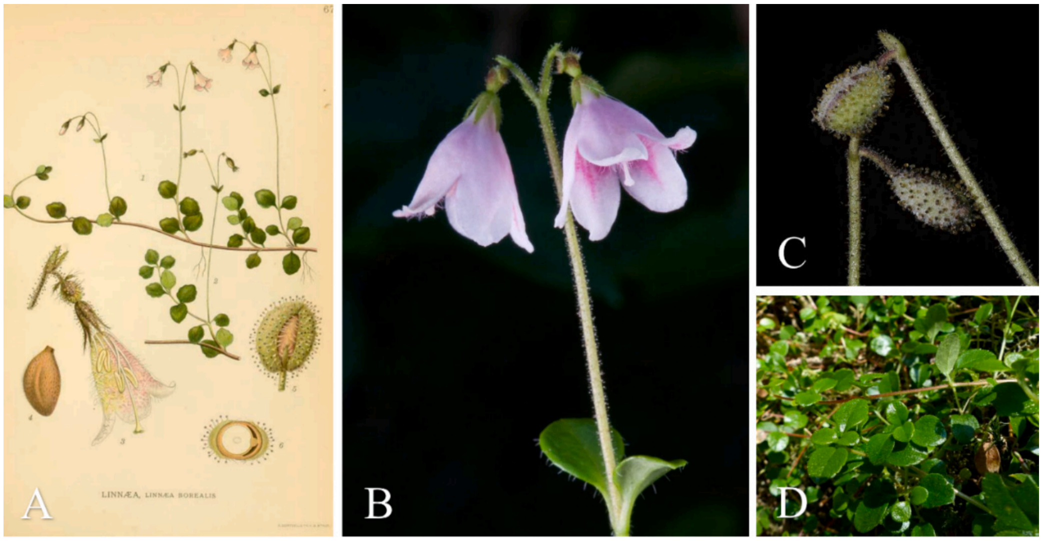

Fig. 2. A: chromolithograph from Carl Lindman's *'Bilder ur Nordens Flora'* (Pictures of Northern Flora), Wahlström & Widstrand, 1905; B: detail of *Linnaea borealis* (common name twinflower; taken from *'Perennial plant database search guide'* accessed on 14th January 2025); C: detail of the capsule (Acta Plantarum, accessed on 14th January 2025. Photo taken in Alta Valtellina (Lombardy), 1890 m a.s.l. in August 2015 – credits by Antonio Mazzoli); D: details of the leaves (Acta Plantarum, accessed on 14th January 2025. Photo taken in Val Bregaglia (SO), 1300 m a.s.l. in July 2015 – credits by Ettore Guarnaroli).

Plantarum, 2025), and Trentino-Alto Adige (Conti et al., 2005; Selvaggi et al., 2024). Regarding the Veneto region, its record was later revised as an identification error (Portal to the Flora of Italy, 2025: Fabrizio Bartolucci and Fabio Conti as responsible for the checklist of native flora). The species is classified as Near Threatened (NT) according to the Red List of the vascular flora of Val d'Aosta (Bovio, 2016). Its presence in Piedmont is a recent discovery, as reported by Selvaggi et al. (2024), overturning the previous belief that it had been extinct in the region. Its first reporting was based on *exsiccata* and bibliographic historical data (such as from Balbis in 1801 as reported in Selvaggi et al., 2023) but was only recently confirmed (Selvaggi et al., 2024). In Lombardy, it is reported as at lower risk, and distribution data are documented, e.g., in the Orobic Alps, at 1460 m a.s.l. (Cretti and Bona, 2015). In Trentino-Alto Adige, and in particular in the Adamello Brenta Natural Park, the species is at lower risk, and it is found both inside and outside the park boundaries (from 1200/1230 m a.s.l at lake Tovel to 1915 m a.s.l on the Peller mount; Festi and Prosser, 2008).

Consequently, giving its ecological requirements and distribution habitat, the finding of this rare mountain species in the north-eastern palaeorecord of Palù di Livenza was counterintuitive. The study area, the Palù basin, is a wetland located in the lowlands called Po Plain, approximately 30 m a.s.l., that played the role of a key archive recording past biodiversity and environmental transformations over millennia. Palù is currently listed in the BRAIN database (Mercuri et al., 2024) with

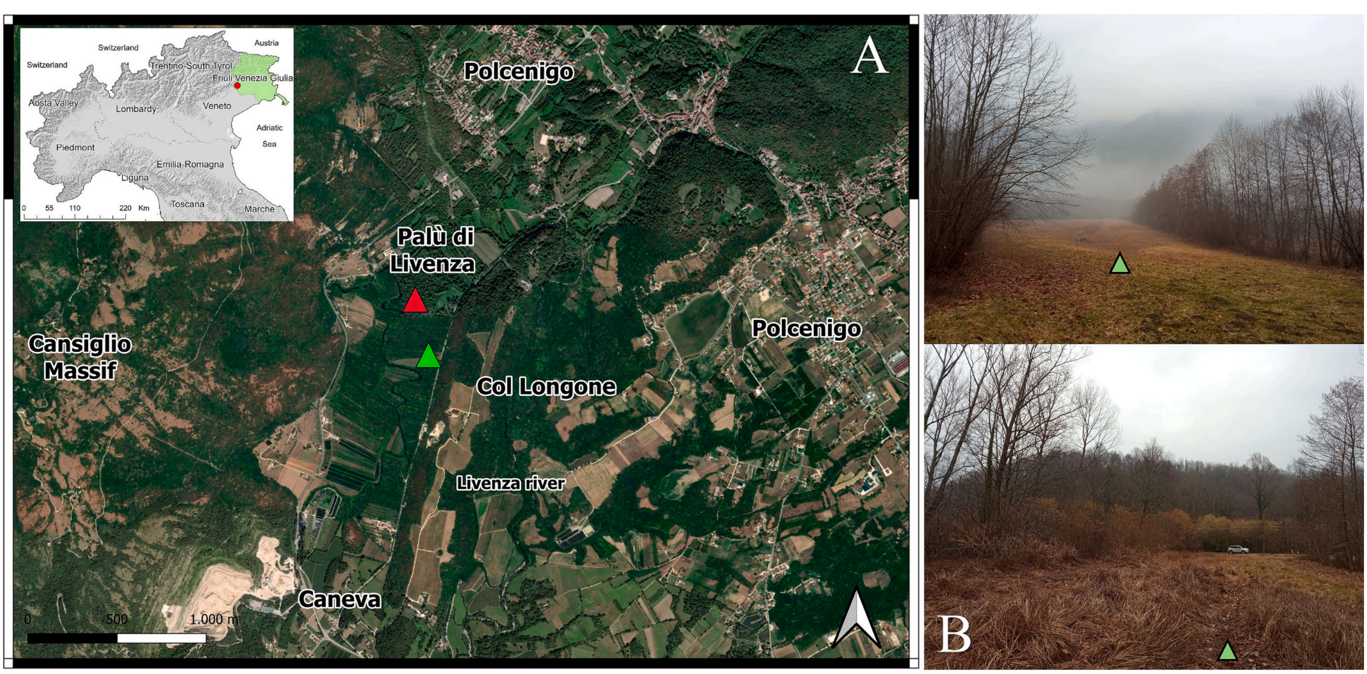

Fig. 3. A: Map showing the Palù di Livenza area in Friuli-Venezia Giulia, north-eastern Italy. The red triangle identifies the excavation area of the archaeological site, while the green triangle identifies the coring location of the PaluOFF1 record (300 m far from the archaeological site); B: photographs of the coring location (taken by J. Zappa on February 22, 2022). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

three ID numbers corresponding to the first palynological on-site study (BRAIN ID: NFV4; Pini, 2004), the more recent on-site research (BRAIN ID: NFV26; Zappa et al., 2023; Zappa, 2025) and the off-site study (BRAIN ID: NFV28; Zappa, 2025). Pollen of *L. borealis* has been found in the off-site core.

2. Materials and methods

2.1. The study site: Archaeological context and vegetation

The study area is located in the Palù basin, in the Polcenigo municipality (Pordenone province, Friuli-Venezia Giulia, north-eastern Italy; Fig. 3). Here, a Late-Neolithic pile-dwelling site was first discovered in the 19th century during drainage operations in the middle of the basin and the importance of the site was immediately acknowledged (Micheli et al., 2023a). In 2011, the site was included in the World Heritage List of UNESCO in the transnational serial property *Prehistoric Pile-Dwellings around the Alps*. Thanks to this inscription, in 2013 a new phase of excavations and research started in order to investigate new sectors of the Neolithic village. The new excavation area, untouched by modern works or disturbances, proved to be an ideal place to investigate a multi-layered pile-dwelling. Multidisciplinary research was conducted aiming at investigating the life of the Neolithic village and their relationship with the territory (Micheli et al., 2023a, 2023b).

According to the Vegetation Chart of Italy (Blasi, 2010), the Palù basin is characterised by three different phytosociological synassociations: *Buglossoido-Ostryo carpinifoliae* sigmentum intertwined with *Mercuriali ovatae-Ostryo carpinifoliae* sigmentum and *Ostryo carpinifoliae-Fraxino orni* sigmentum. Since 2008, the basin has also been recognised as a Regional Biotope, that is an area bearing important environmental, faunistic and vegetational features at regional level. Springs cover almost all the Po Plain (Zappa et al., 2008), originating from the last phases of continental filling of the plains, when rivers transported rocky sediments from mountain catchments to the medium and low plain (Muscio, 2001; Castiglioni and Pellegrini, 2001). In this environment, a variety of habitats is hosted; one is constituted by low alkaline swamps, where stagnation of waters is caused by soil morphology. The most represented families of vascular plants are Cyperaceae, Juncaceae and Poaceae. A typical swamp in the Friulan spring is composed by the sedge *Cladium* swamp (De Luca and Oriolo, 2010).

2.2. The study site: Previous palynological studies

Recent palynological analyses from on-site pollen samplings aimed at reconstructing floristic and vegetation history during the Neolithic (Zappa et al., 2023) and on a longer time range (last 10,000 years; Zappa, 2025) and are in accordance with previous studies carried out at the site (Pini, 2004). Palynological investigation reported in Pini (2004) described the vegetation history between c. 6500 and 5900 cal yr BP at the Neolithic site of Palù. The area was covered by dense oak, beech, and hazelnut forests, with no human impact detected while after the settlement began, forests were cleared, wetlands were reclaimed, and herbaceous communities (including crops, weeds, ruderal and nitrophilous plants, pastures, and meadows) expanded. Coherently, palynological assemblage from PaluON1 (Zappa et al., 2023) describes an environment dominated by mixed oak forests, with abundant swamps and hygrophilous woods. Also, conifer and upland forests were present. During the Neolithic period (c. 6350–5600 cal yr BP), human activity and the development of the local economy led to a significant change in vegetation: cereal crops, flax, and other cultivated plants became widespread, along with animal husbandry. Human influence also promoted the spread of synanthropic plants and the occurrence of local and regional fires. After the site was abandoned, probably due to environmental changes, the area was gradually re-occupied by swamps and hygrophilous woods, as it is today (Zappa et al., 2023; Zappa, 2025). In the two on-site records studied, shrub communities included small amounts of *Lonicera xylosteum* type and *L. coerulea* type (Pini, 2004); also, in the PaluON1 record, pollen grains belonging to the genus *Lonicera* were found (Zappa et al., 2023). On the contrary, no pollen grains of *Linnaea borealis* were identified in the on-site records, i.e. those located inside the archaeological site. New off-site core PaluOFF1 made it possible to extend the palaeoenvironmental reconstruction to a larger scale. Notably, it is in this record that pollen of *Linnaea borealis* was identified, highlighting both the presence and ecological significance of this rare species.

2.3. Pollen extraction from PaluOFF1 and the palaeoecological research

Palynological analyses were carried out on samples coming from the off-site record PaluOFF1, located 300 m far from the archaeological site of Palù (Fig. 3). It was manually cored with an Ejikelkamp hand auger, using an Edelman head above the groundwater table and a gauge of 1 m of length below the groundwater table (Fontana et al., 2017). The core drilling reached a depth of approximately 6 m, where is located the intersection with the blue clay (*Argille Azzurre*) deposits belonging to the LGM (Last Glacial Maximum; Monegato et al., 2017). Two radiocarbon dating was performed on seeds at ETH/AMS Facility in Zurich and calibration was carried out using the latest version of OxCal 4.4.4 (Ramsey, 2009) and the IntCal20 calibration curve of atmospheric data from Reimer et al. (2020). An age-depth model (Fig. 4) was performed using R software (BChron package) adding the date 2020 AD as modern surface layer (as normally applied in palaeoecological studies; Lacourse and Gajewski, 2020). The model obtained is consistent with the archaeological chronology (Micheli et al., 2023a, 2023b), the stratigraphic and sedimentological description of the core, as well as with the sedimentation rate for the Palù peat bog. The stratigraphy of this core, the sedimentological description of layers and sediments composing the core suggest that PaluOFF1 belongs to a stratified peat, without hiatuses and characterised by a continuous sedimentation rate.

Pollen samples were selected along the 6-m core and treated for palynological extraction. About 1–2 g of sediment from each sample were treated through sieving, acetolysis and separation with heavy liquid (Na-metatungstate hydrate) to allow pollen flotation (Florenzano et al., 2012). *Lycopodium* spores were added to calculate concentrations, which are expressed as pollen per gram (p/g). The residues were included in glycerol jelly and were mounted in permanent slides. The routine pollen analysis was performed at 1000× magnification at the optical microscope, and performed for palaeoenvironmental research (Zappa, 2025). Pollen of *Linnaea borealis* was identified in some samples during the routine counts. Therefore, in this study, the slides of all samples were re-examined to check for the presence of this pollen and morphological study. Well preserved pollen grains of *L. borealis* were also measured at the Nikon digital microscope to allow comparison with reference specimens from herbaria (see below 2.4). Furthermore, the presence of *L. borealis* in Europe in the same chronological period as the core studied (from c. 10,000 to c. 2000 yrs. BP) was verified by a search of the Neotoma database (Williams et al., 2018); since, considering the variable state of preservation in palaeorecords, within the family Caprifoliaceae, the pollen of the genus *Lonicera* may be similar to that of *Linnaea* (especially in polar view; e.g., Reille, 1992), all records of this genus were also extracted.

2.4. Reference pollen of Linnaea borealis

The morphology of *L. borealis* pollen was studied to compare the main diagnostic traits of reference specimens with those of the fossil pollen found in PaluOFF1 (Fig. 1). Therefore, a recognition of the availability of specimens of this species was carried out at numerous herbaria in Italy. The Herbaria of Florence (Herbarium Centrale Italicum of Florence – FI-HCI) and Pisa (Herbarium of the Botanical Garden of Pisa – PI-HBG) provided 3 and 6 flowers, respectively, from specimens suitable for this study (Figs. 5 and 6). Pollen was carefully extracted

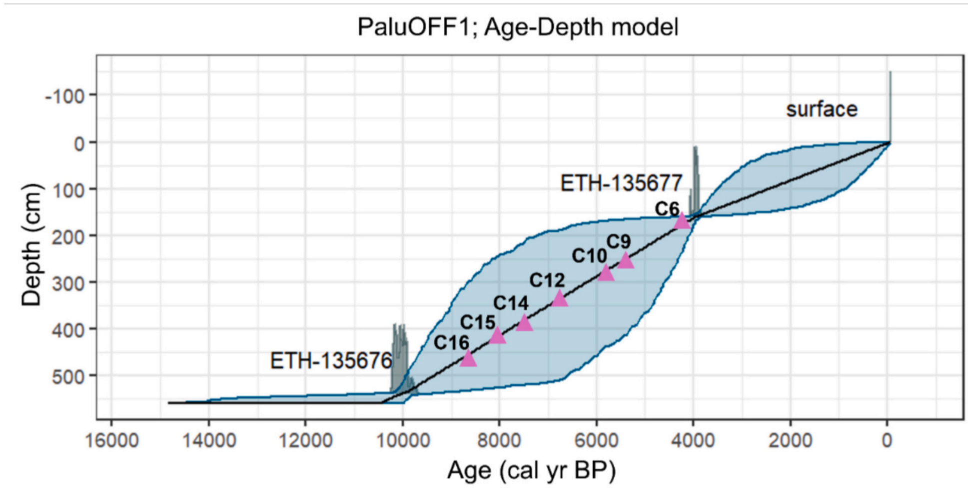

Fig. 4. Age-depth model for PaluOFF1 elaborated with BChron package using R software and relying on two radiocarbon dates and the date 2020 AD as modern surface layer. Violet triangles identify the depth and ages of samples where *L. borealis* pollen was found (between 8600 and 4200 cal yr BP). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Fig. 5. Examples of herbarium sheets. Herbarium Centrale Italicum of Florence (FI-HCI) A: specimen FI068582; B: specimen FI068583 (FI-HCI); Herbarium of the Botanical Garden of Pisa (PI-HBG) C: specimen PI062716; D: specimen PI062719 (PI-HBG).

from anthers under a stereomicroscope at 40 × magnifications. Then, it was acetolysed after dehydration (Erdtman, 1960), and the residue was mounted on permanent slides. Morphological analysis was carried out at 1000 × magnifications with a Digital Optical Microscope (Nikon eclipse Ni-E with integrated NIS Elements L imaging software). Pollen parameters were described according to Punt (1976) and were measured using the above-mentioned optical microscopy, which is the more suitable instrument for applications in routine pollen analysis for palaeoecological studies. Pollen grains were measured in both Equatorial (EV) and Polar (PV) views, when in a suitable position (Fig. 7). Measurements were considered valid only when the pollen grains were intact, showing no signs of folding, breaking, or structural damage. In addition, the grains had to be free from any interference such as overlapping debris, adjacent grains, or underlying material masking their perimeter. In polar view were measured: (i) Exine thickness (Ex); (ii) Mesocolpium (MES); (iii) Equatorial diameter 1 (E1); (iv) Equatorial diameter 2 (E2); (v) distance among apices of two continuous colpi (DAC), which area gives the Apocolpium. In equatorial view, the measurements taken were: (i) polar axis (P); (ii) equatorial axis (E); (iii) exine thickness (Ex).

3. Results

3.1. Reference pollen of Linnaea borealis from historical herbaria

The herbarium material was rather scarce and not always in a good state of preservation, so measurements were taken only on well preserved pollen grains. In two samples (no.1, no.3) pollen was very fragmented, thus preventing any usable measurement (Table 1). Depending on the state of preservation, 30 pollen grains were successfully measured in equatorial or polar view in samples no. 4,5,6, and 7, while a smaller number was measured in sample no.2 (26), no.8 (12) and no.9 (19). A total of 177 pollen grains were measured in 7 of the 9 reference samples. Below, unless otherwise stated, the measurements are the average value of each parameter calculated all pollen grains measured in the sample.

In Equatorial view (EV), the polar axis (P) has a value of 53.8 ± 6.5 μm and the equatorial diameter (E) is 54.9 ± 7 μm. In Polar view (PV) the two diameters (E1 and E2) have values of 61.4 ± 7.6 and 61.5 ± 8.1 μm, respectively. The pollen is isopolar, ranging in shape from spheroidal (45.1% of measured pollen grains), oblate-spheroidal (24.5%), prolate-spheroidal (19.6%), suboblate (7.8%) and subprolate (3.0%).

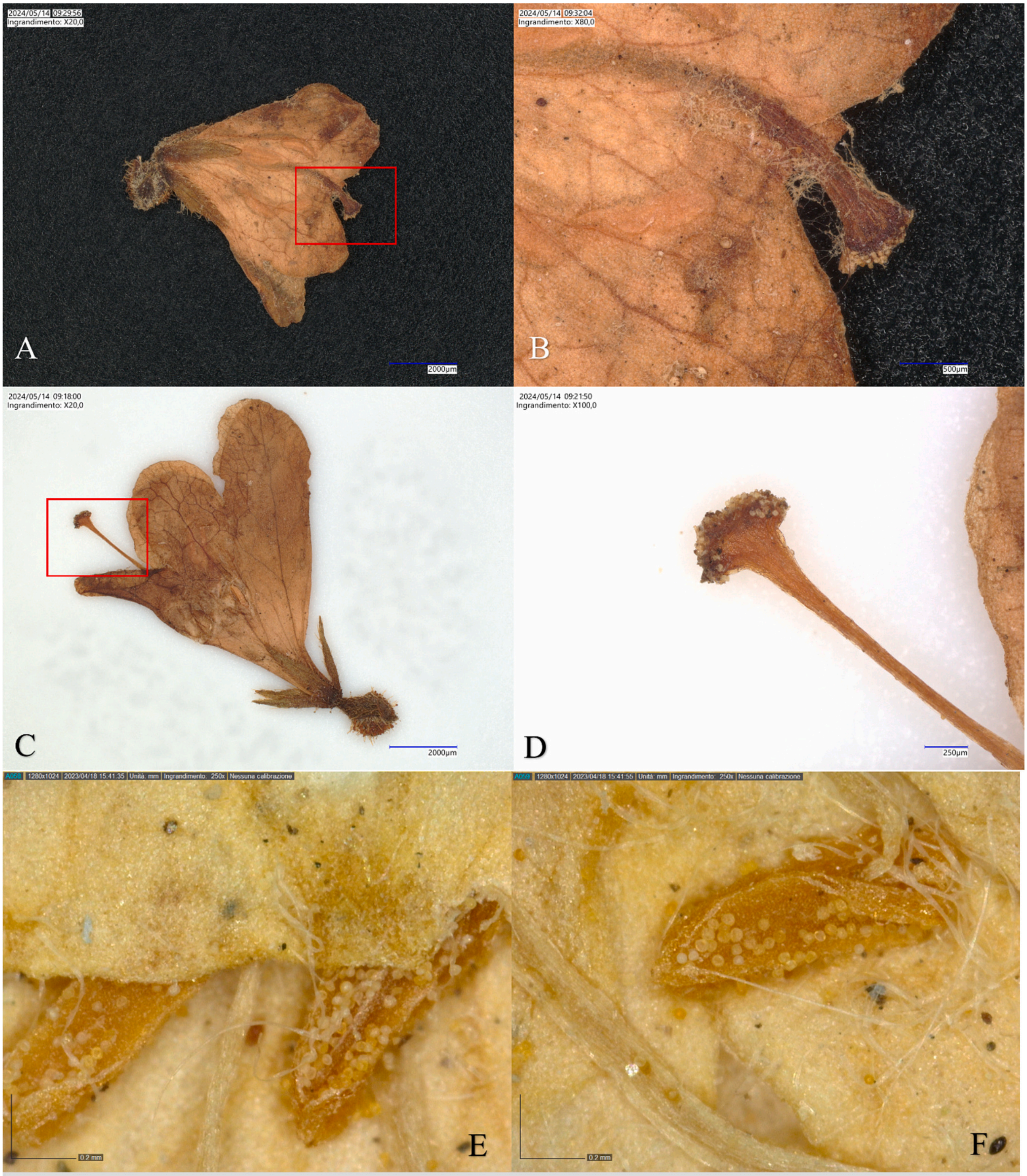

Fig. 6. Flower of *Linnaea borealis* from the Herbarium of the Botanical Garden of Pisa –PI-HBG. A: flower from specimen PI062719; B: detail on specimen PI062719; C: flower from specimen PI062718; D: detail on specimen PI062718; E-F: detail on anthers and pollen grains on specimen PI062719. Photo taken at the Modena's lab with Keyence VHX-7000 Series Digital Optical Microscope.

The mean measure of the exine thickness (Ex), measured both in EV and in PV, is 3.1 ± 0.6 μm. Pollen grains are almost exclusively trizonocolporate with a few exceptions (2.8%) showing four apertures, due to intraspecific diversity. Exine is supra-scabrate and echinate, with the classical sculptures named "echini"(lat: *echinus*, pl. *echini*). Morphometric data (EV and PV) are reported in Table 2.

3.2. Fossil pollen of Linnaea borealis from PaluOFF1

Pollen grains of *Linnaea borealis* were found in the central part of the sequence PaluOFF1, in a chronological interval ranging from about 8600 to 4200 cal yr BP.

Whole pollen grains were measured in seven samples. The pollen has a few echinate, supra-scabrate exine, and trizonocolporate apertures. Pollen preservation was generally good, and only some records were folded or broken but still identifiable. Compared to the pollen grains observed in modern samples, the sculptures (echini) appear less pronounced, likely due to the gradual smoothing over time caused by preservation in ancient sediments. Nevertheless, the echini are still visible, and the distinctive supra-scabrate exine of the grain is even more evident in areas where the echini are less prominent. For those observed in a good condition, pollen parameters were measured (in equatorial or

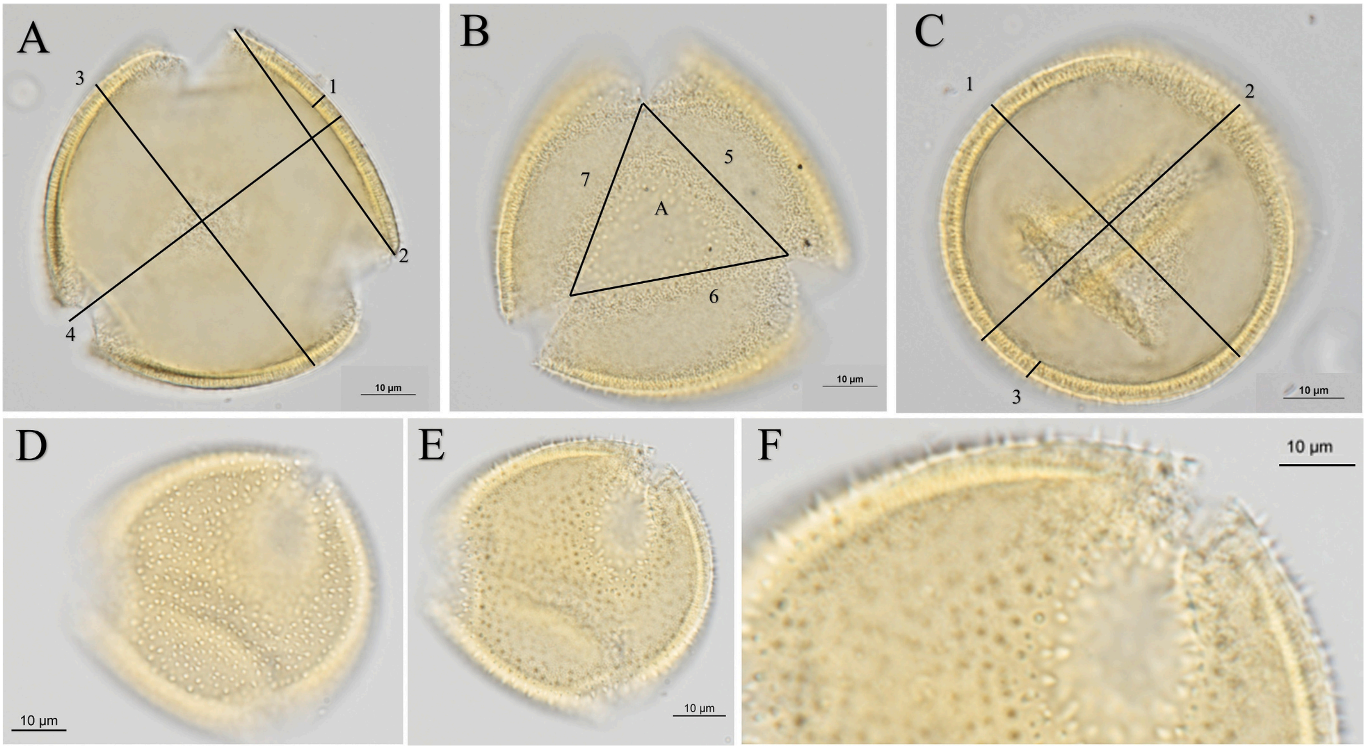

Fig. 7. Pollen parameters of *L. borealis* in polar (A–B) or equatorial view (C). A) Polar view: 1. Exine thickness (Ex); 2. Mesocolpium (MES); 3. Equatorial diameter 1 (E1); 4. Equatorial diameter 2 (E2). B) Polar view: 5, 6 and 7: distance among apices of two continuous colpi (DAC), the resulting area characterise the Apocolpium (A); C) Equatorial view: 1. Polar axis (P); 2. Equatorial axis (E); 3. Exine thickness (Ex). D,E,F: photographs showing exine sculpturing. Photos and measurements taken at Modena's lab with Nikon Digital Microscope.

Table 1
List of reference samples, with sample number, their label in the Herbarium they come from, provenance of the sample, year of collection, herbarium in which it is conserved (Firenze – FI-HCI; Pisa – PI-HBG), number of measured pollen grains in this study (NA = Not Applicable, due to the poor state of preservation).

No. sample	Sample name	Location	Year	Herbarium	No. of measured pollen grains
1	FI068582	Val d'Aosta - Italy	1935	FI-HCI	NA
2	FI068583	Slovenia	1964	FI-HCI	26
3	FI068584	Trentino - Italy	2018	FI-HCI	NA
4	PI062715	Germany	1867	PI-HBG	30
5	PI062716	Lombardy - Italy	1863	PI-HBG	30
6	PI062717	Trentino - Italy	1920	PI-HBG	30
7	PI062718	Germany	1838	PI-HBG	30
8	PI062719	Sweden	1847	PI-HBG	12
9	PI062720	Unknown	Unknown	PI-HBG	19

polar view, Fig. 8). In Equatorial view (EV), the polar axis (P) has a value of 60 μm and the equatorial diameter (E) of 59 μm, on average. In Polar view (PV) the two diameters (E1 and E2) have mean values of 55 and 59 μm, respectively. Pollen grains are exclusively trizonocolporate and the exine is supra-scabrate and echinate.

In the pollen diagram, missing from the bottom and top zones (PAL5, PAL1), pollen of *L. borealis* is present with <1% in each sample in the pollen zones PAL2 and PAL3 and have a sporadic presence in pollen zone PAL4 (Fig. 9). The mean forest cover of the three zones is 58%, mainly consisting of mixed oakwood (deciduous *Quercus*, *Carpinus betulus, Ostrya carpinifolia/Carpinus orientalis* type, *Tilia*), and minor contributions of upland forest (*Abies*, *Picea abies*, *Pinus*, *Fagus sylvatica, Betula*; Zappa, 2025). Wetlands are well testified in PAL2 where hydrophytes reach their maximum (4.3%), while they decrease in PAL3 and almost disappear in PAL4. Conversely, hygrophilous trees increase in PAL3, PAL4a, replacing the gradually declining oak forest in the forest cover.

4. Discussion

The case study presented with this research is of special interest to underline the role of long-time scales in the study of systematics, ecology and conservation, which has classically employed palaeoecological methods and new strategies to improve its scientific potential (Birks, 1993, 1996, 2012; Mercuri et al., 2025b). A growing interest in the refinement of pollen identification is increasingly characterising palynology, which, from the classical development of quantitative techniques for extensive palaeoecological syntheses (e.g., Deza-Araujo et al., 2021; Githumbi et al., 2021; Serge et al., 2023 among the most recent ones), is directing its efforts towards the harmonisation of the pollen florula as well as possible to a specific level (Birks et al., 2023; Flantua et al., 2023; Herzschuh et al., 2022). Attention to pollen identification and nomenclatural standardisation efforts are crucial when it comes to studying biodiversity. Research focused on biodiversity is becoming increasingly important, as it provides in-depth insights into the environmental features and represents a cornerstone for an effective planning of its management and conservation. Since every site is unique and has its own specific needs, a deep understanding of its features should include the plant biodiversity and its relationship with other environmental factors, and this long-term perspective can significantly support the conservation of each unique context (Mercuri et al., 2025a).

Below, the key role of both high detail palynological analyses and herbaria collections for the correct identification of rare species is discussed, followed by the palaeoecological implications of the presence of *Linnaea borealis* in environmental reconstructions.

Table 2
Morphometric data of *L. borealis* pollen from historical herbaria. Each value is the average of the measurements of the pollen grains in the sample, ± standard deviation: A. Equatorial view. P = Polar axis; E = Equatorial axis; P/E = polar and equatorial axis ratio; Ex = exine thickness. B. Polar view. E1 = equatorial diameter 1; E2 = equatorial diameter 2; Ex = exine thickness; MES = mesocolpium; DAC1 (2,3,4) = distance among apices of two colpi 1 (2,3,4). The column 'Accepted measurements' reports the number of pollen grains whose measurements were deemed reliable for the purposes of the morphometric study; partially deformed or imperfectly preserved grains were excluded.

A. EQUATORIAL VIEW

Pollen sample	Accepted measurements	P	E	P/E	Ex
2	11	53.4 ± 6.5	57.2 ± 6.5	0.9 ± 0.1	2.9 ± 0.5
4	19	57.7 ± 4.0	55.7 ± 3.5	1.0 ± 0.04	3.0 ± 0.5
5	18	46.2 ± 4.0	47.7 ± 6.1	1.0 ± 0.1	3.4 ± 04
6	19	50.4 ± 4.0	53.1 ± 5.8	1.0 ± 0.1	3.4 ± 0.5
7	19	56.6 ± 4.4	56.2 ± 5.3	1.0 ± 0.1	3.3 ± 0.7
8	6	55.4 ± 3.9	54.7 ± 4.6	1.0 ± 0.1	2.8 ± 0.5
9	10	60.5 ± 6.8	65.2 ± 5.4	0.9 ± 0.1	3.6 ± 0.4

B. POLAR VIEW

Pollen sample	Accepted measurements	E1	E2	Ex	MES	DAC1	DAC2	DAC3	DAC4
2	15	64.0 ± 5.5	65.6 ± 5.5	2.3 ± 0.6	47.7 ± 5.1	38.2 ± 6.0	36.9 ± 5.4	40.5 ± 4.6	32.7 ± 1.5
4	11	60.9 ± 5.4	59.4 ± 6.3	2.7 ± 0.5	49.1 ± 5.1	38.1 ± 4.1	35.0 ± 4.6	37.6 ± 5.4	/
5	12	52.1 ± 5.0	50.9 ± 4.9	3.2 ± 0.4	42.2 ± 3.4	34.9 ± 4.4	35.0 ± 4.0	34.7 ± 3.4	/
6	11	58.5 ± 5.5	60.0 ± 7.0	3.1 ± 0.6	50.3 ± 3.9	42.3 ± 4.4	41.5 ± 6.1	43.3 ± 5.0	/
7	11	64.1 ± 5.3	63.6 ± 5.7	3.2 ± 0.4	51.3 ± 5.5	37.4 ± 5.7	35.2 ± 4.4	42.4 ± 5.9	/
8	6	64.4 ± 9.6	66.6 ± 8.4	3.0 ± 0.4	54.6 ± 6.6	41.7 ± 7.0	41.1 ± 8.6	38.3 ± 3.4	/
9	9	68.1 ± 8.3	66.9 ± 8.9	3.4 ± 0.6	50.6 ± 7.6	39.1 ± 4.7	37.6 ± 8.2	40.7 ± 7.7	37.9 ± 5.3

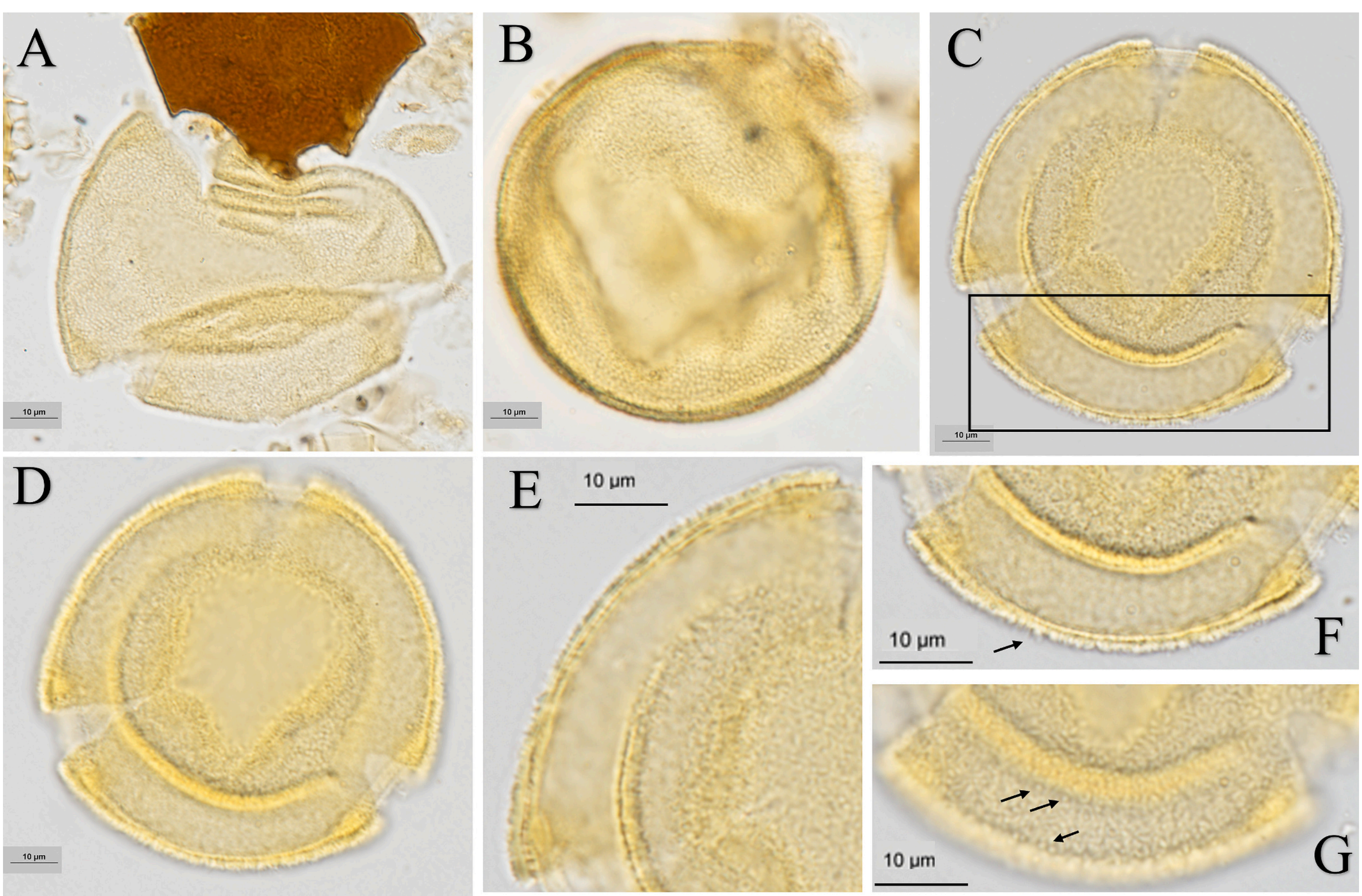

Fig. 8. A,B,C,D: pollen grains of *Linnaea borealis* in PaluOFF1 core (slides n. 11572-2024; 11574-2024) and E, F, G: details on echini (some are pointed by black arrows); photos taken with Nikon Digital Microscope.

4.1. The importance of detailed palynological analyses in biodiversity and palaeoecological studies

In this study, pollen analyses of both the palaeoecological study and the reference material were conducted at 1000× magnification using optical and digital optical microscopes, respectively. The decision to employ maximum magnification, although significantly more time-consuming than routine analyses typically performed at 400× or 600×, was driven by the aim of achieving the highest possible taxonomic resolution for each pollen grain. This approach enabled a more

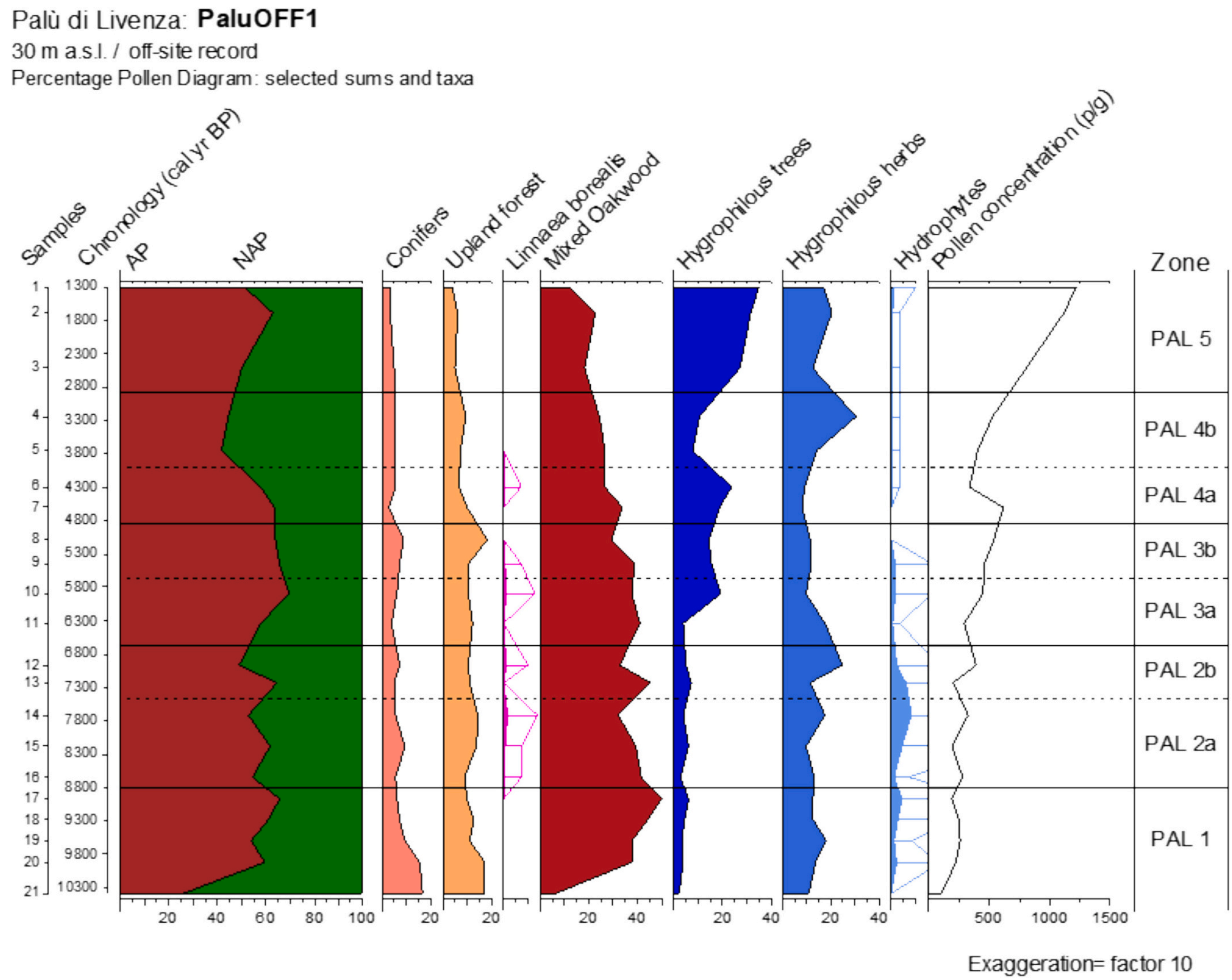

Fig. 9. Synthetic pollen diagram of the PaluOFF1 off-site core reporting some selected sums and taxa. AP includes arboreal pollen (trees, shrubs and lianas), NAP the non-arboreal pollen (herbs). *Linnaea borealis* curve is reported in pink. Other useful sums are presented such as: Conifers (including *Abies*, *Picea abies*, *Pinus*), upland forest (conifers + *Fagus sylvatica* and *Betula*), Mixed oakwood (*Acer campestre* type, *Carpinus betulus*, *Corylus avellana*, deciduous *Quercus*, *Ostrya carpinifolia/Carpinus orientalis* type, *Fraxinus excelsior* type, *Tilia platyphyllos* type, *Tilia cordata* type, *Ulmus*), hygrophilous trees (*Alnus*, *Populus*, *Salix*), hygrophilous herbs (Cyperaceae, *Lilium martagon*, *Lythrum*, *Pancratium* cf., *Paris* type, *Phragmites australis*, *Scilla* type, *Scirpus* type, *Sparganium emersum* type, *Typha latifolia* type) and hydrophytes (*Butomus umbellatus, Myriophyllum*, *Potamogeton, Sparganium erectum* type). Depth bars represent 10x exaggeration. Chronology is based on the age-depth model (Fig. 4) performed on radiocarbon dates and reported in cal yr BP. The diagram was drawn with Tilia software (Grimm, 2004). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

accurate identification process and led to the re-evaluation in permanent slides of some initial determination, ultimately resulting in the identification of *Linnaea borealis*.

In this sense, this research can be taken as an example of how palynological analyses carried out in past environments can stimulate new morphological research on pollen grains of target species that gave unexpected, interesting and useful results. In literature, there are numerous examples of studies of past contexts that document in-depth morphological novelties in palaeorecords. In prehistoric sites of northern Italy, Tecchiati et al. (2022) reports the identification of a peculiar *Tilia* pollen grain exhibiting morphological characteristics intermediate between those of *T. platyphyllos* type and *T. cordata* type (Beug, 2015; Punt et al., 1988) and led to the recognition of *Tilia* hybrids in the site of Colombare di Negrar di Valpolicella (Veneto); this finding shed light on the composition of the Neolithic floristic assemblage revealing new aspects of the local vegetation history. More southern, Mercuri et al. (2021) studied the dimorphism of *Vitis* pollen observed in the Bronze Age samples from the Terramara of Poviglio (Emilia-Romagna, central Po Plain): inaperturate pollen grains are produced by functionally female flowers while male and hermaphroditic flowers (as in domestic grapevine) usually produce tricolporate pollen; this can be a marker for possible discrimination between wild and domesticated *Vitis* (sub) species.

The occurrence of multiporate pollen in the Poaceae family, which usually is monoporate and uniform across different genera, has been reported for the prehistoric Takarkori rock shelter (Libya, Central Sahara; Mercuri et al., 2022; Florenzano et al., 2025); this morphologically distinct type of pollen can be interpreted as bioindicator of past environmental stresses, such as those that occurred with the climatic and ecological changes of the Early–Middle Holocene in the region. Another study on Poaceae (pollen size, shape, and surface ornamentation; Nazish and Althobaiti, 2022) was carried out on pollen grains of halophytic grasses allowing the discrimination of different species from saline environments, demonstrating that these features can effectively be used to distinguish between species, and offering a valuable tool for taxonomic and ecological studies in salt-affected habitats.

Recent palynological studies demonstrate the broad applicability of detailed morphological analyses of pollen, from reconstructing medieval plant diversity in Greece (e.g., Lamiaceae family; Comegna et al., 2024) and confirming honey consumption in medieval Belgium (Deforce, 2010), to supporting forensic investigations through high-resolution species identification. Notably, pollen evidence of specific taxon has been crucial in linking suspects to crime scenes (Mildenhall, 2006) and, in the cold case of Cangrande della Scala (Fornaciari et al., 2015) supported the hypothesis of poisoning through medicinal plants. These examples highlight the scientific and legal value of precise taxonomic pollen identification in archaeological and forensic contexts.

In our case, the application of in-depth morphological study of pollen to a plant species with well-defined climatic and ecological requirements (found beyond the boundaries of its optimal habitat) demonstrates the significant potential of palaeofloristic data in addressing complex biogeographical questions. Specifically, it highlights how high-resolution palynological analyses can contribute to identifying the temporal and spatial distribution patterns of rare and relict taxa. The study made it possible to address specific research questions, such as whether *L. borealis* truly inhabited the Friulian plain during the Neolithic (see below). This, in turn, contributes to a deeper understanding of the region's past biodiversity, and by extension, its vegetation and ecological dynamics.

4.2. The herbaria specimens supported the identification of *Linnaea* pollen

The study of herbarium specimens to learn about the pollen morphology of rare species is very useful to verify the reliability of problematic palynological identifications in past contexts. Several studies focus on one taxon (e.g., *Verbascum*: Mungan Kılıç, 2024; *Erigeron*: Noyes et al., 2015). Johnson et al. (2019) characterised pollen on stigmas of herbarium specimens from remnant native species and indirectly evaluated pollination interactions for plants in disturbed habitats on a century timescale. The information provided on herbarium vouchers has increased in recent years to improve knowledge on floristic lists from regions with conservation issues, also considering specimens of rare plants to develop habitat suitability models or predict range shifts as response to environmental changes (Molano-Flores et al., 2023). A list of de-extinction plant species candidates has been recently compiled from the current availability of herbarium specimens of globally extinct species (Albani Rocchetti et al., 2022). Jarzen and Jarzen (2006) underlined the importance to collect pollen or spore samples from vouchered herbarium specimens for systematic/basic or applied palynology (sensu Mercuri et al., 2015) because the plant specimens have been identified by trained systematists and the useful data on location and date of collection are usually associated with vouchers. However, the same authors point out that the collected material may not always contain well-preserved pollen, and in this sense indeed not all the herbarium samples studied here returned pollen useful for morphological analysis.

The herbarium specimens used in this study offered a good success rate (78%), but the low pollen production of this species and the presence of many pollen grains in poor condition meant that only a limited number of pollen grains could be measured. Nevertheless, the values recorded made it possible to clearly identify the discriminating factors of *Linnaea* pollen, distinguishing it from other similar pollen grains such as *Lonicera* or Caprifoliaceae (Punt, 1976). As one challenge that can arise when analysing past pollen samples is low preservation of pollen grains in ancient sediments (Dimbleby, 1985), the morphological study of reference pollen gave an important contribution to the correct identification of *Linnaea* pollen. The mean values of all parameters in the measured pollen grains are quite similar among the samples (Fig. 10), within the values reported in the reference morphological keys (Punt, 1976; Beug, 2015). Only a few exceptions were recorded (one in the P length, and 6 in E) where the P or E resulted to be longer (5 cases) or shorter (2 cases) than the limits described in the keys. These exceptions can be attributed to the state of preservation of the samples or intraspecific variability.

The criteria for distinguishing between similar taxa in pollen species may seem subtle because they can only be appreciated at high definition, but even small (descriptive and morphometric) variations in parameters have great phylogenetic value (Erdtman, 1954; Wodehouse, 1928). The most useful criteria in our study are known to be: i) the type of sculptures of the exine, which appears less echinate and supra-scabrate in *L. borealis*, whereas it is characterised by echini with no scabrae in all other Caprifoliaceae (Punt, 1976); ii) the pollen size, which on average is smaller in *L. borealis* than, for example, in *Lonicera*. Following Punt (1976), *L. borealis* has an average P and E of 40–50 μm while in the different types of the family, including *Lonicera* species, these measures are never less than 60 μm and 68 μm, respectively for P and E.

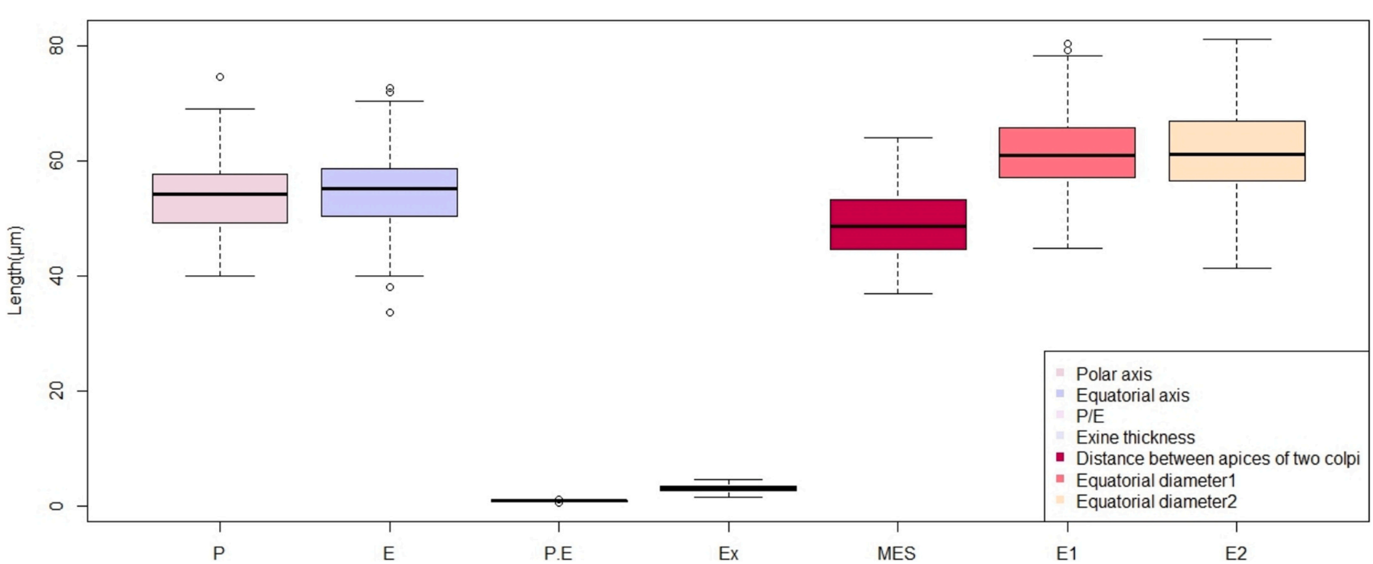

Fig. 10. Boxplot reporting the measured parameters in all pollen grains of *Linnaea borealis* from herbaria specimens. P = Polar axis (EV); E = Equatorial axis (EV); P/E = polar and equatorial axis ratio (EV); Ex = exine thickness (PV and EV); MES = mesocolpium (PV); E1 = equatorial diameter1 (PV); E2 = equatorial diameter 2 (PV).

Furthermore, in *Linnaea* the two axes P and E are almost equal, while in *Lonicera* types the longest axis is E. However, the largest *Linnaea* pollen size may overlap with the size range of *Lonicera* (e.g., following Beug, 2015): the mean size of the species included in *Lonicera periclymenun* Typ are 58.3–83 μm, and in *Lonicera xylosteum* Typ are 47–66.5 μm. In such cases, the best method of distinction is the examination of exine features. While both *Lonicera* and *Linnaea* exhibit echinate exines, the echini of *Linnaea* are smaller and finer (never more than 1 μm, while in the *Lonicera* types they can be up to 1.5 μm; Punt, 1976). Even so, it is possible that when the preservation is not ideal, *Lonicera* pollen have thinned-smaller echini too. In these cases, the key feature to consider for accurate identification is the exine ornamentation: *Linnaea* has scabrae on its exine, which are absent in *Lonicera* and other Caprifoliaceae pollen grains (Punt, 1976; Beug, 2015).

4.3. Did Linnaea borealis really live in the plain of Palù di Livenza?

In the Holocene core PaluOFF1, pollen records of *Linnaea borealis* are few (the average percentage in samples being 0.3% with only two samples reaching percentages >1.0%, i.e. 1.3% and 1.4% in sample no.10 and 14, respectively). This agrees with the fact that this is an entomophilous, and therefore low-pollen producer, species. By extracting DNA from many single leaves of *L. borealis*, researchers of the University of Edinburgh (UK) mapped the distribution of clones in highlands and established that many populations were at risk of local extinction due to limitations in reproduction and because the pollen dispersal distance of the species is only about 30 m (Wiberg et al., 2016).

Due to the low pollen production and low pollen dispersal, the record of this rare species in past pollen samples is very informative of the local growing of these plants in the off-site location. In fact, as mentioned above, no pollen of *L. borealis* was observed in the on-site records (Pini, 2004; Zappa et al., 2023). This allowed to infer that the species distribution during the Neolithic period was preferably in the southern part of the Palù basin. Moreover, in the off-site record, *L. borealis* is limited to the chronological period between c. 8600 and 4200 cal yr BP, which includes the Late Neolithic period (c. 6350–3600 cal yr BP) when pile-dwelling communities were settled in the basin (Fig. 9). For this period, the PaluOFF1 pollen diagram depicts a highly forested environment where woods were composed mainly by elements of the mixed oakwood and upland vegetation forests (conifers and other hilly-mountains trees such as *Fagus sylvatica* and *Betula*). Furthermore, wet environments were spread in the basin (Zappa et al., 2023; Zappa, 2025); the local appearance of *L. borealis* is concurrent to the maximum in the expansion of hygrophytes (PAL2a) and an increase of conifer and upland forest. Pollen data suggests that this species, that today thrived among mosses in acidic conifer and mixed oakwood forests, in the past was widespread in cool mixed forests that were widely distributed, on acidic soils and in colder climatic conditions. Based on local and global records from the Holocene (Walker et al., 2012), it is known that during the Middle and Late Holocene (8200–4200 cal yr BP and 4200 cal yr BP to the present), phases of humid and cold conditions alternated with warmer and arid periods. Local records (e.g., Magny et al., 2012; Vannière et al., 2013) also confirm significant regional variability. In the PaluOFF1 sequence, in the period between approximately 8600 and 4200 cal yr BP, the local pollen assemblage suggests that colder conditions persisted in the basin, even as climate changes were already occurring in other regions, and records of *Linnaea borealis* support this inference during the Neolithic period. However, *L. borealis* pollen has not yet been recorded in the on-site records. This means that there is no direct evidence that local populations used or tended this plant, even though its medicinal uses are currently known (Thiem and Buk-Berge, 2017). The Palù basin appears to have been visited occasionally for hunting and gathering by people, who may have been aware of some of the plant's uses.

In general, in northern Italy *L. borealis* is not often identified in palynological analyses in natural or archaeological sites. This could be attributed to the fact that it is an entomophilous species that produces and disperses less pollen than anemophilous plants. Additionally, the species' distribution has historically been limited due to its specific climatic requirements, as already mentioned, which further hindered its detection in sediment samples. Differently, *Lonicera* is normally found in Quaternary studies of natural sites, albeit in relatively low quantities (e.g., several lakes and bogs cores in Trentino region; Seiwald, 1980).

4.4. Records of Linnaea vs Lonicera in European palaeorecords

Widening research to Europe, using the Neotoma Paleoecological Database (Williams et al., 2018), some palynological studies report *Linnaea borealis* in the period from 10,000 to 2000 cal yr BP, whereas *Lonicera* is present in a larger number of studies (Fig. 11). Most of the sites where *L. borealis* was found are peatbogs and lakes in the Scandinavian peninsula (14 sites), Poland (2), Russia (1), Romania (2), Austria (1), Switzerland (1) and United Kingdom (1).

The closest records to our study area are located in Austria (Krisai, 1975, 2010) and Switzerland (Gobet et al., 2003). The first one refers to a study performed in a raised bog at c. 500 m a.s.l. in Salzburg, where one pollen grain of *L. borealis* was found in one sample dated to c. 9490 cal yr BP. The second one refers to a palynological study by Gobet et al. (2003) in the Upper Engadine Valley located in the central Alps at c. 1700 m a.s.l., where one pollen grain of *L. borealis* was found in a sample dated at c. 2380 cal yr BP. This pollen was found in a pollen zone characterised by high forestation cover with majority of conifers and upland species. This seems to confirm the difficulty of the finding of pollen grains of this species even in an upland environment, possibly with ideal ecological and climatic conditions to the proliferation of this species.

As the occurrence of *Linnaea borealis* is extremely rare in palynological records, the presence in multiple samples from the PaluOFF1 core is particularly significant. The findings of *Linnaea* in the Palù record are a further proof of the noteworthy local presence or persistence of the species during the Neolithic period.

More northern in Europe, given the difficulty of finding plant remains of this species, also molecular analysis has been useful to detect its presence. This is the case of the study by Salonen et al. (2024), who identified *Linnaea borealis* among other shrubs thanks to sedaDNA (sedimentary DNA) analysis from lakes and peat bogs in Finland. SedaDNA allowed to identify, among other plants, the presence of *L. borealis* at 4400 cal yr BP helping in reconstructing the environmental and climatic history of the region and revealing changes in vegetation throughout the Holocene (Salonen et al., 2024).

Tsymbalyuk and Bezusko (2017) performed a palaeofloristic study aiming at evidencing the distribution of *L. borealis* in forest and forest-steppic environments in Ukraine. *L. borealis* pollen was documented in both lowlands and, on the Carpathians, in forest and forest-steppic environments. Data confirmed a highly relevant presence of the species in the floristic assemblage during the Late Pleistocene period, and during the Early and Middle Holocene (with a limit in its distribution at c. 2900 cal yr BP). In the last 800–1000 years, the pollen of *L. borealis* has been no longer found in lowlands areas, but it was only limited to upland zones. They concluded that palaeofloristic data are crucial to investigate and solve the problem of the temporal and spatial distribution of relict species (Tsymbalyuk and Bezusko, 2017). This pattern also applies to our study area, the lowlands of north-eastern Italy. While today *Linnaea borealis* has a highly restricted distribution, confined to high-mountain habitats above approximately 1300 m a.s.l. due to its specific climatic and environmental requirements, it is likely that at the beginning of the Holocene its range was significantly broader, potentially extending into lower-altitude areas as a result of more favourable environmental conditions for its surviving and spreading at that time.

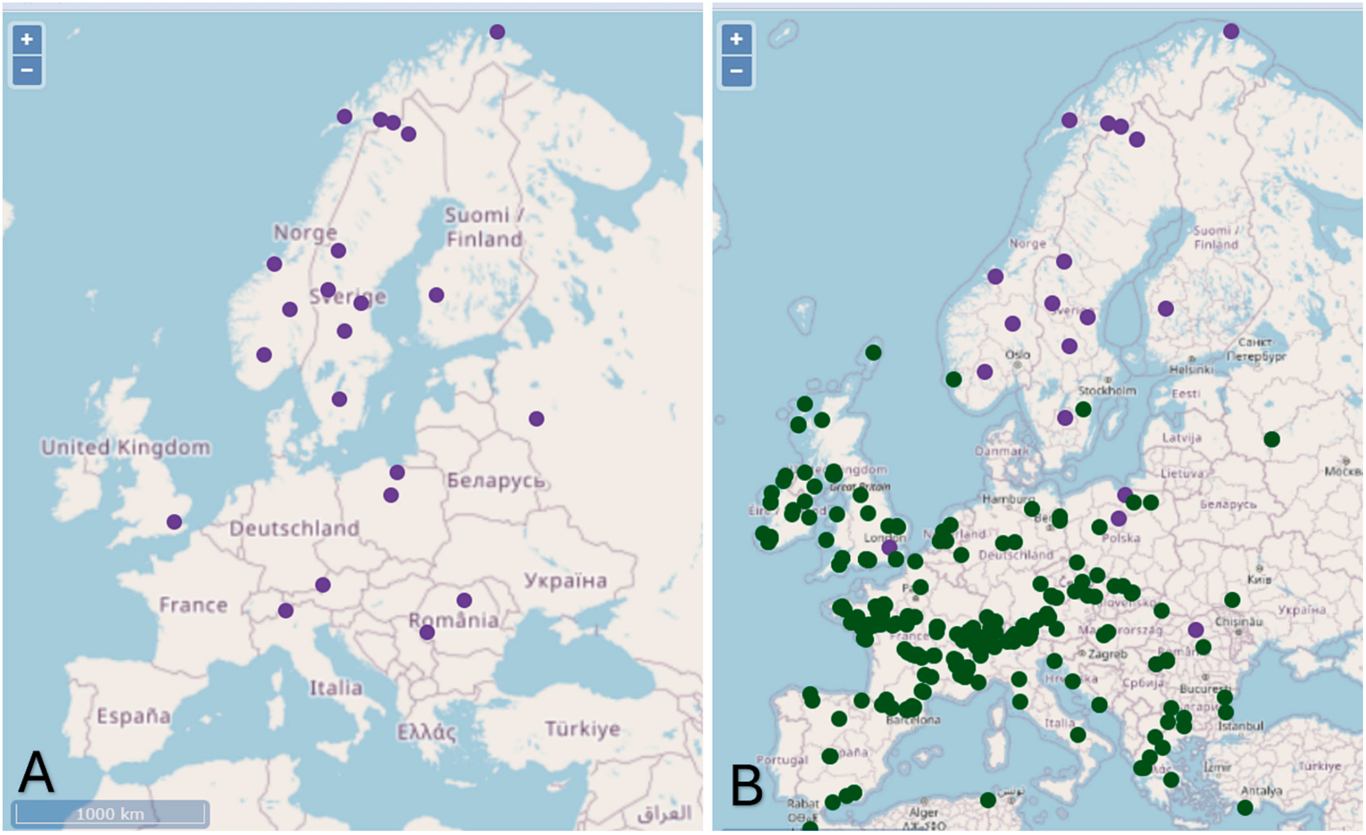

Fig. 11. Search for *Linnaea borealis* and *Lonicera* pollen in the Neotoma Paleoecology Database (Williams et al., 2018; http://www.neotomadb.org), considering palynological studies with a chronology between 10,000 and 2000 cal yr BP. A: *L. borealis* in (purple dots); B: *Lonicera* (green dots), added to *L. borealis* (purple dots). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

5. Conclusions

This research emphasises the uniqueness of the record of *Linnaea borealis* pollen in the lowland context Palù di Livenza in north-eastern Italy. The identification was supported by a morphological study that was carried out on pollen from herbaria and from palaeorecords. Pollen parameters (e.g., dimensions, shape, structure, exine thickness and exine sculpturing) were measured in modern and fossil samples. The exine structure and pollen size were found to be the most diagnostic pollen characters for the identification of this target species. The identification of pollen of *L. borealis* in the off-site PaluOFF1 in the palaeoecological record suggests that this species was quite spread locally in the Early-Middle Holocene period (Zappa, 2025). In accordance with the chronology, this species is a marker of the permanence of cool conditions in this basin where the species was significantly present; furthermore, the concomitance of its presence with the Neolithic settlement suggests a possible exploitation of the plant for its medicinal properties.

The use of herbarium specimens to study target species has proven to be invaluable in biodiversity research. Herbarium collections, which often include detailed historical and geographical data, can offer critical insights into species that are now rare, threatened, or endangered. In our study, access to floral specimens from herbarium collections provided essential reference material, enabling a detailed analysis of pollen grain features. In addition, the rigorous methodology (in our study, permanent slides and 1000 × magnifications) applied in palynological analyses of palaeoecological records demonstrates the potential of pollen analysis to provide valuable insights into past biodiversity, the distribution of plant species, and the environmental conditions in which these species thrived or disappeared often uncovering unexpected, intriguing, and practically relevant findings.

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Declaration of competing interest

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

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Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

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