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Tracing hydrological and ecological dynamics in a volcanic barrier-lake system in NE Iberia during the Late Glacial–Early Holocene using non-pollen palynomorphs☆

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ABSTRACT

The environmental evolution of volcanic barrier-lake systems is shaped by complex interactions between climate forcing and local geomorphological processes. This study presents a high-resolution multi-proxy record from the sedimentary sequence of Pla de les Preses volcanic barrier-palaeolake (Vall d'en Bas, NE Iberia), spanning the Late Glacial–Early Holocene transition. Particular emphasis is placed on the contribution of non-pollen palynomorphs (NPPs) to palaeoenvironmental reconstruction.

Pollen data indicate that regional vegetation dynamics broadly follow the expected transition from open Late Glacial landscapes to temperate deciduous forests during the Early Holocene. However, notable deviations occur, including a marked decline in broadleaf forests, suggesting a strong influence of local disturbance processes.

Sedimentological and palaeobiological proxies document the formation of a volcanic barrier lake following the damming of the Fluvià River, and its subsequent evolution through three main stages: (i) shallow, unstable conditions with pioneer aquatic communities, (ii) progressive deepening and establishment of a persistent lacustrine system, and (iii) lake shallowing, wetland expansion and final terrestrialisation linked to barrier erosion and fluvial reactivation. Hydrological changes do not always align with regional climatic trends, indicating a decoupling between climate and local environmental processes.

NPP assemblages provide key insights into these dynamics, recording variations in water depth, aquatic productivity, trophic conditions and lake–catchment interactions. Algae and cyanobacteria reflect limnological variability, while pteridophyte spores and fungal remains document wetland development, soil erosion processes and terrestrial inputs. In addition, NPPs capture short-term ecological responses to volcanic activity and fire. This study demonstrates the value of NPPs for reconstructing highly dynamic lacustrine systems, complementing pollen-based approaches and enabling a more detailed understanding of palaeoenvironmental change.

1. Introduction

Non-pollen palynomorphs (NPPs) constitute a diverse group of organic-walled microremains preserved in sedimentary archives, including fungal spores, algae, cyanobacteria and other non-pollen microfossils. Unlike pollen, which often reflects regional vegetation patterns and long-distance dispersal processes, many NPPs derive from local production and are deposited close to their source (van Geel, 2001). As a result, NPP assemblages provide sensitive indicators of local environmental conditions, including hydrological fluctuations and nutrient status (van Geel et al., 1994; McCarthy et al., 2018), local-scale soil disturbance and catchment-scale soil erosion (van Geel et al., 1989; Hillbrand et al., 2012), decomposition processes (Barthelmes et al., 2006), wetland development and lake-level variability (Revelles and van Geel, 2016; Torres-Rodríguez et al., 2018), animal husbandry and grazing intensity (van Geel et al., 2003; Gauthier et al., 2010), and fire disturbance (Innes and Blackford, 2003; Blackford et al., 2006). Continuous improvements in taxonomic identification and ecological

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calibration have further strengthened their interpretative potential in palaeoenvironmental research.

The La Garrotxa Volcanic Field (GVF), located in NE Iberia, represents the youngest monogenetic volcanic area of the Iberian Peninsula. Volcanic activity during the Late Pleistocene and Early Holocene produced lava flows that repeatedly dammed the Fluvià River, forming lacustrine basins in the Vall d'en Bas valley (Fig. 1). Recent multiproxy research on the Pla de les Preses (PdP) core demonstrated that volcanic damming around 14 ka cal BP triggered the formation of a barrier lake whose evolution was shaped by climatic oscillations and recurrent explosive activity until ca. 8.4 ka cal BP (Iriarte et al., 2023). This sequence also revealed previously undocumented Early Holocene eruptions, extending the eruptive chronology of the GVF and identifying the youngest known volcanic activity in Iberia (Iriarte et al., 2023).

Previous studies based on the PdP sequence reconstructed the sedimentological, geochemical and aquatic palaeoecological evolution of this barrier-lake system (Iriarte et al., 2023) and assessed the broader socioecological consequences of volcanic disturbances using selected pollen taxa and grouped palaeoecological indicators (Revelles et al., 2023). However, neither study presented the complete palynological dataset or a comprehensive analysis of the non-pollen palynomorph assemblages. Here, we report the full pollen and NPP record, including all identified taxa, and provide the first detailed assessment of the ecological significance of NPPs. NPPs are particularly sensitive to local ecological responses, including shoreline displacement, subaerial exposure, peat initiation and trophic shifts, thereby providing key insights into the processes governing the evolution of highly dynamic lake–basin systems.

This study presents a comprehensive analysis of NPP assemblages from the PdP core. Building upon the established chronostratigraphic and sedimentological framework (Iriarte et al., 2023), we aim to:

1. Characterise NPP assemblage changes across the main geomorphological phases of the Vall d'en Bas barrier-lake system.
2. Assess the ecological responses of aquatic and wetland communities to repeated volcanic disturbances.
3. Evaluate the sensitivity of NPPs to Early Holocene rapid climate changes (9.3 and 8.2 ka events).
4. Demonstrate the value of NPPs as key proxies for reconstructing hydrological and ecological transitions in volcanic landscapes.

2. Study area

The study area is located in the Vall d'en Bas valley, within the GVF, on the southern flank of the Eastern Pre-Pyrenees (NE Iberia). La Garrotxa is a mountainous region characterised by a complex topography that combines tectonic depressions and volcanic landforms with surrounding relief exceeding 1500 m a.s.l.

The Vall d'en Bas constitutes a structural depression formed within a fault-controlled basin, clearly differentiated into a flat plain (mean altitude ~500 m a.s.l.) bordered by steep slopes and mountainous ridges. During the Quaternary, successive basaltic lava flows descending from the GVF repeatedly obstructed the Fluvià River, generating temporary lacustrine basins (Fig. 1). These volcanic barriers played a key role in shaping the geomorphological evolution of the valley and promoted the accumulation of thick sedimentary sequences.

The region acts as an orographic barrier to moist Mediterranean air masses, resulting in relatively high annual precipitation (ca. 800–1000 mm) compared to surrounding lowlands. Present-day vegetation reflects this humid mountainous setting and includes mixed deciduous forests dominated by *Fagus sylvatica*, *Quercus robur* and *Quercus pubescens*, alongside *Pinus sylvestris* and evergreen *Quercus ilex* on sunnier slopes. Riparian communities composed of *Alnus glutinosa*, *Salix* spp. and *Corylus avellana* develop along fluvial corridors.

This geomorphological and climatic setting provides favourable conditions for the preservation of lacustrine and wetland sedimentary archives, making the Vall d'en Bas valley an exceptional site for investigating Late Glacial and Early Holocene environmental dynamics.

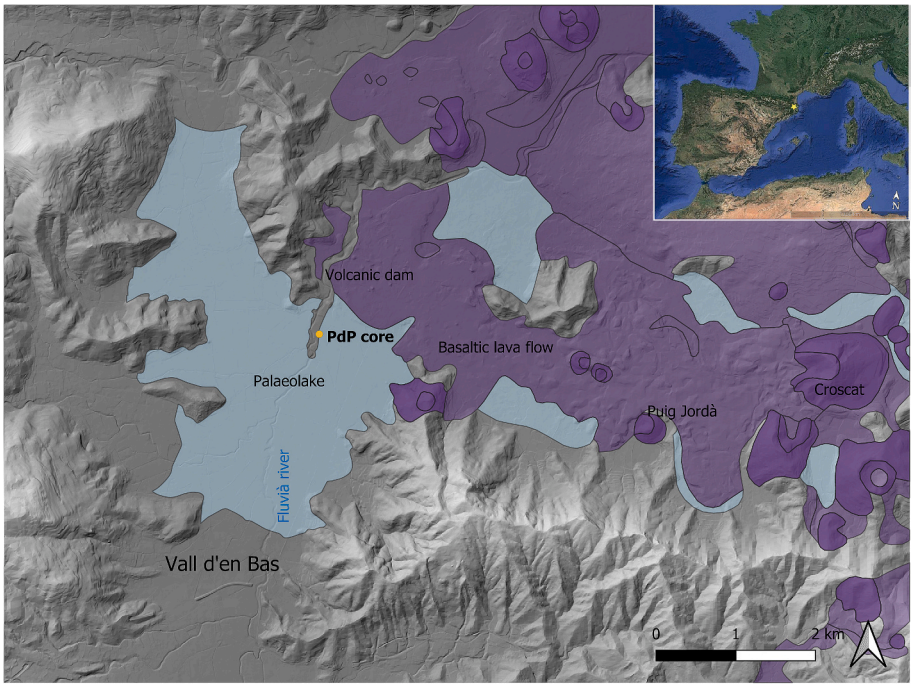

Fig. 1. Location and geomorphological context of the Pla de les Preses (PdP) core in the Vall d'en Bas basin (NE Iberian Peninsula). The map shows the approximate extent of the palaeolake formed by the volcanic damming of the Fluvià River, the position of the PdP core, and the distribution of basaltic lava flows associated with the Garrotxa Volcanic Field (GVF), including key volcanic centres such as Croscat and Puig Jordà. Shaded relief illustrates the local topography. The inset indicates the geographical location of the study area within southwestern Europe.

3. Material and methods

3.1. The Pla de les Preses core

The sedimentary sequence analysed in this study corresponds to the PdP core (UTM 455189.0 X/4667356.0 Y/458.1 m a.s.l.), retrieved from the Vall d'en Bas valley within the GVF (NE Iberia). The core (15 m length) documents the formation and evolution of a volcanic barrier-lake system spanning from the Late Glacial to the Middle Holocene. Core recovery, lithostratigraphy, sedimentological facies, geochemical analyses (XRF) and the detailed chronostratigraphic framework have been described extensively in Iriarte et al. (2023). The sequence is constrained by 15 AMS radiocarbon dates and a Bayesian age–depth model constructed using rBacon (Blaauw and Christen, 2019) allowed to calculate the age of the entire core, ranging from present to ca.14 ka cal. BP, covering the Late Glacial to the Late-Holocene.

3.2. Multi-proxy methodology

The palaeoenvironmental and limnological evolution of the PdP sequence has previously been investigated through an integrated multi-proxy approach (Iriarte et al., 2023; Revelles et al., 2023). These studies combined sedimentological, geochemical and micropalaeontological analyses to reconstruct lake formation, hydrological fluctuations, volcanic disturbances and ecosystem dynamics.

Sedimentological analyses included lithofacies characterisation and stratigraphic description of carbonate-rich lacustrine muds, organic horizons, volcaniclastic deposits and fluvial sediments. Geochemical variability was assessed using X-ray fluorescence core scanning (XRF-CS), allowing identification of minerogenic input, carbonate content and volcanic layers.

Biological proxies (apart from pollen and NPPs) comprised aquatic microfossils such as ostracods, diatoms and charophytes (macroalgae) to infer limnological conditions, including water depth, temperature and trophism. Previous work also incorporated charcoal analyses to assess fire activity and its ecological implications. The methodological procedures, laboratory protocols and analytical settings for these proxies are described in detail in Iriarte et al. (2023) and Revelles et al. (2023). In the present study, we focus specifically on the systematic analysis and ecological interpretation of non-pollen palynomorph (NPP) assemblages within this established multi-proxy framework.

3.3. Pollen and non-pollen palynomorphs analysis

The present study focuses on pollen and NPP assemblages from the Late Glacial and Early Holocene interval (~14–8 ka cal BP), corresponding to the lacustrine and wetland phases of the Vall d'en Bas paleolake system. Younger deposits (above 650 cm), which represent the subsequent floodplain phase, were not considered because they are characterised by very low pollen concentrations. This is consistent with the sedimentological characteristics of this interval, which is dominated by silty floodplain deposits with low organic matter content. Deposition under fluctuating hydrological conditions likely promoted oxidation and pollen degradation, leading to poor pollen preservation and consequently low pollen concentrations.

Palynological samples were taken at 3–5 cm intervals within organic clayish and peaty facies and at 10 cm intervals within inorganic silts corresponding to fluvial deposits. Laboratory preparation followed standard palynological procedures (Girard and Renault-Miskovsky, 1969) including treatment with HCl and NaOH, flotation in Thoulet heavy liquid, HF digestion, and final mounting in glycerine. A minimum of 300 terrestrial pollen grains per sample were counted using an Olympus Bx43 microscope equipped with 10x oculars and 40/60x objectives. The pollen sum included terrestrial taxa only, while hygrophytic taxa (Cyperaceae, *Ranunculus*, *Typha latifolia* and *Typha angustifolia/Sparganium*) and aquatic plants (*Myriophyllum, Nuphar, Nymphaea, Potamogeton*) were excluded. Pollen identification was based on standard atlases and reference collections. Non-pollen palynomorphs were identified following established morphological criteria (see Table 1). Full taxonomic nomenclature and NPP type classification are provided in Figs. 2 and 3 and in Table 1, while simplified names are used in the Discussion for text clarity.

Pollen and NPPs percentages were calculated relative to the terrestrial pollen sum, and diagrams were produced using Tilia software (Grimm, 1991-2011). Although pollen analysis was conducted throughout the sequence, samples from the upper 650 cm yielded low pollen concentrations; therefore, only the interval between 14.0 and 8.0 ka cal BP is considered here. Pollen assemblage zones were defined using CONISS stratigraphically constrained cluster analysis (Grimm, 1987). For the pollen dataset, zonation was performed on square-root transformed percentage data to reduce the dominance effect of high-abundance taxa while preserving relative compositional structure. For the NPP dataset, Orloci's chord distance was used in order to minimise the influence of extreme abundance peaks (in some cases reaching 300–800%) and to reduce the disproportionate effect of these values on hierarchical clustering. Pollen and NPP zonations were therefore calculated independently to assess whether local-scale ecological dynamics paralleled or diverged from regional vegetation trends.

3.4. Statistical analysis

Relationships among non-pollen palynomorph (NPP) taxa were explored through correlation and ordination analyses. Pairwise correlations between taxa were calculated using Spearman's rank correlation coefficient using the vegan package in R (Oksanen et al., 2022), which is appropriate for ecological datasets characterised by non-normal distributions and a high proportion of zero values. Correlations were computed on the matrix of relative abundances of NPP taxa.

To explore the structure of the NPP assemblages, identify potential ecological gradients, and evaluate the relative contribution of different NPPs to differentiation between zones we used between-group Principal Component Analysis (bgPCA) and multiple Linear Discriminant Analysis (LDA) (Boulesteix, 2004; Taranu et al., 2023). Before ordination, the dataset was transformed using the Hellinger transformation, which reduces the influence of highly abundant taxa and makes species abundance data suitable for linear ordination methods (Legendre and Gallagher, 2001). bgPCA was performed using the correlation matrix in PAST v. 5.0 (Hammer et al., 2001). LDA with stepwise selection of significant NPPs variables contributing most to zone discrimination was performed in IBM® SPSS® Statistics v. 28.0 (IBM Corp., 2021).

4. Results

4.1. Pollen

Two main pollen zones (A and B), subdivided into four sub-zones, were defined through CONISS cluster analysis (Fig. 2).

- Sub-zone A1 (1013–1267 cm; 12.4–14.0 ka cal BP). This interval is characterised by the predominance of *Pinus*, accompanied by relatively high values of *Betula* in several samples and occasional peaks of *Juniperus*. *Quercus pubescens*-type and *Corylus* occur sporadically and at very low percentages. Open-land taxa reach their highest representation in this sub-zone, particularly Poaceae and *Artemisia*, with Amaranthaceae present but consistently lower than the former two (Fig. 2). Hygrophilous taxa show notable fluctuations, with peaks of Cyperaceae and high values of *Myriophyllum* between 1030 and 1180 cm (ca. 13.5–12.5 ka cal BP),
- Sub-zone A2 (917–1006 cm; 11.7–12.3 ka cal BP). *Pinus* remains dominant but displays a declining trend compared to Sub-zone A1. *Betula* shows a slight expansion, while *Acer* increases and *Juniperus* forms a continuous curve. *Quercus pubescens*-type also becomes

Table 1
Nomenclature and classification of non-pollen palynomorphs (NPPs) identified in this study. The table includes taxonomic or morphotype names, corresponding laboratory codes (e.g. HdV, UAB, EMA), and bibliographic references to their original descriptions or standard identification sources. Fern spores (pteridophytes) are reported following conventional palynological nomenclature (e.g. Moore et al., 1991; Reille, 1992), whereas other non-pollen palynomorphs are classified according to the morphological typology established by several studies.

Group	Taxon/Morphotype	Lab. Code	Reference
Pteridophytes	Monoletes		Moore et al. 1991; Reille 1992
Pteridophytes	*Polypodium*		Moore et al. 1991; Reille 1992
Pteridophytes	*Asplenium*-type		Moore et al. 1991; Reille 1992
Pteridophytes	*Pteridium*		Moore et al. 1991; Reille 1992
Pteridophytes	*Ophioglossum*-type		Moore et al. 1991; Reille 1992
Pteridophytes	*Lycopodium*-type		Moore et al. 1991; Reille 1992
Pteridophytes	*Selaginella*-type		Moore et al. 1991; Reille 1992
Pteridophytes	*Osmunda*-type		Moore et al. 1991; Reille 1992
Plant remains	Suberized basal cells of hairs of Nymphaeaceae	HdV-127	Pals et al., 1980
Plant remains	Cyperaceae root hair		Revelles and van Geel, 2016
Plant remains	Coniferous tracheids	HdV-218	van Geel et al., 1989
Algae	*Botryococcus*		Kuhry, 1997
Algae	*Spirogyra*	HdV-130	Pals et al., 1980
Algae	*Spirogyra*	HdV-210	van Geel et al., 1989
Algae	*Mougeotia*		Pals et al., 1980
Algae	*Mougeotia laetevirens*	HdV-373	van Geel and van der Hammen, 1978
Algae	*Zygnema*-type	HdV-314	van Geel et al., 1981
Algae	*Tetraëdron*	HdV-371	van Geel et al., 1981
Algae	*Closterium idiosporum*	HdV-60	van Geel, 1978
Algae	*Pseudoschizaea*		Scott, 1992
Cyanobacteria	*Gloeotrichia*	HdV-146	van Geel et al., 1983
Cyanobacteria	*Anabaena*	HdV-601	van Geel et al., 1994
Cyanobacteria	*Aphanizomenon*	HdV-600	Ralska-Jasiewiczowa and van Geel, 1992
Cyanobacteria	*Rivularia*-type	HdV-170	van Geel et al., 1983
Fungi	*Glomus*	HdV-207	van Geel et al., 1989
Fungi	*Gaeumannomyces*	HdV-126	Pals et al., 1980
Fungi	*Diporotheca rhizophila*	HdV-143	van Geel et al., 1989
Fungi	*Sphaerodes*	TM-020	Cugny, 2011
Fungi	*Melanographium*	TM-111	Cugny, 2011
Fungi	*Thecaphora*	HdV-364	van Geel et al., 1981
Fungi	Type 361	HdV-361	van Geel et al., 1981
Fungi	*Sporormiella*	HdV-113	van Geel et al., 2003
Fungi	*Sordaria*-type	HdV-55A	van Geel, 1978
Fungi	*Sordaria*-type	HdV-55B	van Geel, 1978
Fungi	*Podospora*-type	HdV-368	van Geel et al., 1981
Fungi	*Cercophora*-type	HdV-112	van Geel et al., 1981
Fungi	*Apiosordaria verruculosa*	HdV-169	van Geel et al., 1983
Fungi	*Arnium*-type	HdV-261	van Geel et al., 2003
Fungi	*Delitschia*	UAB-34A/B	Revelles et al., 2016
Fungi	*Coniochaeta* cf. *C. ligniaria*	HdV-172	van Geel et al., 1983
Fungi	*Coniochaeta xylariispora*	HdV-6	van Geel, 1978
Fungi	*Gelasinospora*	HdV-1	van Geel, 1978
Fungi	*Gelasinospora* cf. *G. retispora*	HdV-2	van Geel, 1978
Fungi	*Chaetomium*	HdV-7a	van Geel, 1972
Fungi	*Kretzschmaria deusta*	HdV-44	van Geel, 1978
Fungi	*Neurospora*	HdV-55C	van Geel, 1978
Fungi	Type 2	UAB-2	Revelles et al., 2016
Fungi	Type 4	UAB-4	Revelles et al., 2016
Fungi	Type 8	UAB-8	Revelles et al., 2016
Fungi	Type 9	UAB-9	Revelles et al., 2016
Fungi	Type 10	UAB-10	Revelles et al., 2016
Fungi	Type 11	UAB-11	Revelles et al., 2016
Fungi	Type 12	UAB-12	Revelles et al., 2016
Fungi	Type 14	UAB-14	Revelles et al., 2016
Fungi	*Brachysporium britannicum*	EMA-120/ UAB-17	Prager et al., 2012/ Revelles et al., 2016
Fungi	*Bactrodesmium*-type	UG-1091/ UAB-18B	Gelorini et al., 2011/ Revelles et al., 2016
Fungi	Type 20	UAB-20	Revelles et al., 2016
Fungi	Type 21	UAB-21	Revelles et al., 2016
Fungi	Type 30 A	UAB-30A	Revelles et al., 2016
Fungi	*Savoryella lignicola*	UG-1118/ UAB-35	Gelorini et al., 2011/ Revelles et al., 2016
Fungi	Type 36	UAB-36	Revelles et al., 2016
Fungi	Type 38	UAB-38	Revelles et al., 2016
Fungi	*Xylomices chlamydosporus*-type	KNG-7/ UAB-40	Shumilovskikh et al., 2017/Shumilovskikh et al., 2017
Fungi	Type 41A	UAB-41A	Revelles et al., 2016
Fungi	Type 41B	UAB-41B	Revelles et al., 2016
Fungi	Type 41C	UAB-41C	Revelles et al., 2016
Fungi	*Ityorhoptrum*	UY-119/ UAB-50	Leal et al., 2021/ Revelles et al., 2016
Other	Type 128	HdV-128	Pals et al., 1980
Other	Type 182	HdV-182	van Geel et al., 1983
Other	Type 988	HdV-988	Carrión and van Geel, 1999
Animalia	Oribatida (Type 36)	HdV-36	van Geel, 1978
Animalia	*Trichuris* sp.		van Geel et al., 1983

continuous, although still represented by very low percentages. Open-land taxa (Poaceae and *Artemisia*) remain important but decrease relative to the previous sub-zone. Hygrophilous elements, particularly Cyperaceae, decline markedly, and *Myriophyllum* becomes scarce.

- Sub-zone B1 (754–910 cm, 9.1–10.5 ka cal BP). This sub-zone is marked by the abrupt expansion of *Corylus*, which becomes the dominant taxon, accompanied by increasing values of *Quercus pubescens*-type and significant representation of *Ulmus*. In contrast, *Pinus* undergoes a sharp decline, together with *Betula*, *Acer* and *Juniperus*. Open-land taxa (Poaceae and *Artemisia*) reach very low percentages, reflecting forest expansion. Hygrophilous taxa are also scarce, although aquatic plants such as *Nuphar* and *Nymphaea* appear (Fig. 3).
- Sub-zone B2: 670–746 cm (8.1–9.1 ka cal BP). This interval records an abrupt decline in *Corylus* and *Quercus pubescens*-type, accompanied by a regression of *Ulmus*. Conversely, *Pinus* expands markedly, and slight increases in *Abies* and *Tilia* are observed. *Poaceae* percentages rise again, indicating a partial reopening of the landscape. Hygrophilous taxa, particularly Cyperaceae, increase significantly.

4.2. Non-pollen palynomorphs

Two main NPP zones were identified (Zones A and B). Zone A was subdivided into two subzones (A1 and A2), with subzone A1 being divided into three additional subzones (A1a–A1c) (Figs. 3, 4):

- Sub-zone A1 (922–1267 cm; 11.7–14.0 ka cal BP).
  - ◆ A1a (1191–1267 cm; 13.5–14.0 ka cal BP). This interval is characterised by the occurrence of cyanobacteria and green algae, including *Gloeotrichia* (type 146, HdV), *Aphanizomenon* (type 600, HdV), *Botryococcus*, *Zygnema*-type (type 314, HdV) and *Spirogyra* (type 130, HdV) (Fig. 3). High peaks of *Ophioglossum*-type spores and elevated values of Oribatida (type 36C, HdV) are recorded (Fig. 3). *Glomus* is abundant, while fungal

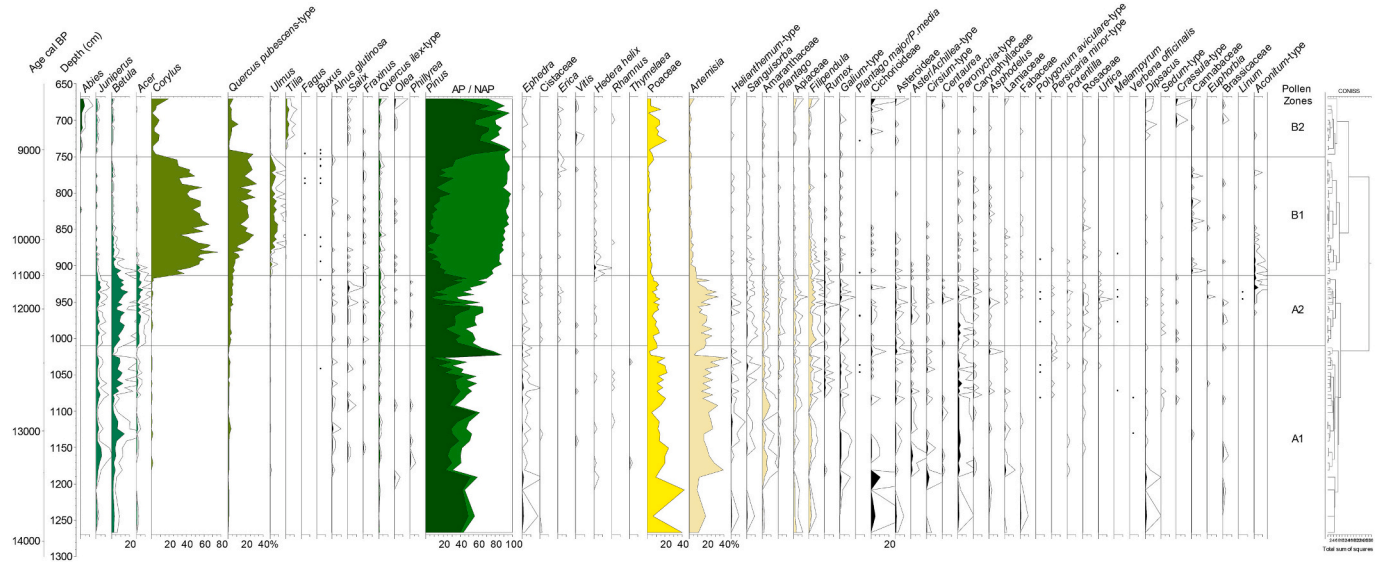

Fig. 2. Pollen percentage diagram of the Pla de les Preses (PdP) core showing the main terrestrial taxa and selected ecological groups plotted against depth (cm) and calibrated age (cal BP). Pollen assemblage zones (A1–B2) were defined using stratigraphically constrained cluster analysis (CONISS). Exaggeration curves are shown as hollow (white) silhouettes to enhance low-percentage taxa: these correspond to ×3 exaggeration when associated with coloured curves and ×10 exaggeration when associated with black curves.

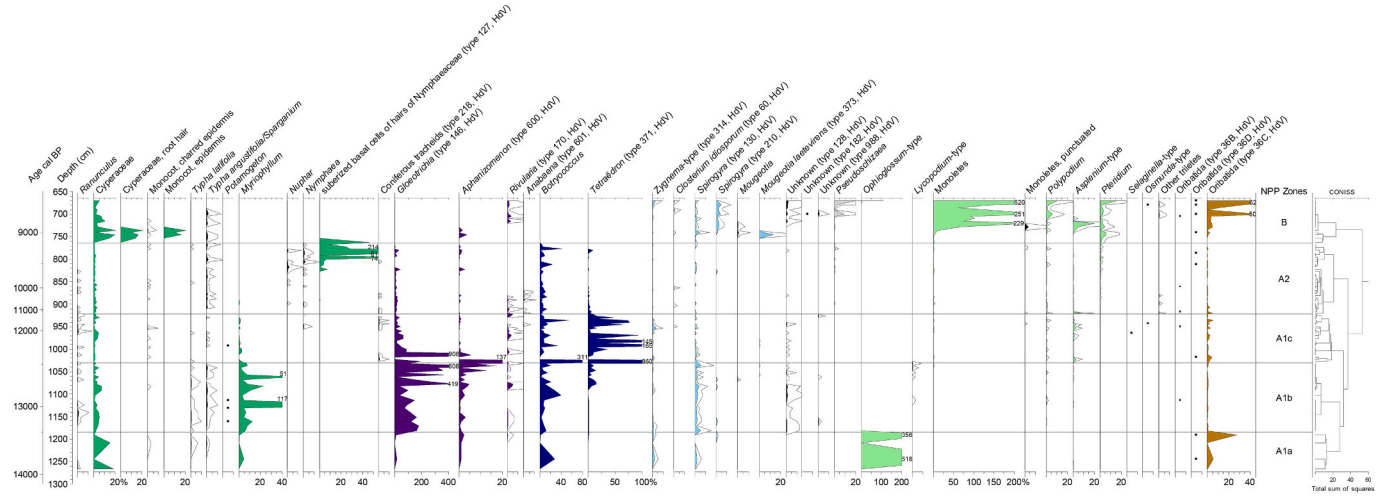

Fig. 3. NPP percentage diagram of the Pla de les Preses (PdP) core showing aquatic plants, cyanobacteria, algae, pteridophytes and other microfossils. NPP assemblage zones (A1a–B) were defined using stratigraphically constrained cluster analysis (CONISS). Exaggeration curves enhance low-percentage taxa, corresponding to ×3 and ×10 exaggeration.

spores are generally scarce and sporadic, including *Coniochaeta* cf. *C. ligniaria* (type 172, HdV), *Sordaria*-type (type 55 A, HdV), type 2 (UAB) and type 41B (UAB) (Fig. 4).

- A1b (1037–1181 cm; 12.5–13.5 ka cal BP). This subzone shows very high values of *Gloeotrichia* (type 146, HdV), forming a continuous curve with minimum values around 100% and peaks reaching 400–600%. *Aphanizomenon* (type 600, HdV) also forms a continuous curve with an increasing trend. *Rivularia* (type 170, HdV) appears. *Botryococcus* maintains a continuous curve with intermittent peaks, while *Tetraëdron* (type 371, HdV) first appears and increases towards the top of the subzone. *Spirogyra* (type 130, HdV) and type 128 (HdV) display continuous curves (Fig. 3). Fungal spores occur sporadically and without clear peaks, including *Gelasinospora* cf. *G. retispora*, (type 2, HdV), *Diporotheca rhizophila* (type 143, HdV) and type 41A (UAB) (Fig. 4).
- A1c (922–1032 cm; 11.7–12.5 ka cal BP). Coniferous tracheids (type 218, HdV) are recorded. This interval contains the highest peaks of *Gloeotrichia* (type 146, HdV) and *Aphanizomenon* (type 600, HdV), followed by decreasing trends. *Rivularia* (type 170, HdV) persists. *Botryococcus* remains abundant and *Teträedron* (type 371, HdV) reaches its highest values with pronounced peaks. In contrast, *Spirogyra* (type 130, HdV) and type 128 (HdV) decline (Fig. 3). *Asplenium*-type occur and fungal spores increase in diversity and concentration. Small peaks of *Glomus* are recorded, together with continuous curves of *Coniochaeta* cf. *C. ligniaria* (type 172, HdV) and *Kretschmaria deusta* (type 44, HdV). Frequent occurrences include *Coniochaeta xylariispora* (type 6, HdV), *Savoryella lignicola* (type 35, UAB/type 1118, UG), type 38 (UAB) and *Delitschia* (type 34B, UAB) (Fig. 4).

- Sub-zone A2 (768–920 cm; 9.2–10.5 ka cal BP). At the base of the sub-zone, *Rivularia* (type 170, HdV) occurs together with *Anabaena* (type 170, HdV), while *Teträedron* (type 371, HdV) persists in very

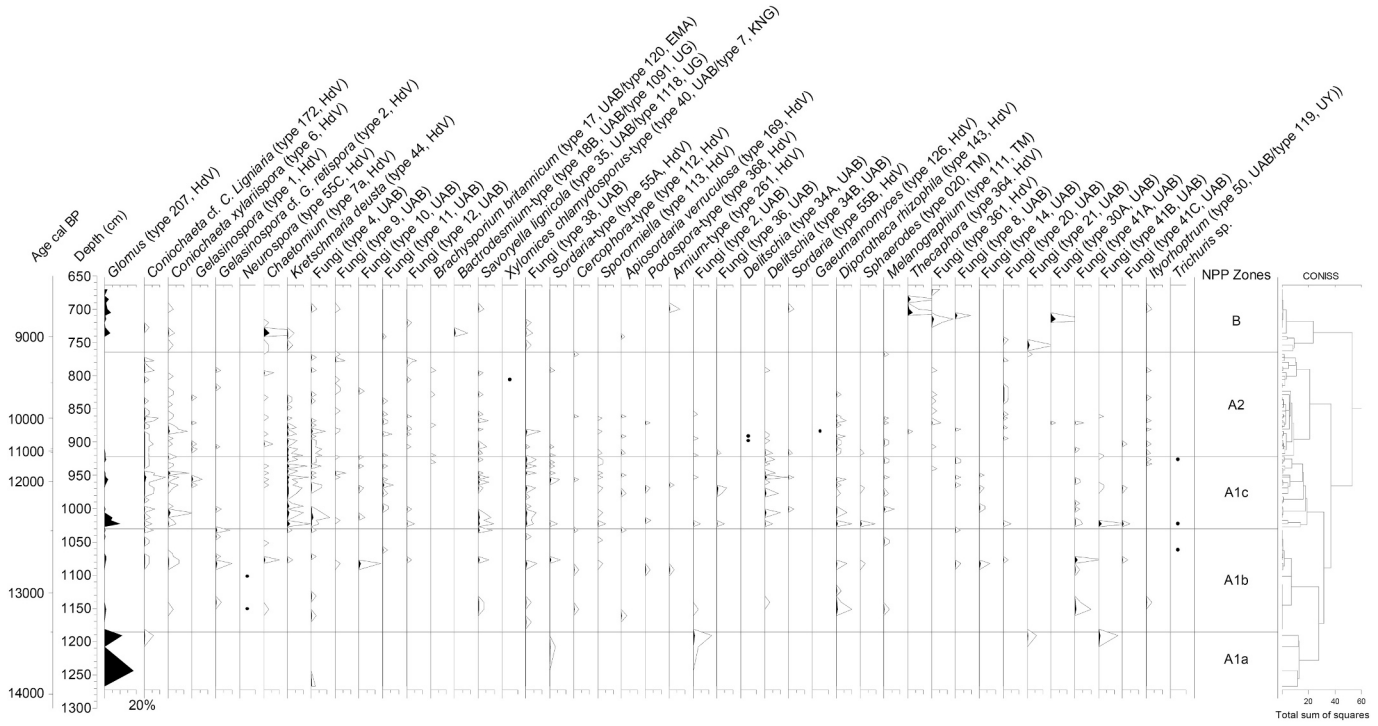

Fig. 4. NPP percentage diagram of the Pla de les Preses (PdP) core showing fungal remains. NPP assemblage zones (A1a–B) were defined using stratigraphically constrained cluster analysis (CONISS). Exaggeration curves enhance low-percentage taxa, corresponding to ×10 exaggeration.

low values (Fig. 3). *Gloeotrichia* (type 146, HdV) shows a decreasing trend, *Aphanizomenon* (type 600, HdV) becomes sporadic and *Botryococcus* maintains a continuous curve. *Spirogyra* (type 130, HdV) and type 128 (HdV) are scarce. Pteridophytes (*Polypodium*, *Asplenium*-type, *Pteridium*) are present in low abundances. Fungal spores display relatively high diversity, but lower concentrations compared to A1c. *Coniochaeta* cf. *C. ligniaria* (type 172, HdV) and *Kretschmaria deusta* (type 44, UAB) occur with decreasing trends (Fig. 4). A marked concentration of suberized basal cells of hairs of Nymphaeaceae (type 127, HdV) between 760 and 820 cm corresponds with the presence of *Nymphaea* pollen (Fig. 3).

- Zone B (670–763 cm; 8.1–9.2 ka cal BP). At the base of the zone, Cyperaceae root hairs and monocot epidermis increase, together with the occurrence of *Aphanizomenon* (type 600, HdV). Peaks of *Mougeotia* and *Mougeotia laetevirens* (type 373, HdV) are recorded, along with high values of *Pteridium*. Subsequently, monolete spores become dominant. Continuous curves of *Spirogyra* (type 130, HdV; type 210, HdV) and type 128 (HdV) are recorded, together with *Pseudoschizaea* (Fig. 3). A succession is observed from peaks of *Asplenium*-type to peaks of *Polypodium* and a continuous curve of *Pteridium*. Oribatida (type 36C, HdV) shows pronounced peaks. Among fungal remains, *Glomus* displays continuous moderate values. Peaks of *Chaetomium* (type 7A, HdV) and *Kretschmaria deusta* (type 44, UAB) occur at the base of the zone, followed by peaks of *Thecaphora* (type 364, HdV) (Fig. 4).

4.3. Statistical analysis

4.3.1. Correlation analysis

Spearman correlation analysis revealed several significant positive associations among NPP taxa. The strongest positive correlations were observed between *Myriophyllum* and *Gloeotrichia* ($\rho = 0.75$), as well as between *Tetraëdron* and *Gloeotrichia* ($\rho = 0.73$). A positive correlation was also identified between *Myriophyllum* and *Aphanizomenon* ($\rho = 0.60$). Negative correlations were less frequent but included moderate negative relationships between *Pteridium* and *Gloeotrichia* ($\rho = -0.66$) and between *Pteridium* and *Tetraëdron* ($\rho = -0.62$). Most other taxa showed weak or moderate correlations, and a large proportion of taxa displayed low pairwise correlation coefficients (Suppl. Mat. 1).

4.3.2. Between-groups principal component analysis

Between-group PCA (bgPCA) and Linear Discriminant Analysis (LDA) reveal a clear separation of NPP assemblages among the defined zones. The bgPCA performed on the Hellinger-transformed dataset revealed that the first two principal components explained a substantial proportion of the variance in the NPP dataset. The first principal component (PC1) accounted for 36.9% of the total variance, while the second principal component (PC2) explained 27.8%, together representing 64.7% of the total variance. These axes capture the main structure of the dataset, discriminating several groups of samples that correspond to the different stratigraphic zones.

The combined interpretation of the bgPCA ordination of samples (Fig. 5a) and the distribution of taxa (Fig. 5b) reveals a coherent relationship between sample grouping and NPP composition across the different stratigraphic zones. Samples assigned to A1a are closely associated with taxa such as Cyperaceae, *Glomus*, *Ophioglossum*-type and *Typha latifolia*. Zone A1b occupies an intermediate position in the bgPCA and is primarily associated with taxa such as *Aphanizomenon* and *Myriophyllum*, reflecting a distinct but transitional assemblage. Samples from zone A1c show a strong association with taxa including *Gloeotrichia* and *Tetraëdron*. *Botryococcus* occupies an intermediate position between zones A1c and A2, indicating a shared affinity with both groups.

Zone A2 is characterised by its association with taxa such as *Nymphaea* and suberized basal cells of hairs of Nymphaeaceae, together with *Polypodium*, reflecting a distinct cluster of NPPs. Notably, zones A1c and A2 are associated with a greater diversity of taxa, particularly in terms of fungal spores, which show a wider dispersion in the ordination. Finally, samples from zone B are clearly differentiated from the other groups and are associated with taxa such as Monoletes, Oribatida (type 36C, HdV), *Pteridium* and *Pseudoschizaea*.

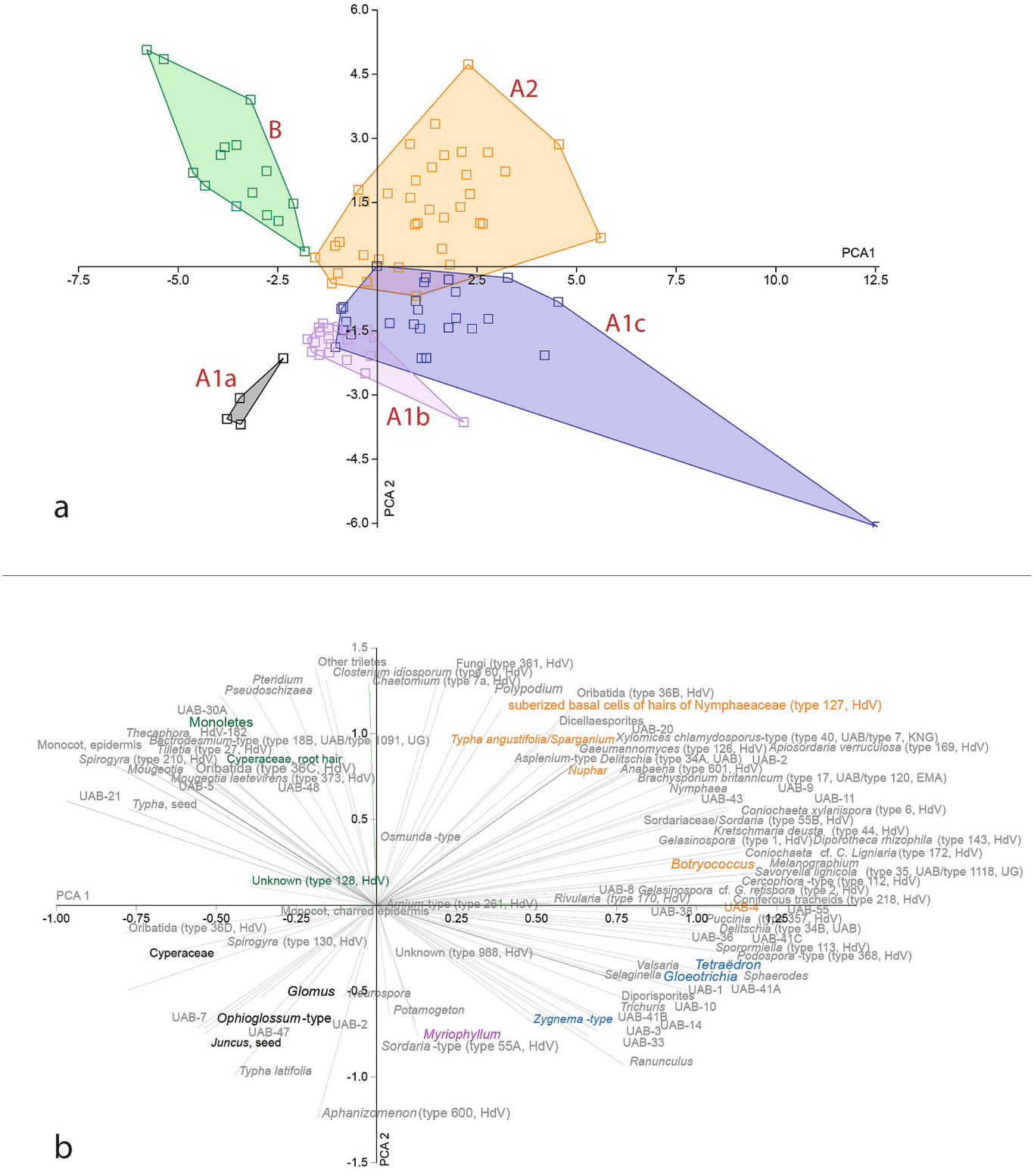

Fig. 5. Multivariate analysis of non-pollen palynomorph (NPP) assemblages from the Pla de les Preses sequence based on between-group Principal Component Analysis (bgPCA). (a) Distribution of samples according to stratigraphic zones (A1a, A1b, A1c, A2 and B). Convex hulls represent the dispersion of samples within each group. (b) Distribution of NPP taxa projected onto the same ordination space. Taxa identified as significant in the Linear Discriminant Analysis (LDA) are highlighted and coloured according to the stratigraphic zones with which they are most strongly associated (see Supplementary Material 2), whereas non-selected taxa are shown in grey. Each label corresponds to a specific NPP type.

5. Discussion

The multi-proxy record from the PdP provides a detailed reconstruction of environmental changes in the Vall d'en Bas basin during the Late Glacial–Early Holocene transition. By combining pollen data with non-pollen palynomorphs (NPPs) and other palaeobiological proxies and sedimentological information, it is possible to distinguish processes operating at different spatial scales, from regional vegetation responses to climate change to local hydrological and geomorphological dynamics associated with the evolution of a volcanic barrier-lake system and even volcanic activity. While pollen assemblages primarily reflect broader landscape and climatic trends across NE Iberia, NPP assemblages capture more local ecological processes within the basin, including changes in aquatic productivity, wetland development and soil exposure. In this context, the discussion first situates the record within the framework of regional vegetation and climate evolution during the Late Glacial–Early Holocene transition before examining the local palaeoenvironmental dynamics of the Vall d'en Bas palaeolake and the specific contribution of NPPs to reconstructing these processes. This framework allows us to directly address the objectives of this study by (i) tracking NPP changes across geomorphological phases, (ii) evaluating ecosystem responses to volcanic disturbances, and (iii) assessing the sensitivity of these proxies to rapid climatic events.

5.1. Regional vegetation dynamics and climate evolution during the Late Glacial–Early Holocene transition

Understanding the environmental evolution of the Vall d'en Bas basin requires placing the local sedimentary record within the broader context of regional vegetation and climate dynamics. During the Late Glacial–Early Holocene transition, major climatic shifts triggered significant changes in vegetation composition and landscape structure across the northeastern Iberian Peninsula (Pèrez-Obiol and Julià, 1994; González-Sampériz et al., 2017; Rull et al., 2023; Casas-Gallego et al., 2025). Recent syntheses highlight the complexity and spatial heterogeneity of these dynamics, emphasising the persistence of pine-dominated landscapes and the role of Mediterranean areas as refugia for thermophilous taxa even during cold phases (Casas-Gallego et al., 2025). These regional transformations provide an essential framework for interpreting the ecological trajectories observed in the study area, allowing us to distinguish between changes driven primarily by climate forcing and those related to volcanism and local geomorphological processes such as volcanic damming and subsequent basin evolution.

Despite the abrupt climatic oscillations recorded at the global scale, the impact of the Younger Dryas in NE Iberia appears relatively moderate, with many records indicating a certain degree of vegetation resilience and continuity. Pine-dominated woodlands and steppe landscapes persisted throughout this interval, with limited disruption in vegetation composition (Revelles et al., 2023), a pattern also supported by recent modelling and synthesis studies suggesting ecological stability or gradual transitions rather than abrupt shifts (Casas-Gallego et al., 2025). In this context, pollen records from the central Pyrenees further indicate that the Younger Dryas did not result in a complete collapse of forested landscapes despite the expansion of *Artemisia*–Poaceae assemblages during this period, while independent palaeoclimatic proxies instead point to relatively moist environments during this stadial (Rull et al., 2023). This apparent resilience contrasts with the pronounced climatic signal observed in other parts of the Mediterranean, as is the case of the eastern Mediterranean, where the Younger Dryas is generally associated with a marked shift towards colder and drier conditions, leading to the expansion of steppe vegetation and a reduction of woodland cover, as documented by multi-proxy syntheses combining pollen, charcoal and isotopic data (Roberts et al., 2018).

A clear example of the strong influence of local geomorphological processes overriding climatic signals is the evolution of the Vall d'en Bas palaeolake, where the deepest lacustrine phase is recorded during the Younger Dryas. This counterintuitive pattern reflects the dominant role of volcanic damming and basin hydrology in controlling lake development, independently of regional climatic trends (Iriarte et al., 2023).

At the regional scale, the PdP record shows that vegetation dynamics reflected successive climatic oscillations during the Late Glacial- Early Holocene transition. The development of open steppe-like landscapes with high Poaceae and *Artemisia* values, together with the dominance of *Pinus* and the presence of *Betula* and *Juniperus*, is consistent with cold and relatively dry conditions characteristic of the later stages of the Last Glacial period. However, short-term fluctuations in hygrophilous taxa and aquatic elements suggest variable moisture availability at the local scale. The subsequent interval shows a gradual reduction of open-land taxa and a slight expansion of mesophilous trees such as *Betula* and *Acer*, pointing to progressive climatic amelioration prior to the onset of the Holocene. This pattern closely matches the transition observed between sub-zones A1 and A2 in the PdP record (Fig. 2), highlighting the combined influence of regional climatic trends and local hydrological dynamics.

The onset of the Holocene favoured the expansion of temperate deciduous forests, particularly *Quercus pubescens*-type and *Corylus*, marking a major reorganisation of regional ecosystems. Across NE Iberia, this transition is generally expressed as a progressive and sustained increase in forest cover, reflecting warmer and more humid conditions and leading to the consolidation of closed-canopy woodlands. These regional vegetation dynamics are well documented in the PdP sequence and have been described in detail in previous work, which highlighted the strong influence of climatic fluctuations on landscape evolution during this period (Revelles et al., 2023).

However, in contrast to this general regional trend, the PdP record reveals an abrupt decline in deciduous broadleaf taxa during the Early Holocene, particularly during the interval corresponding to sub-zone B2. Such a rapid forest regression is not consistent with the expected vegetation response to climatic amelioration and instead points to the influence of local disturbance factors. Previous work in the Vall d'en Bas basin has demonstrated that this decline is associated with recurrent volcanic eruptions and increased fire activity, which triggered a two-step ecological response involving (i) the collapse of deciduous forests and expansion of *Pinus* woodlands, followed by (ii) the development of open landscapes dominated by Poaceae under intensified fire regimes (Revelles et al., 2023). The persistence of these disturbance processes prevented the rapid recovery of broadleaf forests, in contrast with regional records where deciduous woodland expansion continued under favourable Holocene climatic conditions (Pèrez-Obiol and Julià, 1994; Revelles et al., 2015).

This decoupling between regional vegetation trends and local ecological dynamics highlights the dominant role of volcanic activity, fire and associated geomorphological processes in shaping the landscape of the Vall d'en Bas basin during the Early Holocene, often overriding the effects of climate at the local scale. While regional vegetation dynamics provide an essential climatic framework, the evolution of the basin was strongly controlled by these local processes, particularly volcanic damming and subsequent hydrological changes. Disentangling climate-driven vegetation patterns from locally driven geomorphological and hydrological dynamics is therefore crucial for understanding the palaeoenvironmental evolution recorded in the sequence.

5.2. Palaeoenvironmental evolution of a volcanic barrier-lake ecosystem: Insights from non-pollen palynomorphs

The Vall d'en Bas palaeolake developed as a consequence of volcanic damming of the Fluvià River by lava flows from the GVF. The resulting barrier lake created a highly dynamic sedimentary basin in which hydrological conditions, aquatic ecosystems and marginal wetlands evolved in response to both regional climatic changes and local geomorphological processes. While pollen data primarily reflect regional vegetation dynamics driven by climate change, non-pollen

palynomorphs provide key information on local hydrological, ecological and geomorphological processes within the lake basin.

5.2.1. Formation of a volcanic barrier lake and colonisation by pioneer aquatic communities (Zone A1)

The earliest phase of the sequence (subzone A1) reflects the formation and progressive development of a volcanic barrier lake under highly dynamic hydrological conditions. During subzone A1a, the system is characterised by a shallow palustrine to lacustrine environment with fluctuating water levels and episodes of subaerial exposure. The occurrence of hygrophilous taxa and aquatic plants such as *Myriophyllum* indicates the presence of emergent wetlands, while NPP assemblages document the rapid colonisation of the basin by pioneer phototrophic communities. Cyanobacteria and green algae, including *Gloeotrichia*, *Aphanizomenon*, *Botryococcus* and *Zygnema*-type (Fig. 3), are consistent with relatively shallow and nutrient-rich water bodies (van Geel et al., 1996). High values of *Glomus* (Fig. 4) and the presence of oribatid mites indicate enhanced soil erosion and input of terrestrial material from lake margins. The abundance of *Ophioglossum*-type spores suggests the development of moist, periodically waterlogged substrates along the lake margins, while the scarcity of fungal remains indicates limited accumulation of organic matter.

Subzone A1b marks a phase of progressive deepening and increasing hydrological stability. Sedimentological and geochemical data indicate the development of a shallow but persistent lacustrine system in the core area, with enhanced carbonate production and continued fluvial terrigenous input (Fig. 6). Biological proxies support the expansion of littoral habitats, and the ostracod assemblage (Fig. 6) include species common in permanent, deep freshwater lakes, especially from Central and Northern Europe at present (Meisch, 2000), indicating cooler temperatures during the Late Glacial. The NPP assemblages indicate sustained aquatic productivity dominated by nitrogen-fixing cyanobacteria such as *Gloeotrichia* and *Aphanizomenon* (van Geel et al., 1994) and the persistence of green algae suggests relatively stable water conditions, although variability in their abundance (Figs. 3 and 6) reflects ongoing fluctuations in lake level and chemistry. Notably, this phase spans the transition to the Younger Dryas, yet no evidence of lake-level lowering is observed, highlighting the dominant control of volcanic damming and basin hydrology over regional climatic forcing.

Subzone A1c represents the culmination of the lake deepening trend and the establishment of maximum water depth. Sedimentary facies indicate continuous aggradation under deeper-water conditions, with increased siliciclastic input and reduced carbonate production, likely reflecting enhanced runoff and lower phytoplankton productivity. Aquatic assemblages show a shift towards Chlorophyta-dominated communities (*Botryococcus*, *Tetraedron*), while the decline of *Spirogyra* and Cyperaceae suggests a reduction in shallow littoral habitats (Fig. 6). This interpretation is supported by the ecology of *Spirogyra*, which typically inhabits stagnant, shallow mesotrophic to eutrophic waters, including small lakes, pools and the littoral zones of larger lakes (Gelorini et al., 2011). In contrast to earlier phases, fungal remains show a marked increase in both diversity and concentration. The occurrence of lignicolous and saprotrophic taxa such as *Coniochaeta* cf. *C. ligniaria*, *Kretschmaria deusta* and *Savoryella lignicola* suggests enhanced input and decomposition of terrestrial organic matter, likely linked to the accumulation of plant debris along lake margins (Fig. 4). Together with minor peaks of *Glomus*, these patterns suggest a stronger coupling between the lake and its catchment, involving both minerogenic and organic inputs.

Overall, Zone A1 records the transition from an unstable, shallow and intermittently exposed environment to a deeper and more stable lacustrine system, strongly controlled by volcanic damming processes. NPP assemblages are key to reconstructing this evolution, providing detailed insights into hydrological variability, aquatic productivity and the progressive coupling between the lake and its surrounding landscape.

5.2.2. Lake shallowing and transition to marshy environments (Subzone A2)

Subzone A2 records a major reorganisation of the Vall d'en Bas palaeolake system, characterised by progressive shallowing and the transition from a relatively deep lacustrine environment to marshy and littoral-dominated conditions. At the beginning of this subzone, at ca. 10.5 ka cal BP, sedimentological and geochemical data indicate the persistence of carbonate-rich muds with the highest Ca values of the sequence (Fig. 6), suggesting enhanced authigenic carbonate production linked to increased organic productivity and photosynthetic activity. This trend is consistent with a general increase in organic matter content and reflects warmer water conditions associated with the onset of the Holocene.

Biological proxies support this interpretation. Changes in aquatic communities, including the disappearance of cold-adapted taxa (*Candona candida*, Fig. 6) (Horne and Mezquita, 2008) and the expansion of eurytopic and warmer water ostracod species (see *Neglecandona neglecta* in Fig. 6), indicate rising temperatures and increased ecological stability. This is confirmed by the increase in the number of gyrogonites (particularly of *Chara vulgaris*), indicating higher fertility in warmer waters (Fig. 6).

From 9.8 ka cal BP onwards, the development of macrophyte-rich environments, including *Nymphaea* and *Nuphar* (Fig. 3), points to more productive and structured aquatic ecosystems, while a reduction in charophyte remains suggests increasing trophic conditions and shading of the water column. Non-pollen palynomorph assemblages provide detailed insights into this transition. The decline of cyanobacteria such as *Gloeotrichia* and *Aphanizomenon*, together with the persistence of *Botryococcus* and low values of other green algae, reflects a shift from open-water productivity towards more complex, macrophyte-dominated systems. The occurrence of *Rivularia* and *Anabaena* at the base of the subzone indicates continued but reduced nitrogen-fixing activity (Fig. 3) (van Geel et al., 1994), while the marked presence of Nymphaeaceae remains confirms the expansion of floating-leaved vegetation.

Fungal assemblages show relatively higher diversity but lower concentrations compared to the previous phase (Fig. 4), suggesting continued terrestrial input but reduced accumulation of organic matter within the basin. The decline of lignicolous taxa such as *Coniochaeta* cf. *C. ligniaria* and *Kretschmaria deusta* indicates a reduction in woody debris input, consistent with the progressive stabilisation of lake margins and the expansion of vegetated littoral zones.

This shallowing trend culminates in a marked lowering of the lake level around 9.3 ka cal BP, leading to the development of peat-forming, vegetated littoral environments. This phase likely reflects a combination of internal basin processes and external forcing, as the 9.3 ka dry event (Bond et al., 2001), previously attested in other Mediterranean lacustrine records (Carrion, 2002; Vegas et al., 2010; Perez-Sanz et al., 2013; Magny et al., 2007, 2011; Revelles et al., 2015) may have contributed to lowering the water table and promoting fluvial incision of the volcanic dam. Consistently, the NPP zonation highlights this interval as the most pronounced ecological threshold in the sequence, with the transition from Zone A to Zone B (Figs. 3, 4, 6) marking the reorganisation of aquatic and wetland communities. This interval provides a clear example of the sensitivity of NPP assemblages to rapid environmental perturbations, as shifts in aquatic and wetland indicators closely track hydrological changes associated with the 9.3 ka event.

Overall, subzone A2 represents a transition from a deep, open lacustrine system to a more productive, shallow and vegetated wetland environment, where NPPs provide key evidence for changes in aquatic structure, trophic conditions and lake–catchment interactions.

5.2.3. Barrier erosion and re-establishment of fluvial dynamics (Zone B)

Zone B records the final stage in the evolution of the Vall d'en Bas palaeolake, characterised by the progressive erosion of the volcanic barrier and the re-establishment of fluvial dynamics. Sedimentological

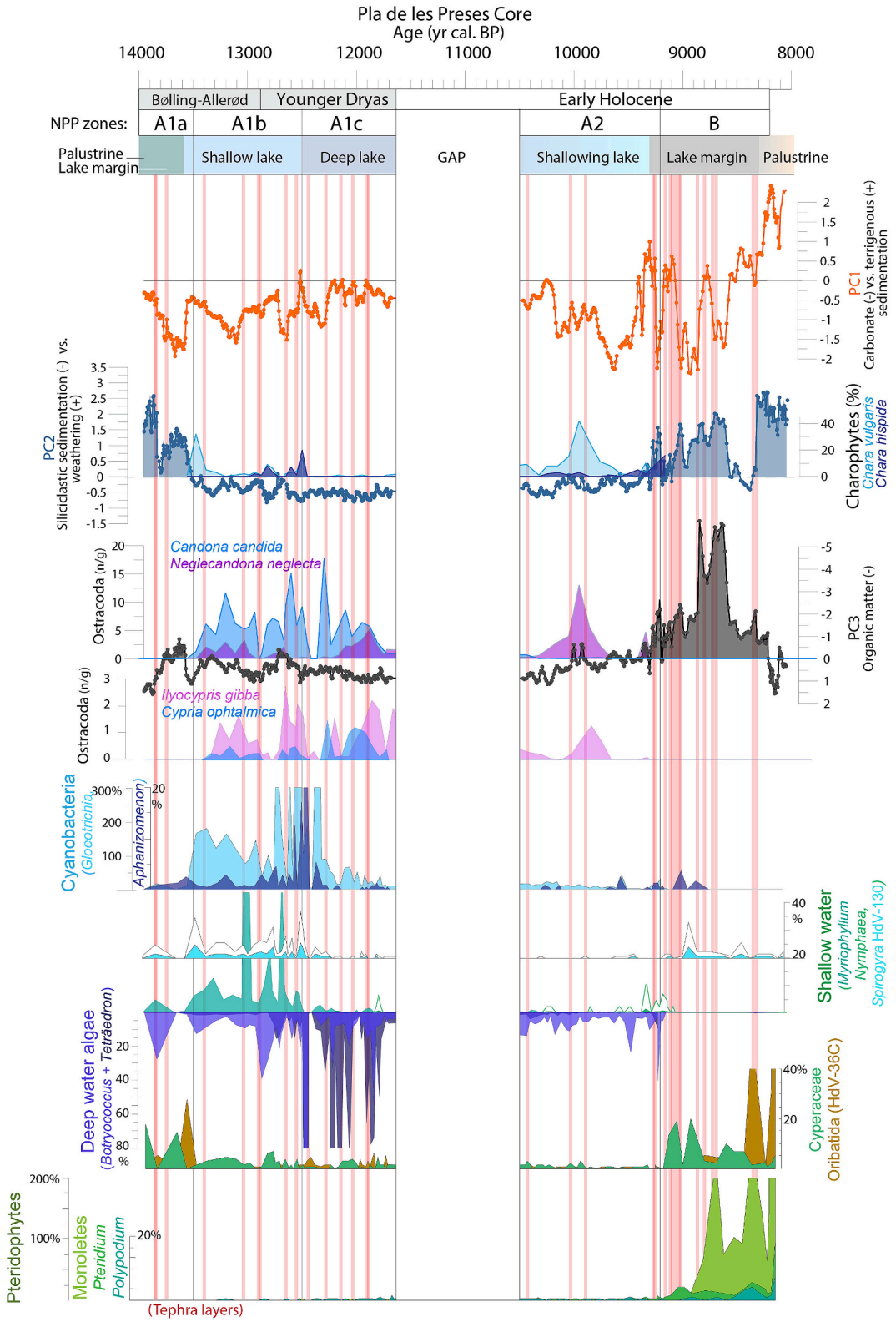

Fig. 6. Multiproxy synthesis of palaeoenvironmental evolution in the Pla de les Preses (PdP) core during the Late Glacial–Early Holocene transition. The diagram integrates principal component analysis (PC1–PC3) of geochemical data (carbonate, siliciclastic and organic matter proxies), aquatic and terrestrial non-pollen palynomorphs (NPPs), cyanobacteria and algae, ostracods, and charophytes, plotted against calibrated age (cal BP). NPP zones (A1a–B) are shown alongside major climatic phases (Bølling–Allerød, Younger Dryas, Early Holocene) and inferred environmental stages (from palustrine/lake margin to shallow and deep lake conditions, followed by lake shallowing, marginal environments, and palustrine development). Red vertical bands indicate tephra layers. The integration of proxies highlights the dynamic evolution of a volcanic barrier-lake system and its response to climatic variability, hydrological shifts and volcanic activity. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

evidence indicates continued shallowing of the basin, with the deposition of organic-rich peaty sediments associated with vegetated lake margins (Fig. 6), intercalated with lacustrine muds and frequent volcaniclastic ash layers. These features reflect a shallow and highly dynamic littoral environment, with recurrent phases of low water level and vegetation colonisation.

Biological proxies confirm this transition. From ca. 9.3 ka cal BP onwards, aquatic assemblages show the disappearance of typical lacustrine indicators such as *Nuphar*, *Nymphaea*, *Gloeotrichia*, *Botryococcus* and *Teträedron*, while the expansion of Cyperaceae, ferns (mainly monoletes but also *Pteridium* and *Polypodium*) and filamentous algae such as *Spirogyra* indicates the development of shallow, marshy and periodically exposed environments (Fig. 6). The absence of ostracods during this interval further supports the interpretation of very shallow and possibly acidic conditions, unfavourable for carbonate preservation.

Non-pollen palynomorph assemblages provide detailed evidence of these environmental changes. The increase in Cyperaceae root hairs and monocot epidermis, together with the dominance of monolete spores and the succession from *Asplenium*-type to *Polypodium* and *Pteridium* (Fig. 3), reflects the expansion of hygrophilous and terrestrial vegetation in the basin. Peaks of *Mougeotia* and related algae, as well as continuous curves of *Spirogyra*, indicate fluctuating water availability and shallow aquatic conditions. At the same time, the occurrence of *Pseudoschizaea* suggests phases of subaerial exposure or weathering and soil development/erosion processes (van de Schootbrugge et al., 2024).

Fungal assemblages and other NPPs indicate increasing terrestrial influence and catchment instability. Continuous values of *Glomus* point to sustained soil erosion, while peaks of taxa such as *Chaetomium*, *Kretschmaria deusta* and *Thecaphora* (Fig. 4) reflect the accumulation and decomposition of organic matter under increasingly subaerial conditions. Pronounced peaks of oribatid mites (Fig. 6) further support the development of exposed and vegetated soils within the former lake basin.

This shallowing process culminates around 8.2 ka cal BP, when the lacustrine system collapses and the study area become fully subaerial. This transition is interpreted as the result of a marked lowering of the water table, likely enhanced by the 8.2 ka climatic event (Bond et al., 2001; Mayewski et al., 2004; Rohling and Palike, 2005), which promoted the incision of the volcanic dam and the reactivation of fluvial dynamics. The lowering of the outflow point led to rapid drainage of the basin and the transformation of the former lake into a palustrine and fluvial environment. The abrupt ecological reorganisation associated with the 8.2 ka event highlights the capacity of NPPs to capture rapid environmental transitions. In that sense, Zone B represents the transition from a shallow, vegetated lake margin to a fully terrestrialised system dominated by fluvial processes. NPP assemblages are key to documenting this transformation, capturing the shift from aquatic to terrestrial conditions and the progressive establishment of soil and vegetation within the former lake basin.

5.3. Insights from non-pollen palynomorphs for reconstructing dynamic lake-barrier ecosystems

These results demonstrate that NPPs are not only complementary to pollen data but constitute key proxies for reconstructing local hydrological and ecological dynamics in highly dynamic environments such as volcanic barrier lakes. While pollen data primarily reflect regional vegetation patterns and broader climatic trends, some taxa—particularly aquatic and hygrophilous indicators such as *Myriophyllum*, Cyperaceae and *Nymphaea*—also provide crucial information on local environmental conditions. In parallel, NPP assemblages offer direct and high-resolution insights into local ecosystem dynamics, particularly hydrological, limnological and shoreline processes. In this sense, both proxies are highly complementary, capturing environmental variability at different spatial scales and contributing jointly to a more complete reconstruction of lake-basin evolution.

Pollen and NPP zonations show markedly different patterns, reflecting their sensitivity to processes operating at different spatial and temporal scales. The main division in the pollen record occurs at the transition from the Late Glacial to the Early Holocene, indicating a strong response to major climatic reorganisation and the expansion of temperate forests. In contrast, the NPP zonation is primarily structured by the transition from Zone A to Zone B at ca. 9.2 ka cal BP, corresponding to a major shift from lacustrine to wetland conditions associated with peat formation and the subsequent reestablishment of fluvial dynamics. This pattern suggests that NPP assemblages are more directly controlled by local hydrological and geomorphological processes linked to the evolution of the volcanic barrier-lake system, rather than by regional climatic forcing alone. While the formation of the volcanic barrier lake and progressive deepening was fundamentally controlled by geomorphological processes following the emplacement of the lava flow, its later evolution appears to reflect an increasing influence of climate. The timing of this ecological transition broadly coincides with the 9.3 and 8.2 ka cooling events, both linked to freshwater perturbations of the North Atlantic circulation and associated with widespread hydroclimatic changes across Europe (Bond et al., 2001; Mayewski et al., 2004). These climatic episodes may have reduced effective moisture and lake levels, accelerating peat development after the 9.3 ka event and favouring the final transition to fluvial conditions following the 8.2 ka event. This interpretation suggests that the late evolution of the Vall d'en Bas palaeolake resulted from the interaction between long-term geomorphological infilling and centennial-scale climatic forcing.

The multivariate analyses provide an objective synthesis of the ecological succession reconstructed from the NPP record. The bgPCA distinguishes well-defined assemblages that closely match the stratigraphic zonation, indicating that each phase of basin evolution was characterised by a distinct combination of local ecological indicators (Fig. 5). The ordination reveals a progressive shift from the Cyperaceae–*Glomus*–*Ophioglossum*-type assemblage of Zone A1a towards communities dominated by aquatic macrophytes and cyanobacteria during Zones A1b and A1c, before reaching the *Nymphaea*-dominated conditions of Zone A2. Finally, Zone B occupies a clearly separated position in the ordination, reflecting the establishment of wetland and floodplain conditions characterised by Monoletes, *Pteridium*, *Pseudoschizaea* and oribatid remains. This succession closely mirrors the geomorphological evolution of the volcanic barrier-lake system from shallow marshes, through a well-developed lacustrine phase, to progressive terrestrialisation and renewed fluvial influence.

Although aquatic algae and cyanobacteria, particularly *Gloeotrichia*, *Botryococcus* and *Teträedron*, account for much of the variance captured by the first ordination axes, the differentiation among palynological zones depends on the combined contribution of aquatic, marginal and terrestrial indicators. The LDA (Suppl. Mat. 2) highlights the importance of additional taxa, including Cyperaceae, *Ophioglossum*-type, Monoletes, *Pteridium* and *Glomus*, which contribute significantly to the discrimination of ecological phases. This pattern indicates that the successive stages of lake evolution involved coordinated responses across multiple ecosystem components rather than shifts in individual taxa alone. The close agreement between the statistical classification and the defined stratigraphic zonation further demonstrates that NPP assemblages reliably capture distinct ecological states associated with the evolution of the volcanic barrier-lake system. The observed assemblage changes reflect shifts in primary productivity, water depth and nutrient availability, indicating that variations in limnological conditions constitute the dominant signal within the NPP record. In contrast, fungal remains play a more limited role in structuring the overall statistical patterns, although they provide valuable complementary information on terrestrial inputs and organic matter dynamics.

Within the Vall d'en Bas sequence, NPPs prove particularly effective for reconstructing hydrological changes associated with the evolution of the volcanic barrier lake. Aquatic algae and cyanobacteria record fluctuations in water depth, permanence and trophic state, allowing the

identification of successive phases of lake formation, deepening and shallowing. At the same time, pteridophyte spores and other indicators of hygrophilous vegetation document the expansion of wetland environments and the progressive terrestrialisation of the basin. Indicators such as *Pseudoschizaea*, *Glomus* and oribatid mites are typically associated with exposed or disturbed soils. Their occurrence in the sequence may therefore reflect both the local development of subaerial conditions and soil exposure around the lake margins, and/or an increased input of terrestrial material into the basin, reflecting phases of soil erosion.

The NPP record also provides key insights into the ecological responses of aquatic and wetland communities to volcanic disturbances, one of the central objectives of this study. Abrupt changes in aquatic communities, including declines in macrophytes, algae and cyanobacteria following eruptive episodes, reflect short-term disturbances in water chemistry and trophic conditions. These disturbances were followed by relatively rapid recovery phases, often characterised by the expansion of pioneer taxa such as nitrogen-fixing cyanobacteria (*Gloeotrichia*) (Fig. 6), indicating high resilience of the system. Such dynamics highlight the sensitivity of NPPs to short-term limnological changes.

Overall, NPP assemblages emerge as a particularly powerful proxy for reconstructing the evolution of highly dynamic environments where local geomorphological processes strongly influence ecosystem development. In the case of the Vall d'en Bas basin, they allow a detailed reconstruction of hydrological variability, aquatic productivity, wetland expansion and catchment–lake interactions, complementing pollen-based reconstructions and providing a more complete understanding of the processes driving palaeoenvironmental change.

6. Conclusions

The multi-proxy record from Pla de les Preses provides a high-resolution reconstruction of the environmental evolution of the Vall d'en Bas basin during the Late Glacial–Early Holocene transition, revealing the complex interplay between regional climatic forcing and local geomorphological processes. While vegetation dynamics in NE Iberia largely followed the expected trajectory from open Late Glacial landscapes to more forested Holocene ecosystems, the Vall d'en Bas sequence demonstrates that local environmental evolution was strongly modulated by volcanic activity and basin hydrology.

Overall, the results directly address the objectives of this study by showing that (i) NPP assemblages effectively track the main geomorphological phases of the barrier-lake system, (ii) they capture ecosystem responses to volcanic disturbances, (iii) they are sensitive to rapid climatic events such as the 9.3 and 8.2 ka episodes, and (iv) they constitute key proxies for reconstructing local-scale environmental dynamics.

The development of a volcanic barrier lake following the damming of the Fluvià River resulted in a highly dynamic open lacustrine system that evolved through three main stages: (i) an initial phase of shallow and unstable conditions with rapid colonisation by pioneer aquatic communities (14–13.5 ka cal BP), (ii) progressive deepening and stabilisation of the lake culminating in maximum water depth (13.5–11.7 ka cal BP), and (iii) subsequent shallowing, wetland expansion and terrestrialisation associated with barrier erosion and the re-establishment of fluvial dynamics (10.5–8.1 ka cal BP). These phases were not always synchronous with regional climatic trends, as illustrated by the persistence of deep lacustrine conditions during the Younger Dryas and the abrupt reorganisation of hydrological conditions during the Early Holocene.

This sequence highlights a clear decoupling between regional vegetation patterns and local ecological dynamics, emphasising the dominant role of volcanic processes, fire activity and hydrological changes in shaping the landscape at the basin scale. In particular, the Early Holocene decline of deciduous forests contrasts with regional afforestation trends and reflects volcanic disturbance-driven processes rather than climatic forcing alone.

Non-pollen palynomorphs prove to be a key proxy for reconstructing these local dynamics. While pollen data provide the regional vegetation framework, NPP assemblages offer detailed insights into hydrological variability, aquatic productivity, wetland development and soil processes. Aquatic algae and cyanobacteria effectively track changes in lake depth and trophic conditions, pteridophyte spores document the expansion of marshy environments, and fungal remains and soil indicators capture terrestrial inputs, erosion and phases of subaerial exposure. In addition, NPPs are particularly sensitive to short-term disturbances, such as volcanic eruptions, allowing the detection of rapid ecological responses and recovery processes.

Overall, this study demonstrates the value of integrating pollen and NPP data for reconstructing complex palaeoenvironmental systems. In dynamic settings such as volcanic barrier lakes, where local processes can override regional climatic signals, NPPs provide essential information for understanding ecosystem evolution and the mechanisms driving environmental change.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.revpalbo.2026.105688.

Data availability

The datasets generated during the current study are available in the Neotoma Palaeoecological Database repository (https://data.neotomadb.org/56691).

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