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# From site to basin: the on–site and off–site palynodiversity to trace vegetation dynamics in the Palù di livenza basin (NE Italy)

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## ABSTRACT

Understanding how human activities transformed wetland ecosystems during the Neolithic requires the integration of palaeoecological records operating at different spatial scales. This study reconstructs the biodiversity and vegetation history of the Palù di Livenza basin, at the foothill of the Cansiglio Plateau in the Prealps (NE Italy), by integrating palaeoecological and archaeological evidence from both on-site and off-site contexts. On-site data derive from the Late Neolithic pile-dwelling settlement, with particular focus on a stratigraphic sequence from Sector 3, an area investigated archaeologically between 2013 and 2021, while off-site information derives from a sediment core retrieved within the basin. The combination of these records provides complementary perspectives: the site sequence documents local environmental modifications directly associated with human activities, whereas the basin core offers a broader framework of regional vegetation dynamics. By integrating palynological, archaeological, and geomorphological data, we trace the development and transformations of the Palù di Livenza basin in relation to the Neolithic settlement and examine their responses to climatic and human-driven changes. New data from on-site record of Sector 3 is compared with off-site sequence to highlight differences and assess the spatial extent of human impact. We also propose a novel workflow for generating land cover suitability maps from pollen data, providing a transferable methodological framework for linking palaeoecological reconstructions with spatial modelling. This integrated approach offers new insights into human-environment interactions and long-term landscape dynamics in Neolithic wetland settings.

## 1. Introduction

The role of palynology in the reconstruction of past environments and landscapes has become, in recent decades, not only well established but also considered crucial, particularly in Southern Europe (Sadori et al., 2013; Revelles et al., 2018; Revelles, 2021; Deza–Araujo et al., 2022). Pollen analysis offers a unique and highly informative window into the past, as it allows to trace changes in flora, vegetation composition, ecological settings, and climate conditions across very different temporal scales, from broad millennial sequences down to finer, decadal variations. This flexibility makes palynology a methodological cornerstone for understanding long-term environmental dynamics (e.g., Roberts et al., 2018; Fyfe et al., 2025). Thanks to this multi-scalar and interdisciplinary potential, palynology can also contribute to a more nuanced understanding of how past societies adapted to and modified their environments. It provides crucial evidence for discussions on resilience, sustainability, and long-term ecological change, making it a vital tool not only for archaeological and paleoenvironmental research, but also for contemporary debates on the relationship between humans and their ecosystems. Palynological studies at archaeological sites are indeed of paramount importance for interpreting the evolution of cultural landscapes and for tracing the local footprint of human activities on vegetation and the environment (Mercuri, 2014; Mercuri et al., 2019a). Valuable insights can be obtained by comparing on-site with off-site records: whilst the former usually provide highly localised signals that reflect the role of human communities in shaping vegetation

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history (Mercuri and Sadori, 2014), the latter captures broader, regional dynamics that are less directly affected by human presence and, therefore, potentially offer less disturbed reconstructions (Colombaroli et al., 2008; Vannière et al., 2008; Vescovi et al., 2010; Marinova et al., 2012; Weiberg et al., 2016; Revelles et al., 2018). Integrating both scales of analysis allows site-specific signals to be placed within their broader environmental context.

The Palù di Livenza site is a Late Neolithic pile-dwelling settlement, first discovered in the 19th century during drainage works and later inscribed in 2011 on the UNESCO World Heritage List as part of the transnational serial property *Prehistoric Pile-Dwellings around the Alps*. Since 2013, it has been the focus of renewed, multidisciplinary excavations, targeting previously undisturbed sectors to investigate its multilayered stratigraphy and the relationship between the Neolithic community and the surrounding landscape.

Apart from its outstanding archaeological importance, previous palaeoenvironmental studies have also highlighted the site's high palaeoecological significance (Pini, 2004; Zappa et al., 2023, Fig. 1). Pollen data were obtained within the archaeological site from a sedimentary core near the Sector 2 (PDL157/‘99, Pini, 2004) and from a pollen sequence in Sector 3 (PaluON1, Zappa et al., 2023). Palynological analyses indicated that prior to the settlement (ca. 6590–5960 cal yr BP) dense oak and mixed forests dominated. The establishment of the pile-dwelling led to forest reduction, wetland reclamation, expansion of herbaceous communities, and local crop cultivation. Comparison with archaeobotanical evidence (wood, charcoal, seed and fruits; Rottoli et al., 2018) further highlights human impact on vegetation, including fire use, crop fields, and plant processing.

The present paper extends previous research at Palù di Livenza by incorporating pollen data from two new sequences, PaluON2 and PaluOFF1, which respectively strengthen the on-site framework and provide, for the first time, a basin-scale off-site perspective. The main aims are: (i) to enhance understanding on biodiversity and vegetation history of the Palù di Livenza basin; (ii) to combine palynological, archaeological and geomorphological information to trace the history of the Neolithic village and their transformations following vegetation and landscape changes, whether climate- or human-driven; (iii) to compare on-site/off-site records to underline differences and infer the range of anthropogenic influence on the territory.

Furthermore, this paper aims at (iv) introducing a new methodological workflow to obtain land cover maps based on palynological data.

Regarding the latter aim, the proposed workflow integrates expert-based knowledge of the ecological significance and habitat preferences of plant species with pollen-based quantitative vegetation reconstruction and land-cover modelling approaches, providing an evidence-based framework for the spatially explicit mapping of land cover classes within the study area. Implemented using open-source software, the workflow is reproducible and flexible, allowing the integration of additional parameters according to the specific aims of the study.

### 1.1. Environmental settings

The Palù di Livenza basin (Fig. 1) is located in north-eastern Italy, in the western sector of the Friuli Venezia Giulia region. It is a wetland of about 100 ha sets within a tectonic depression at ca. 30 m a.s.l., bordered by the Cansiglio Plateau to the west and the Col Longone hills to the east in the Venetian-Friulan Prealps. The basin is filled by about 40 m of Quaternary sediments, largely consisting of lacustrine and swampy deposits that occupied the area because of the temporary blocking of the narrow structural threshold existing between Col Longone and Col del Conte by alluvial deposition (Fig. 1A; Bartolomei, 1997; Bassetti and Cavulli, 2002; Monegato et al., 2023). A rather large lake formed during the Last Glacial Maximum (LGM, 29,000–19,000 years BP), when the aggradation of the external alluvial plain

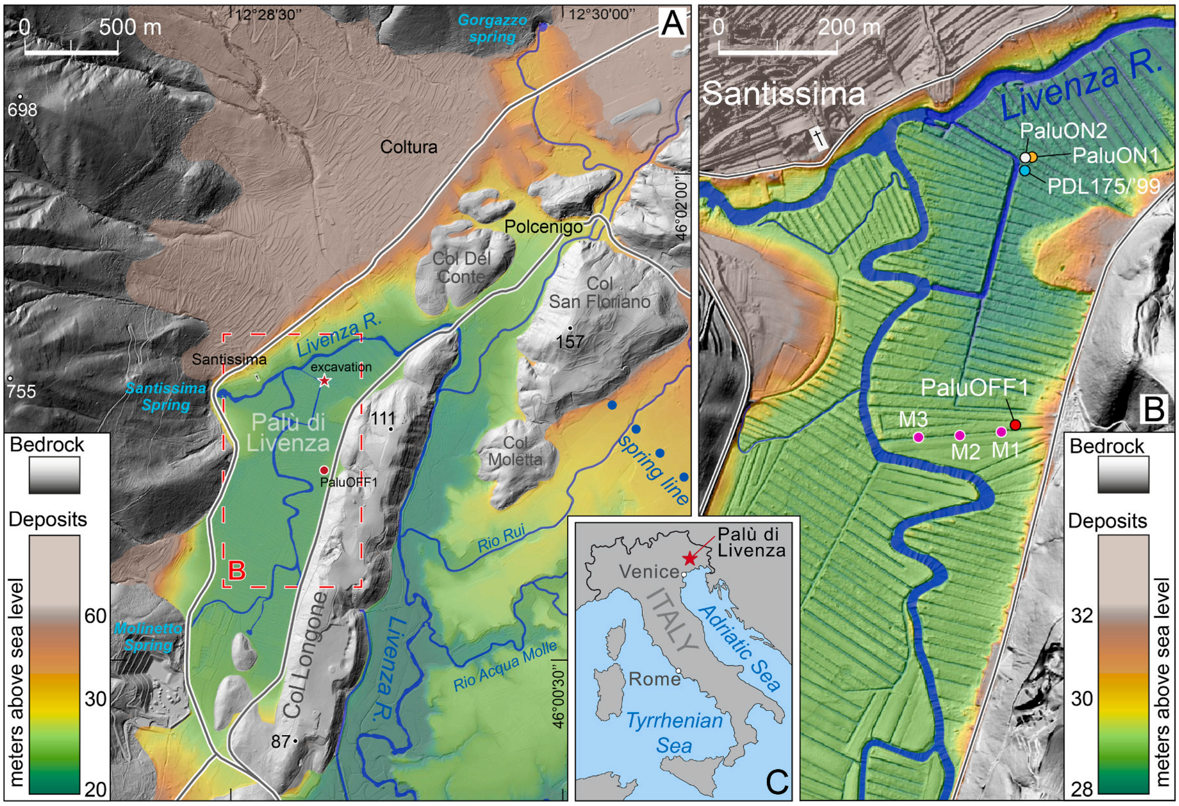

**Fig. 1.** A) Location of the Palù di Livenza basin; B) detailed view of the study area showing the position of the records presented or cited in this study. PDL157/‘99 (near-site pollen record – Pini, 2004); PaluON1 (on-site record – Zappa et al., 2023); PaluON2 (on-site record); PaluOFF1 (off-site record); M1, M2 and M3 (moss samples).

dammed the Palù di Livenza basin and led to the accumulation in it of several meters of laminated blue-greyish clays (Bassetti and Cavulli, 2002; Monegato et al., 2023; Fontana et al., 2024). After the deactivation of the lake and the partial erosion of its deposits, the basin transformed into a peatland during the Holocene due to increasing temperate climatic conditions (Peresani et al., 2009; Monegato et al., 2023). The Holocene stratigraphic sequence, consisting of silts and clays followed by organic deposits, is covered by anthropogenic layers that document periodic submersion, peat development and human activity during the Neolithic period. The anthropogenic layers, consisting of blackish organic mud with abundant plant and woody remains, contain fragments of charcoal, baked clay, and pottery fragments that testify to the existence of a settlement in the area or in the immediate vicinity (Bartolomei, 1997; Bassetti and Cavulli, 2002). This natural archive of palaeoenvironmental and cultural information highlights the interplay between natural processes and human presence since the LGM (Pini, 2004).

The environment of the basin has been strongly altered by the reclamation activities carried out in the first part of the 20th century that dug a dense network of ditches and drained some sectors. Anyhow, the area is protected by regional and national laws as a Biotope since 2018, due to its spring-fed wetland habitats, endangered amphibian populations and hygrophilous woodland communities (Vitri and Visentini, 2002; Fontana et al., 2019). The Palù di Livenza site was inscribed on the UNESCO World Heritage List in 2011 as a component (IT-FV-01) of the *Prehistoric Pile Dwellings around the Alps* series. It was brought to archaeological attention after drainage works in 1965, which revealed the prehistoric site. The settlement extends around 60.000 $m^2$ and partially overlaps with the archaeological constraint area (Comune di Caneva, 2023).

The area has a continental climate, with cold winters, hot summers, and annual precipitation between 1200 and 1600 mm (ARPA FVG–OSMER, 2026). The main vegetation series (147 b; see Blasi, 2010) includes forests of *Ostrya carpinifolia* Scop., *Fraxinus ornus* L., *Quercus pubescens* Willd. And associated shrubs and herbs. The basin hosts ecologically valuable spring-fed wetlands, where clear, alkaline waters give rise to swamps (dominated by wood vegetation, typical of low-elevation floodplains along rivers or slow-moving streams, as the Palù basin is) and *Cladium mariscus* (L.) Pohl stands, forming transitions between wet meadows and reed beds (Zappa et al., 2008; De Luca and Oriolo, 2010). The territory is currently characterised by cultivated fields, uncultivated land and wetland environments.

### 1.2. Archaeological context

The first human evidence at the Palù di Livenza basin is confirmed since after the LGM by some collections of lithic materials attributed to late Palaeolithic and Mesolithic (Epigravettian and Mesolithic foragers) which evidence remains poorly studied. They can be framed within the broader Late Pleistocene–Early Holocene pattern of hunter-gatherer frequentation in north-eastern Italy. In this regional context are documented groups with marked seasonal mobility, who exploited available resources distributed between piedmont and mountain zones (such as the Cansiglio Plateau at Palughetto (Peresani et al., 2009;Peresani et al., 2011), Bus de la Lum (Peresani et al., 1999–2000), and Pian di Landro (Visentin et al., 2018), as well as Piancavallo (Guerreschi, 1975; Duches et al., 2007), the Pradis Plateau at Grotta Clusantin (Peresani et al., 2008; Romandini et al., 2012), and Grotte Verdi (Gurioli et al., 2011; Naudinot et al., 2014; Lugli et al., 2022). At Palù di Livenza, the most extended archaeological evidence is related to the Neolithic settlement that developed in the area, based on the data currently available, between 6350/6250 and 5550 cal yr BP. The greatest concentration of archaeological remains is found in the centre of the basin, in an area crossed by a drainage canal. This zone, divided into three survey sectors, has been investigated archaeologically in several occasions since the early 1980s. Investigations revealed significant evidence of the pile-dwelling settlement and a complex stratigraphy resulting from various phases of occupation during the Neolithic (Fig. 2).

The excavation area considered in this study includes Sector 3–Section 4, with 2 sequences (Fig. 2) where, in 48 $m^2$, five different structural Neolithic phases were recognised (Micheli, 2018; Micheli et al., 2022, 2023). The earliest occupation of the site is represented by phases 1–4, dated between 6350/6250 and 5950 cal yr BP (end of the Middle Neolithic) and associated with the Square Mouthed Pottery (*Vasi a Bocca Quadrata*) culture or SMP culture. Later phases 5a–b, dated between 5850 and 5550 cal yr BP (Late Neolithic), are attributed to the Late Neolithic Alpine Groups.

## 2. Material and methods

In this section, we describe the methods applied to investigate two new sequences (PaluON2 and PaluOFF1). For previously published data, readers should refer to the corresponding profiles PDL157/'99 (Pini, 2004) and PaluON1 (Zappa et al., 2023).

### 2.1. Chronology

*On-site record: PaluON2* – The chronology, based on both radiocarbon dates (Micheli et al., 2018) and archaeological evidence, spans from ca. 6300 to 5600 cal yr BP comprising all the archaeological phases recognised in Sector 3. The 5 phases identified in this sector were recognised on the basis of the structural evidence identified at the various levels in relation to both the stratigraphic contexts of the deposit and the associated archaeological materials. The development of the Neolithic in northern Italy is well known thanks to numerous sites with well-preserved archaeological deposits that have provided good stratigraphic sequences (Ferrari and Visentini, 2002; Visentini, 2018). Comparisons with other Italian Neolithic sites in the Alpine regions or in the Po Valley therefore allow for a reliable chronological-cultural attribution of many ceramic finds found in Sector 3, both for materials associated with the Square Mouthed Pottery culture (Phases 1-4) and for those from the Late Neolithic Alpine Groups (Phase 5). The investigations also allowed to obtain numerous short-lived samples (seeds, acorns and charred apples) used for AMS $^{14}C$ dating. At the moment, seventeen dates are available from samples of different stratigraphic units of the phases identified in Sector 3, most of which have not yet been published pending the results of further dating of dendrochronological samples necessary for wiggle-matching in order to define the most reliable chronological sequence possible for the Palù di Livenza site. What is certain is that after the abandonment of the Neolithic site in the mid-4th millennium BC (c. 5400 cal yrs BP) no new settlements were identified, but it cannot be excluded that this occurred in other areas of the wetland for which there is currently no evidence. The $^{14}C$ dates obtained from archaeological contexts in Sector 3 published in Micheli et al. (2018) and Zappa et al. (2023) are reported in Table S1.

*Off-site record: PaluOFF1* – Eight radiocarbon dates were obtained, two on seeds (performed at the ETH/AMS Facility in Zurich) and six on peat (at ISOCORE laboratory in Campania, Italy). Calibration was carried out using Oxcal 4.4.4 (Ramsey, 2009) and the calibration curve of atmospheric data from Reimer et al. (2020). Details of the samples are provided in the Supplementary Information (Table S2). The age-depth model was performed on all radiocarbon dates using the "Bchron" package (Haslett and Parnell, 2008) performed with R, version 4.1.0 (R Core Team, 2020). Default model settings were applied, including 10, 000 MCMC (=Markov Chain Monte Carlo) iterations, a burn-in of 2000 iterations, thinning result every 8. Prior outlier probabilities were set to 0.01 for each date, and radiocarbon ages were calibrated using the IntCal20 calibration curve.

The PaluOFF1 record spans a broad chronological range, that includes the period represented by PaluON2. The two records can therefore be compared to identify similarities and differences between the on-site and off-site sequences, helping to distinguish local processes

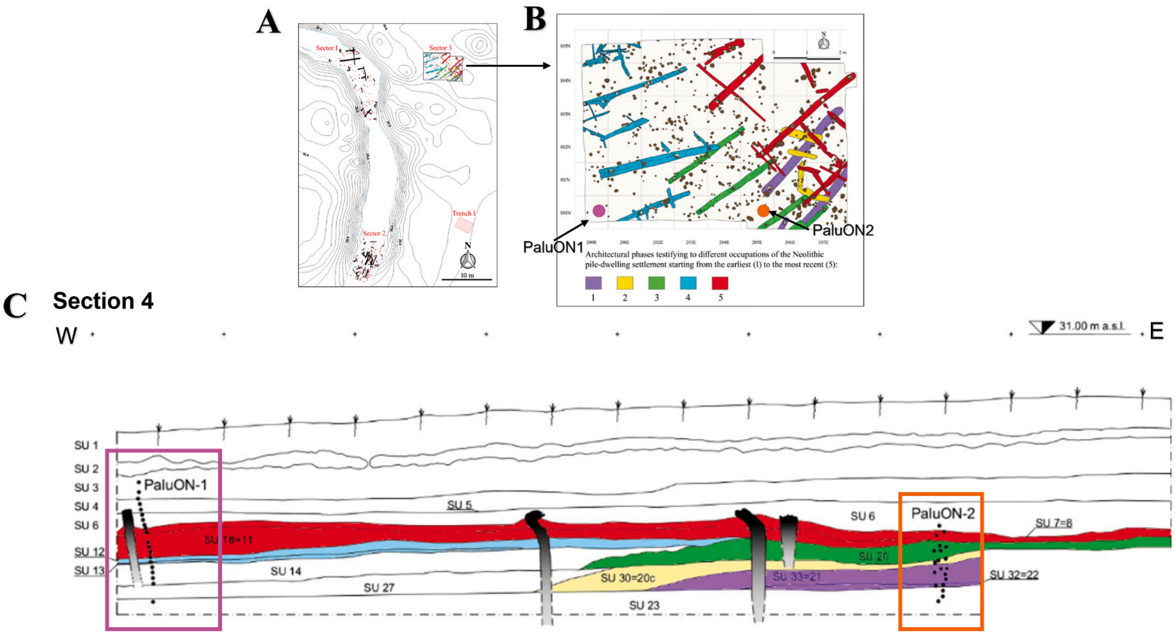

**Fig. 2.** A) Excavation area in the Palù di Livenza basin showing the three investigated sectors (Micheli et al., 2022, 2023). B) Detail of the structural phases recognised in Sector 3. Colours indicate the different phases as follows: red, Phase 5; blue, Phase 4; green, Phase 3; yellow, Phase 2; purple, Phase 1 (Micheli et al., 2022, 2023). See also the Supplementary Material for details on the sedimentology and archaeological phases of each sequence. C) Location and correlation of the two on-site sequences analysed in Sector 3, PaluON1 (fuchsia square; Zappa et al., 2023) and PaluON2 (orange square; this study), with pollen samples marked by black dots. Grey elements represent posts identified during the excavation, whereas the colour of the layers correspond to the structural phases.

occurring within the archaeological site from broader environmental dynamics outside it.

### 2.2. Sampling

The on-site sampling (PaluON2) was conducted in Sector 3, SE corner of Section 4, during the 2021 archaeological excavation campaign (Fig. 2; Table S3). The vertical profile sampled inside the pile-dwelling consists of the stratigraphical units related to the earliest phases in the sector (phase 1 and 2; Micheli et al., 2022, 2023), which are absent in the western part of the sector (PaluON1; Zappa et al., 2023). 20 samples were collected from the profile each 3/4 cm and in each stratigraphic unit. No samples were collected between 85 and 98 cm depth due to the presence of a wooden post in the stratigraphy. This new sequence was sampled and analysed to investigate intra-site variability, localised different depositional conditions, and possible differences in anthropogenic signals within the pile-dwelling area. Unlike PDL157/'99, this sequence was collected from a different sector of the site, potentially reflecting differences in the functional use of the settlement area (living or productive areas).

PaluON2, the second on-site record from Sector 3, was sampled following further excavations, which showed that the previously analysed PaluON1 sequence did not encompass all the archaeological phases identified in this sector. In particular, PaluON1 does not include the earliest phases, archaeological phases 1 and 2, which are instead recorded in PaluON2. The comparison between the two sequences is therefore particularly informative, as they also intercept different archaeological structures, including possible silos, and can provide insights into the spatial variability of activity areas within the site.

The off-site record (PaluOFF1) was manually cored at over 400 m west of the archaeological site, in an area lacking any evidence of archaeological material on the surface and along the stratigraphy. Coring was performed using an Ejikelkamp hand auger, with an Edelman head for sediment above the groundwater table and a gauge of 1 m of length below the groundwater table (cf. Fontana et al., 2017), reaching a depth of ca. 6 m. At this depth, below an erosive surface, the top of the light-bluish overconsolidated clays related to the LGM lake was found. Following the sedimentological description of the core, a subset of 29 samples was selected to ensure a representative coverage of the entire sequence and processed for palynological analysis in this study (Table S4). A broader sampling interval was adopted for this core, because of the greater length of the sequence, with sampling guided by careful observation of sedimentological changes along the sequence. Although we acknowledge this as a limitation, the results appear to be consistent and provide a reliable basis for the comparison between the on-site and off-site records.

Furthermore, three mosses (M1, M2 and M3), collected in the proximity of the sampling point of the off-site record (Fig. 1B), were analysed for assessing the current pollen rain in the site. Moss samples are widely used in Quaternary studies as natural pollen traps, providing a modern reference for comparing present-day pollen rain with fossil pollen assemblages and for interpreting past vegetation, land use, and climate signals (Hicks and Birks, 1996; Räsänen et al., 2004; Davis et al., 2020).

### 2.3. Palynological extraction from sediment and mosses and microscopic analyses

All selected samples were treated for palynological extraction (Florenzano et al., 2012), including deflocculation of clays using a nylon wire with 7 μm meshes, removal of carbonates with 10% HCl and silicates with 40% HF, acetolysis, separation with heavy liquid (Na-metatungstate hydrate), drying in stove at 42 °C.

For the palynological extraction from mosses, 2 g of moss were boiled in 10% KOH for 10 min to remove humic acids. Then mosses were then filtered and repeatedly rinsed with distilled water (Zappa et al. in press.;Zappa et al). *Lycopodium* spore tablets were added prior to chemical treatment in order to allow calculation of pollen concentration (expressed in p/g). Slides were examined under an optical microscope at 1000× magnification. Pollen grains (Fig. S1) were identified using atlases, keys (e.g., Moore et al., 1991; Reille, 1992; Beug, 2015), and the reference collection of the laboratory of Modena. Pollen grains were identified at the most specific taxonomic level. When the identification at species or genus level was not possible, pollen grains were identified through the use of groups and types following Moore et al. (1991) and Beug (2015). The fenestrate pollen of Cichorioideae is identified as Cichorieae according to Florenzano et al. (2015). Pollen counts include all counted pollen grains, averaging 300 per sample. This pollen count proved to be sufficient to capture the main vegetation trends and to compare the on-site and off-site records. Microcharcoals were analysed following the method reported in Mercuri et al. (2019b) based on the measuring of the length of the minor axis of particles and their concentrations were expressed in CHAC (=CHarcoal Concentration) calculated as number of charcoals $cm^{-3}$. In addition, Non-Pollen Palynomorphs (NPPs) were identified and counted when relevant (Van Geel, 2001; Gelorini et al., 2011; Shumilovskikh and Van Geel, 2020; Shumilovskikh et al., 2021, 2022).

### 2.4. *Data elaboration*

Palynological data (PaluON2 and PaluOFF1) were elaborated using Tilia software (Grimm, 2015).

Pollen zones (LPAZ) were identified following the cluster analysis (Grimm, 1987), and were labelled as follows: PAL (PaluOFF1, off-site core – six Local Pollen Zones – LPAZ) and PDL (Palù di Livenza, on-site records), with W indicating the western record (PaluON1– four LPAZ, Zappa et al., 2023) and E the eastern one (PaluON2 – four LPAZ). Sums useful for environmental and land use reconstructions were calculated (Table 1; Pignatti et al., 2017; Mazier et al., 2006, 2009; Mercuri et al., 2013; Florenzano et al., 2015; Kouli et al., 2015). Principal Component Analysis was performed using XLStat on the three records (PaluON1, PaluON2 and PaluOFF1) to discriminate contexts based on their pollen assemblage.

Palynological data from all the sites are stored in the BRAIN database (Mercuri et al., 2024) with unique identifiers: PDL157/’99 = NFV4, PaluON1 and PaluON2 = NFV26, and PaluOFF1 = NFV28.

#### 2.4.1. *REVEALS on PaluOFF1 data*

The basin context of PaluOFF1 record was chosen to apply step 1 (REVEALS – Regional Estimates of VEgetation Abundance from Large Sites; Sugita, 2007) of the LRA (Landscape Reconstruction Algorithm) using the program REVEALS. v5.0. win 64 (Sugita, 1994, 2007). The algorithm was applied only to the off-site record, because REVEALS is designed to reconstruct regional vegetation composition from off-site pollen archives (in its original formulation, developed for large lake records). Whereas, in on-site archaeological sequences the pollen assemblage is strongly influenced by local human activities and depositional processes (Sugita, 2007). Plant species to be used in the application of the algorithm were selected based on the availability of parameters in literature for northern Europe and Mediterranean area (e.g., Mazier et al., 2012; Abraham et al., 2014; Kuneš et al., 2015, 2019; Githumbi et al., 2021). The application of REVEALS algorithm in Mediterranean landscapes is constrained by the availability of suitable pollen productivity and dispersal parameters, which may not fully represent high diversity of Mediterranean mosaic landscapes. Moreover, entomophilous taxa, that include several fruit-trees for example, were excluded from the application as parameters are not present in literature. Therefore, only a selected subset of the taxa found in the palynological record was used for REVEALS application and subsequent spatial modelling.

For this record, 17 Arboreal Pollen (AP) and 12 Non-Arboreal Pollen (NAP; Table 2) taxa with available and appropriate parameters (Table S5) were included. Pollen sums of the selected taxa in a single sample were lower than required by the algorithm. To address this issue, samples were grouped into “Time Windows–TW” that were identified based on the Local Pollen Zones (see above). The selected TW correspond to the six LPAZ identified (Table S6), ordered from the youngest (PAL6) to the oldest one (PAL1).

#### 2.4.2. *Cartographic elaborations: workflow*

The elaboration followed the following steps (Fig. 3).

1) A Digital Terrain Model (DTM) was created to represent the elevation gradient of the area, ranging from approximately 20 to 980 m a.s.l. Raw data correspond to a raster obtained from LiDAR survey with a horizontal pixel of 0.5 m and represented in the coordinate system RDN2008/UTM33, freely available from the web portal of the Regione Autonoma Friuli Venezia Giulia (www.eaglefvg.regione.fvg.it). A circular area with a 2500 m radius (= estimated area of influence in the Palù di Livenza basin and a small portion of the nearest

**Table 1**

Sums used for environmental and land use reconstruction. Taxa found in both records are reported in black, those found only in PaluON2 record in orange, and those found only in the PaluOFF1 core in blue. The colours in the first column correspond to the described pollen sums and are consistently applied in the pollen diagrams presented below.

| | POLLEN SUM | TAXA INCLUDED |
|---|---|---|
| 🟫 | 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* |
| 🟥 | Conifers | *Abies*, *Picea abies*, *Pinus*, *Juniperus* type |
| 🟥 | Upland forest (Kouli et al., 2015) | *Abies*, *Picea abies*, *Pinus*, *Fagus sylvatica*, *Betula* |
| 🟦 | Hygrophilous trees | *Alnus*, *Populus*, *Salix* |
| 🟦 | Hygrophilous herbs | Cyperaceae, *Scilla* type, *Scirpus* type, *Lilium martagon, Lythrum, Pancratium* cf., *Paris* type, *Phragmites australis*, *Sparganium emersum* type, *Typha latifolia* type, *Veratrum* type |
| ⬜ | Hydrophytes (Pignatti et al., 2017) | *Alisma*, *Butomus umbellatus*, *Callytriche*, *Myriophyllum*, *Potamogenton*, *Sparganium erectum* type |
| 🟥 | API – Anthropogenic Pollen Indicators (Mercuri et al., 2013; Florenzano et al., 2015) | *Artemisia*, *Centaurea nigra* type, *Plantago* (*P. atrata, P. lanceolata* type, *P. albicans, P. bellardii*), *Trifolium* type, *Urtica*, cereals, Cichorieae |
| 🟨 | Cereals | *Avena/Triticum* group, *Hordeum* group, *Panicum* |
| 🟩 | Cereal weeds | *Alchemilla* type, *Anagallis arvensis* type, *Papaver, Persicaria maculosa* type |
| ⬜ | LPPI – Local Pastoral Pollen Indicators (Mazier et al., 2006, 2009) | Asteraceae (*Anthemis* type, *Aster* type, *Centaurea nigra* type, Cichorieae, *Taraxacum*, *Carduus* type, *Cirsium* type, *Senecio* type, *Xanthium* type), Ranunculaceae (*Pulsatilla, Thalictrum flavum* type), *Trifolium* type, *Trifolium stellatum* type, *Potentilla* type, *Galium* type |
| ⬜ | Grasslands | Apiaceae, Chenopodiaceae/Amaranthaceae, Poaceae wild grass group |
| 🟪 | Possibly cultivated trees (Kouli et al., 2015) | *Cornus mas*, *Corylus avellana*, *Prunus*, *Rubus*, *Sorbus*, *Vitis vinifera* |

**Table 2**
The selected taxa (17 A P and 12 NAP) included in the land cover types used for the cartographic elaborations. The name of taxa are reported accordingly to the cited literature (see also Table S5).

| LAND COVER TYPE | TAXA INCLUDED | PLANT FUNCTIONAL TYPE (PFT - Wolf et al., 2008) | PFT DEFINITION |
|---|---|---|---|
| DECIDUOUS FOREST | *Acer* | IBS | Shade-intolerant summer-green trees |
| | *Carpinus betulus* | TBS | Shade-tolerant summer-green trees |
| | *Corylus* | TBS | Shade-tolerant summer-green trees |
| | *Carpinus orientalis* | TBS | Shade-tolerant summer-green trees |
| | deciduous *Quercus* | TBS | Shade-tolerant summer-green trees |
| | *Tilia* | TBS | Shade-tolerant summer-green trees |
| | *Fraxinus* | TBS | Shade-tolerant summer-green trees |
| | *Ulmus* | TBS | Shade-tolerant summer-green trees |
| UPLAND FOREST | *Abies* | TBE2 | Shade-tolerant evergreen trees |
| | *Picea* | TBE1 | Shade-tolerant evergreen trees |
| | *Pinus* | IBE | Shade-intolerant evergreen trees |
| | *Juniperus* | TSE | Tall shrub-evergreen |
| | *Betula* | IBS | Shade-intolerant summer-green trees |
| | *Fagus sylvatica* | TBS | Shade-tolerant summer-green trees |
| ANTHROPOGENIC ENVIRONMENT | Cerealia-t | AL | Agricultural land – cereals |
| | Chenopodiaceae | GL | Grasslands – all herbs |
| | *Artemisia* | GL | Grasslands – all herbs |
| | *Plantago lanceolata* | GL | Grasslands – all herbs |
| | *Rumex acetosa*-t | GL | Grasslands – all herbs |
| | Fabaceae | GL | Grasslands – all herbs |
| | *Filipendula* | GL | Grasslands – all herbs |
| | *Potentilla*-t | GL | Grasslands – all herbs |
| | Cichorioideae | GL | Grasslands – all herbs |
| WETLANDS | *Alnus* | IBS | Shade-intolerant summer-green trees |
| | *Salix* | TSD | Tall shrub, summer-green |
| | *Populus* | IBS | Shade-Intolerant Summergreen Tree |
| | Cyperaceae | GL | Grasslands – all herbs |
| MEADOWS | Poaceae | GL | Grasslands – all herbs |
| | Apiaceae | GL | Grasslands – all herbs |

mountains that probably contribute to the local pollen rain; Fig. S2) was selected and imported into the QGIS environment for further processing. From the DTM, additional layers were derived in GRASS GIS environment and are (Fig. S3):

- Slope: showing inclination values expressed in degrees (Hofierka et al., 2009).
- Digital terrain modeling: a review of hydrological, geomorphological, and biological applications. The one I put as Moore, Grayson, & Ladson, 1991 in the original draft. This one is related to this part, while for palynological analyses is the (Moore et al., (1991))

2) Land cover types were selected based on existing inventories (e.g., CLC 2018; Copernicus Land Monitoring Service) and adapted to the taxa recorded in the PaluOFF1 palynological sequence, for which production and dispersal parameters were available for use in the REVEALS model (see Table S5). The chosen land cover types include deciduous forest, upland forest, anthropogenic environments (comprising synanthropic plants and species related to human activities, such as cereals), wetlands, and meadows. A detailed list of the taxa included in each land cover type is provided in Table 2.
3) Creation of suitability maps (Fig. S4): For each land cover type, suitability maps were generated using elevation, slope, and wetness index maps (0–1 scale being 0 the lowest and 1 the highest suitability) taking into account the ecological and environmental requirements of the species included in each land cover type; then combined suitability was produced by combining the suitability maps based on the three geomorphological variables (0–3 scale); a 5 m buffer was applied around main streams to exclude areas near watercourses and avoid misclassification.
4) The palynological data derive from the PaluOFF1 core and were divided into six pollen zones based on cluster analysis. For each pollen zone, the counts from the included samples were summed to achieve a sufficient total for application of the REVEALS algorithm (Table S6).
5) Application of REVEALS algorithm on palynological data: the algorithm was applied to each pollen zone, obtaining regional cover percentage of the taxa involved. To derive the land cover proportions used as input for the GIS analyses, REVEALS-based estimates for individual taxa were summed within the selected land cover classes for each pollen zone (e.g., upland forest is the sum of the REVEALS percentages of *Abies*, *Picea abies, Pinus*, *Betula* and *Fagus sylvatica*).
6) After calculating the total surface of each land cover type based on the percentages of REVEALS (point 5), the combined suitability maps (point 3) were used to distribute each land cover types in the most suitable locations; to prevent the model from assigning the same pixels to different land cover types with similar suitability in specific sectors, a priority ranking was developed for the land cover types (e.g. anthropogenic environments are mapped before natural environments); a moving window was also used to reclassify each pixels according to the value of its nearest neighbour, thus removing isolated pixel surrounded by pixels of different land cover type; these steps were repeated until the distribution of land cover type in the area matched the surface estimations derived from REVEALS.

## 3. Results

### 3.1. Chronology

The age depth model for PaluOFF1 core relies on eight radiocarbon dates (Fig. 4). Sediments appear to have accumulated slowly and steadily, with no abrupt changes evident in the model. That suggests that the record spans approximately 11,800 to 1500 cal yr BP.

### 3.2. Pollen, NPP and microcharcoal analyses

Pollen preservation was generally good in both the analysed records, with high biodiversity and pollen concentrations. Mean pollen

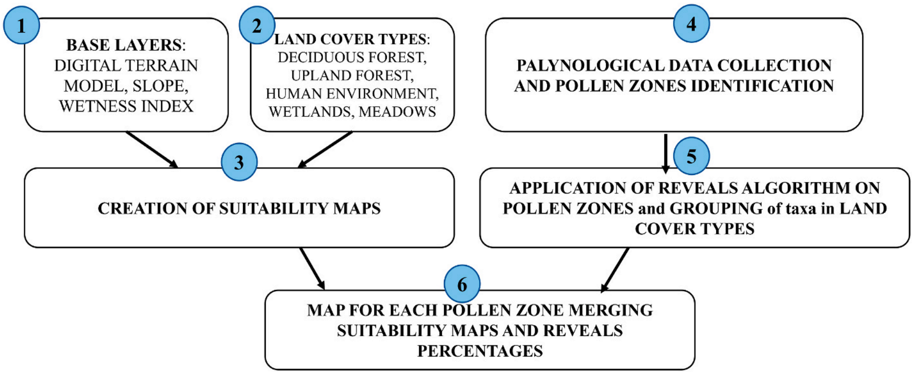

**Fig. 3.** Workflow of the cartographic elaborations performed, from the selection of the base layers and land cover types, to the final maps with land cover percentages obtained from REVEALS.

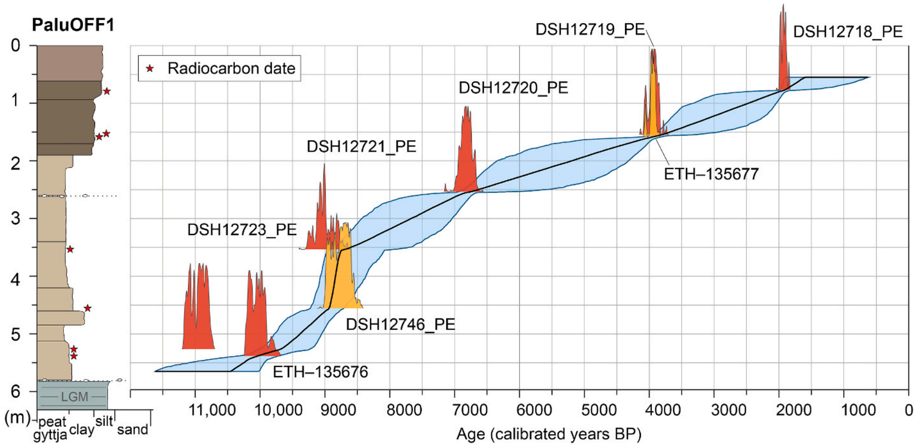

**Fig. 4.** Age depth model carried out with BChron package in R environment, based on eight radiocarbon dates (Table S2), with associated stratigraphic log.

concentrations were similar in the two sequences, and the floristic lists indicate high biodiversity in both sequences (Table 3). The forest cover was lower in the on-site record (AP = 38.4% on average; Fig. 5) compared to the off-site record (58.4%; Fig. 6).

### 3.2.1. *Main features of palynological diversity*

The natural environment is mostly clear reflected in the off-site sequence (Fig. 6), although it is also well represented in the on-site record (Fig. 5). Woods are mainly composed by elements of the oakwood (mainly deciduous *Quercus* followed by the other mixed oakwood elements (21.3% and 33.3% in PaluON2 and PaluOFF1 respectively), upland forest (conifers and hilly-mountain trees such as *Betula* and *Fagus sylvatica* – 4.5% and 7.7%) and hygrophilous woods (*Alnus*, *Populus* and *Salix* – 8.6% and 12.5%). Hygro-hydrophilous NAP communities are also well represented (12.4% and 13.9%). In PaluOFF1, the presence of *Linnaea borealis* in 7 samples throughout the sequence is noteworthy, representing an important boreal relict (Zappa et al., 2025a, 2025b).

Human influence is more pronounced in the on-site record (Fig. 5). Anthropogenic Pollen Indicators (API; Mercuri et al., 2013) account for 11% in PaluON2 and 4.5% in PaluOFF1, while Local Pastoral Pollen Indicators (LPPI; Mazier et al., 2006, 2009) reach 6.9% in PaluON2 and 4% in PaluOFF1. Probable cultivated trees (Kouli et al., 2015) show comparable values in both sequences (6.2% in PaluON2 and 7.0% in PaluOFF1) and are largely represented by *Corylus avellana*, a species naturally widespread in the basin and likely exploited as a food resource. Additional evidence of human activities is provided by the occurrence of *Linum usitatissimum* in two on-site samples from PaluON2, together with a complete anther of the *Hordeum* group and one of *Mentha* type in the same sequence, suggesting the collection and storage of these plants within the village.

### 3.2.2. *Local Pollen Zones (LPAZ)*

In this section, each zone for both sequences is described, reporting the average values of the main and most representative taxa.

#### 3.2.2.1. *PaluON2: PDLE1–4 (Figs. 5 – S5).*

- PDLE1 (samples no. 20–19; 6330–6300 cal yr BP). AP is 44.4% on average and NAP 55.6%. Woody taxa are dominated by mixed oakwood (21%), followed by conifers (9.8%) and hygrophilous trees (8.8%). Wet habitats are further indicated by hygrophilous herbs (23.6%) and hydrophytes (1.8%). Anthropogenic indicators include API (6.1%; cereals 3.5%) and LPPI (3.2%); possibly cultivated trees are 5.1%.

- PDLE2 includes three samples (no.18–16; 6280–6230 cal yr BP). AP decreases slightly to 39.3%, while NAP increases to 60.7%. Woody taxa are still dominated by mixed oakwood (22.7%), followed by hygrophilous trees (7.0%) and conifers (5.8%). Wet habitats are mainly indicated by hygrophilous herbs (20.2%). API and LPPI both reach 5.3%, with cereals at 4.0%, while possibly cultivated trees remain stable at 4.3%.

- PDLE3 includes eight samples (no.15–8; 6190–6080 cal yr BP) divided in two subzones (PDLE3a and PDLE3b). Overall, PDLE3 is characterised by a dominance of NAP over AP, woodland largely represented by mixed oakwood with a consistent hygrophilous

**Table 3**
The 10 most abundant taxa (both AP and NAP) in the PaluON2 and PaluOFF1 records, and their average abundances in samples.

| | | PaluON2 | PaluOFF1 |
|---|---|---|---|
| | Concentration (p/g) | 56,400 | 58,800 |
| | Pollen florula (no. taxa) | 122 | 133 |
| | AP – NAP | 37 A P – 85 NAP | 37 A P – 96 NAP |
| **AP – Arboreal Pollen** | Deciduous *Quercus* | 10% | 19.8% |
| | *Alnus* | 7.3% | 11.7% |
| | *Corylus avellana* | 5.7% | 6.8% |
| | *Abies* | 2.8% | 4.0% |
| | *Pinus* | 1.6% | 3.5% |
| | *Fagus sylvatica* | 1.6% | 3.4% |
| | *Fraxinus excelsior* type | 2.5% | 2% |
| | *Carpinus betulus* | 0.6% | 2% |
| | *Tilia platyphyllos* type | 0.4% | 0.9% |
| | *Ulmus* | 0.4% | 0.7% |
| **NAP – Non - Arboreal Pollen** | Poaceae wild grass group | 17% | 11.5% |
| | Cyperaceae | 4.9% | 5% |
| | *Sparganium emersum* type | 4.8% | 3.4% |
| | *Hordeum* group | 4.6% | 2.1% |
| | *Scilla* type | 1.2% | 1.7% |
| | *Scirpus* type | 0.7% | 1.6% |
| | *Butomus umbellatus* | 0.2% | 1.1% |
| | *Mentha* type | 2.1% | 1.1% |
| | *Brassica* type | 4% | 1.1% |
| | *Ranunculus* type | 2.3% | 1.1% |

component, and wet habitats mainly indicated by hygrophilous herbs. Anthropogenic indicators (API and LPPI) increase through the zone, with cereals representing the majority in the API signal. In PDLE3a, AP is 37.5% and NAP 62.5%; mixed oakwood reaches 21.4% (with hygrophilous trees 7.9% and conifers 4%), hygrophilous herbs decline to 9.7%, while API increase to 10.9% (with cereals 10.2%) and LPPI to 7.0%; possibly cultivated trees has a peak at 7.8%. In PDLE3b, openness increases further (AP: 30.5%, NAP: 69.5%): mixed oakwood decreases to 17.3%, hygrophilous trees remain similar (8.2%), and conifers halve (2.2%); hygrophilous herbs stay stable (9.5%). Human indicators intensify (API: 17.5% with cereals being the 13.0%; LPPI: 7.4%), while possibly cultivated trees decrease to 6.0%.

- PDLE4 (samples no.7–1; 5980–5670 cal yr BP) divided in two subzones (PDLE4a and PDLE4b). In general, PDLE4 is characterised by a substantial woody component dominated by mixed oakwood, a persistent hygrophilous signal and relatively high anthropogenic indicators (API and LPPI). Across the whole zone, it is also worth noting the very high presence of heterocysts of *Rivularia* type. In PDLE4a, AP is 37.2% and NAP 62.8%, with mixed oakwood at 23.1%, hygrophilous trees at 6.5%, conifers at 3.6%, hygrophilous herbs at 9.5%, and high API (14.2%, with cereals 9.7%) and LPPI (8.7%). In PDLE4b, AP rises to 44.5% (NAP decrease to 55.5%), mixed oakwood slightly decreases (21.2%) while hygrophilous trees increase (14.5%) and conifers increase to 4.4%; API declines to 9.1% (cereals 5.2%) and LPPI to 7.5%, with possibly cultivated trees remaining broadly stable (6.5% vs 6.2%).

#### 3.2.2.2. *PaluOFF1 – PAL1–6 (Fig. 6 – S6).*

- PAL1 (samples no. 29–26; 11,800–10,790 cal yr BP). AP is 48.8% and NAP 51.2%. Woody taxa are largely represented by mixed oakwood (23.9%) and upland forest (21.5%), together with abundant conifers (20.7%), while hygrophilous trees are low (2.4%). Also, wet indicators among herbs are limited (hygrophilous herbs 8.9%; hydrophytes 0.6%); API are 11.0%, with a majority of *Artemisia.*

- PAL2 (samples no. 25–23; 10,790–9060 cal yr BP). AP increases to 60.5% (with NAP 39.5%). Woodlands are dominated by mixed oakwood (44.1%), with upland forest (11.2%) and conifers (7.5%), while hygrophilous trees are still low (4.6%). Wet habitats are indicated also by hygrophilous herbs (14.5%) and hydrophytes (2.6%); API and LPPI are very low 2.1% and 3.7% (with cereals 1%).

- PAL3 (samples no. 22–18; 9060–8200 cal yr BP). This zone is divided in two subzones (PAL3a and PAL3b). In general, is characterised by high AP with prevalently mixed oakwood with consistent upland and conifer forests and wet environments. PAL3b shows slightly higher mixed oakwood (39.0% vs 37.5%) and hygrophilous trees (6.3% vs 4.5%), and a stronger wet signal in hygrophilous herbs (17.9% vs 13.5%), while PAL3a has a slightly higher upland forest (12.4% vs 10.8%), higher conifers (6.7% vs 6%), and higher API and LPPI (5.4% and 5% vs 4.5% and 3.2%).

- PAL4 (samples no. 17–8; 8200–5600 cal yr BP). This zone is divided in two subzones (PAL4a and PAL4b). Overall, PAL4 is dominated by AP (AP 65.0–67.2%; NAP 32.8–35%) and characterised by a substantial woody component, with mixed oakwood as the main forest type, accompanied by hygrophilous trees and a moderate conifer signal. PAL4a shows higher mixed oakwood (42.6% vs 33.8%) and slightly higher hygrophilous herbs (10.9% vs 8.2%), whereas PAL4b is characterised by markedly higher hygrophilous trees (18.7% vs 12.8%), a stronger conifer component (7.7% vs 3.8%), and higher upland forest (12.4% vs 8%); API is similar, while LPPI is slightly lower in PAL4b (2.1% vs 2.5%).

- PAL5 (samples no. 7–4; 5600–2890 cal yr BP). This zone is divided in two subzones (PAL5a and PAL5b). Overall, PAL5 shows a variable balance between AP and NAP with mixed oakwood remaining important but reduced (25.6–30.4%) and a prominent hygrophilous component. Anthropogenic indicators are moderate, with cereals around 2.5–3.9%. PAL5a AP cover is higher (AP 60.8% vs 43.8%) and features higher hygrophilous trees (21.7% vs 9.3%) and higher API and cereals (5.6%; cereals 3.9%), whereas PAL5b shifts toward openness (NAP 56.8% from 39.2% of the previous subzone) and is distinguished by a strong increase in hygrophilous herbs (22.2% vs 8.6%) and slightly higher conifers (5% vs 3.9%); LPPI remains similar but slightly lower in PAL5b (1.8% vs 2.2%).

- PAL6 (samples no. 3–1; 2890–1500 cal yr BP). AP is 54.8% (with NAP 45.2%). The woody signal is dominated by hygrophilous trees (31.4%), while mixed oakwood is reduced (17.6%); upland forest and conifers are consistently lower (5% and 3.6%). Hygrophilous herbs remain relatively high (16.5%), while API and LPPI are lower (3.5% and 2.1%).

### 3.2.3. *The NPP records – Fig. 5b-6b*

The most common non-pollen palynomorphs identified are morphotypes belonging to the cyanobacteria *Rivularia* type, the mycorrhizal fungi *Glomus* type, some algae (*Arcella*, *Pediastrum* and *Pseudoschizaea*) and *Trichuris* resting eggs (the latter, found only in the on-site record).

### 3.2.4. *The microcharcoal records – Fig. 5b-6b*

Charcoal particles average 295,049 ch*cm$^{-3}$ in the PaluON2 sequence, whereas they are nearly absent in the PaluOFF1 sequence, with an average CHAC of 6882 ch*cm$^{-3}$ (consisting only of small and few medium sized class).

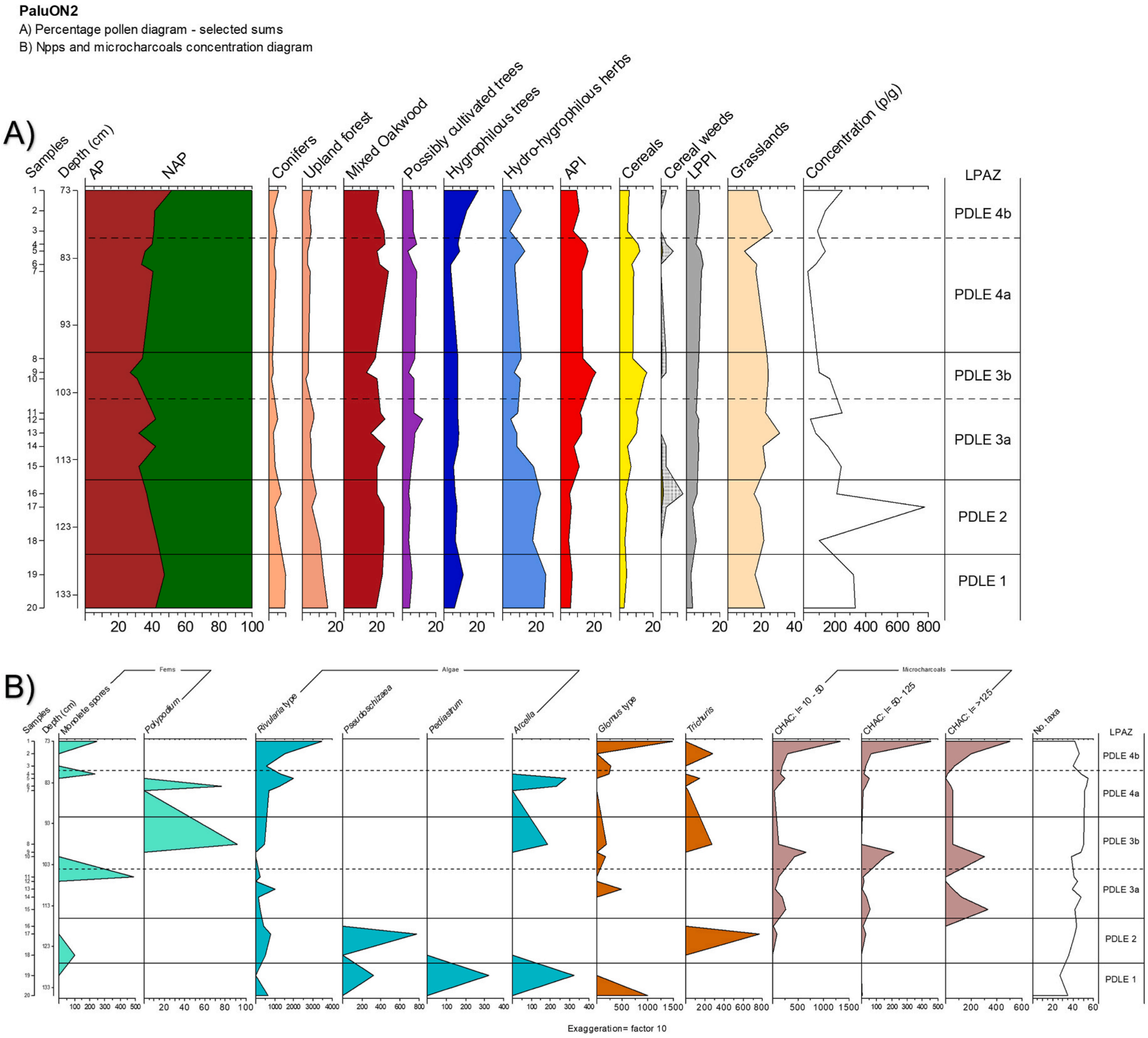

**Fig. 5.** PaluON2 – A) Percentage pollen diagram of selected sums: for taxa included in sums refer to Table 1; B) Concentration of microcharcoals and most relevant NPPs.

### 3.3. *Moss samples*

Across the three moss samples, an average of 504 pollen grains, representing 48 taxa (20 A P and 28 NAP), was counted. Ubiquitous taxa reflecting the current pollen rain in the area include ten woody plants (in decreasing order; Fig. S7): *Alnus* (34.0% on average), *Platanus* (22.1%), *Corylus avellana* (7.5%), deciduous *Quercus* (3.8%), *Ostrya carpinifolia/Carpinus orientalis* type (1.8%), *Salix* (1.2%), *Pinus* (1.1%), *Abies* (1.1%), *Carpinus betulus* and *Ulmus* (0.7% each) and seven non arboreal taxa (Fig. S7): *Brassica* type (2.3%), Poaceae wild grass group and Chenopodiaceae/Amaranthaceae (1.5% each), *Myriophyllum* (1%), *Aster* type (0.7%), *Mentha* type and *Stachys sylvatica* type (0.3% each). These pollen taxa reflect the main vegetation groups characterising the area, namely hygrophilous wood, mixed oakwood, conifer forest and natural grasslands (European Environment Agency, 2018).

### 3.4. *Regional cover (REVEALS)*

The quantitative reconstruction for the six LPAZ is in accordance with the interpretation of the pollen assemblage described from pollen diagrams (Figs. 7 and 8). For the most ancient pollen zone, PAL1, a forested environment composed by upland forests (50.8%) and deciduous forests (14.6%) is attested. In PAL2 upland forest are quite the same, but deciduous ones increase (29.6%). In PAL3 and PAL4 anthropogenic environments (15.6% and 9.5% respectively) are well attested, while deciduous and upland forests decrease (29% and 33.8% respectively). An increasing humidity is also recorded (9.6%), continuing to rise in PAL5 (14.7%) and PAL6 (25%). This last pollen zone marks the expansion of hygrophilous trees and wetlands, accompanied by general decrease of anthropogenic environment (8.4%), upland forests (24.9%) and deciduous forests (17.1%).

### 3.5. *Cartographic elaborations*

The application of the proposed method to generate land cover maps based on pollen percentages derived from the REVEALS algorithm yielded promising results, supporting and improving the visualization of the spatial distribution of selected taxa within the study area.

PAL1 (11,800–10,790 cal yr BP) is characterised by a pre-Holocene high forest cover dominated by upland forest taxa, followed by deciduous forest with meadows and very few wet areas. PAL2 (10,790–9060 cal yr BP) marking the onset of the Holocene, shows the expansion of deciduous forests and an increase in wetland areas. In PAL3 (9060–8200 cal yr BP), wetlands and anthropogenic environment start increasing, a trend that continues into PAL4 (8200–5600 cal yr BP). In PAL5 (5600–2890 cal yr BP), the mixed oakwood decreases significantly in favour of grasslands typical of meadows and wetlands. Finally, in PAL6 (2890–1500 cal yr BP), wetlands dominate the landscape, while

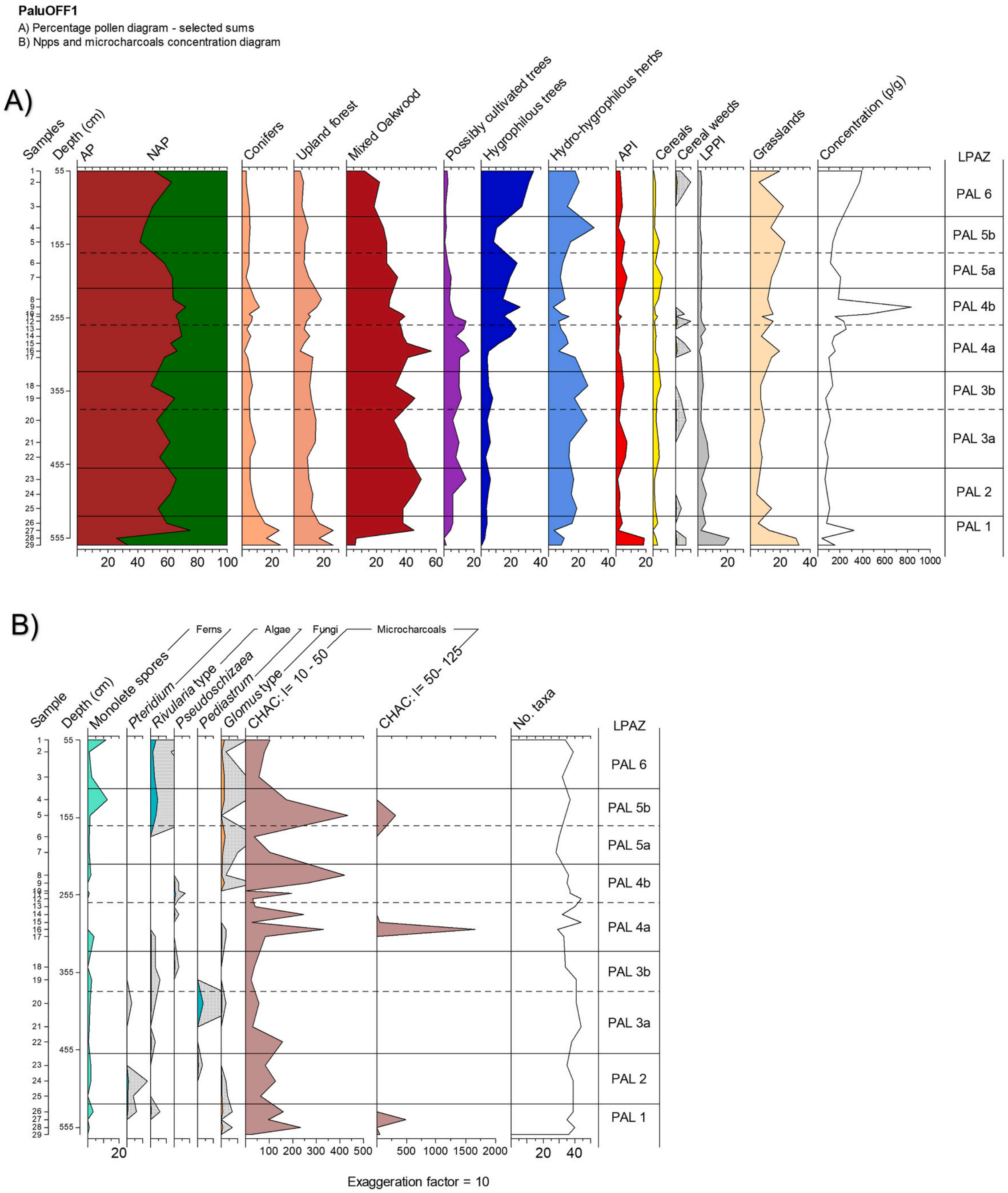

**Fig. 6.** PaluOFF1 – A) Percentage pollen diagram of selected sums: for taxa included in sums refer to Table 1; B) Concentration of microcharcoals and most relevant NPPs.

mixed oakwood and anthropogenic environment decrease.

## 4. Discussion

The on-site palaeoenvironment was reconstructed phase by phase by integrating the new sequence (PaluON2) with the previously studied record (PaluON1; Zappa et al., 2023) (Table 4). Strong consistencies in floristic composition emerged between the two sequences, supporting a robust site-scale palaeoenvironmental reconstruction. Comparison with the off-site record (PaluOFF1) subsequently allows this framework to be extended to the basin scale. In the following discussion, chronologies are presented in calibrated years before present (cal yr BP).

### *4.1. Palaeoenvironment and palaeoecological inferences at basin and site scale*

Pollen spectra from Palù di Livenza record biodiversity, environmental and climatic changes which occurred in the basin from ca. 11,800 cal yr BP to recent times. The reconstruction shows that, since the onset of the Holocene, the landscape was largely dominated by mixed oak forests with coniferous woodlands at higher elevations. During the Neolithic occupation, human impact on the environment is detectable as increased frequencies of cereal pollen and other anthropogenic indicators, pointing to the presence of cultivated fields in the surroundings of the pile-dwellings. These signals are particularly pronounced in the on-site samples, reflecting intensive local activity

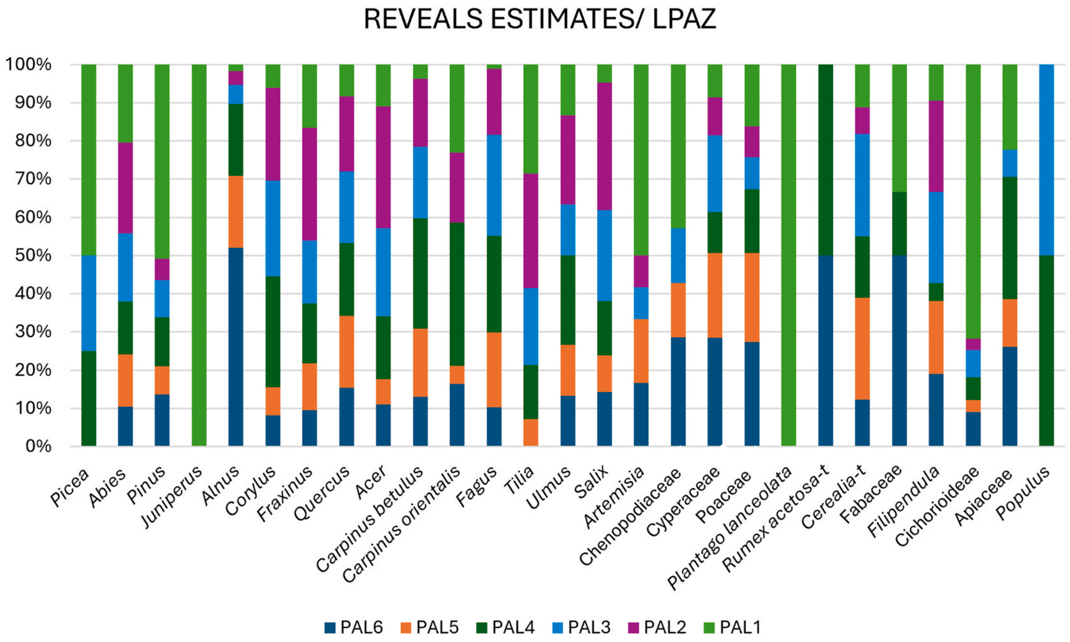

**Fig. 7.** Regional vegetation estimates for the taxa included in the six pollen zones (LPAZ) of PaluOFF1. Colours correspond to the pollen zones obtained by the cluster analysis (CONISS). *Betula* and *Potentilla*, although part of the taxa included in the application of the algorithm, occur in very low abundances and are therefore not visible in the graphical output.

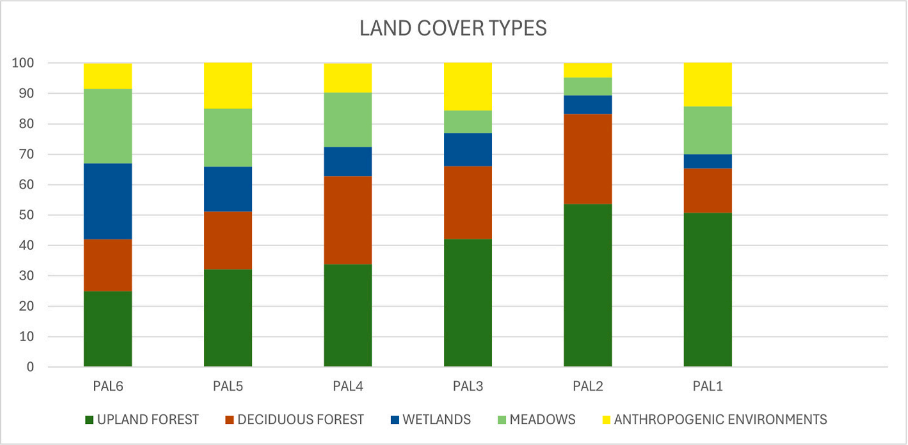

**Fig. 8.** Histogram of land-cover proportions obtained by summing regional vegetation estimates of individual taxa within the selected land-cover classes; these values were used as input for the algorithm and subsequent GIS analyses.

(including plant processing), but are also evident in the off-site record. Their presence in the off-site record may suggest that human influence extended limitedly beyond the settlement area into the nearby surrounding landscape. From 5000 cal yr BP onwards, vegetation dynamics shifted towards wetter environmental conditions, likely driven by climatic changes that favoured the development and expansion of a wetland system. This shift is interpreted as the result of both regional mid-to late-Holocene hydroclimatic changes and local basin evolution, including progressive infilling, swamping, and rising water-table conditions. In the broader northern Italian and southern Alpine context, palaeohydrological records indicate increasing hydrological instability during the mid-to late Holocene, with more frequent phases of higher lake levels after ca. 4000 cal yr BP (Magny et al., 2009, 2012). This environmental transition may have progressively reduced the suitability of the area for human occupation and ultimately led to the permanent abandonment of the site. Following this abandonment, forest cover gradually recovered, accompanied by continued wetland expansion, marking the establishment of a predominantly natural ecosystem dominated by hygrophilous woodland communities.

### *4.1.1. Long-term natural environment and human presence (11,800–8200 cal yr BP)*

At basin scale, the PaluOFF1 core records phases during which the basin was probably only sporadically occupied by late Palaeolithic and Mesolithic groups during their seasonally frequentation of the area, with no detectable imprint in the pollen record. Accordingly, the palaeoenvironment inferred for the first pollen zone (PAL1; ca. 11,800–10,790 cal yr BP; Fig. 6) is dominated by dry steppe communities, pointing to relatively arid conditions. The occurrence of conifer taxa further suggests persistently cold conditions, whereas mixed oakwood remains poorly represented. Overall, this assemblage is consistent with late-glacial vegetation patterns (e.g., Vescovi et al., 2007), when temperate mixed oak forests had not yet fully established.

Starting from PAL2 phase (from ca. 10,790 to 9060 cal yr BP; Fig. 6) a significant environmental change is recorded in the basin. The landscape became largely forested, with upland forests and deciduous mixed

**Table 4**

Comprehensive table that summarises the pollen zones of the two on-site sequences (PaluON1: acronym PDLW; PaluON2: acronym PDLE) in chronological order. Depth (cm), stratigraphic unit, associated archaeological or natural phase and the characterising palynological taxa are also reported.

| Chronological range (cal yr BP) | Phase | Pollen Zone | Depth (cm) | SSUU | Main AP taxa | Main NAP taxa |
|---|---|---|---|---|---|---|
| 7140–6370 | Pre-settlement | PDLW1 | 116–129 | 23<br>14<br>bottom | *Abies, Pinus, Betula, Fagus sylvatica* type, *Alnus, Corylus avellana,* deciduous *Quercus, Tilia platyphyllos* type | Cyperaceae, *Galium* type, *Hornungia* type, *Phragmites australis, Potamogeton, Scirpus* type, *Sparganium emersum* type, Poaceae wild grass group |
| 6330–6300 | Pre-settlement | PDLE1 | 130–135 | 23 | *Abies, Pinus, Fagus sylvatica, Alnus, Salix, Corylus avellana,* deciduous *Quercus, Fraxinus excelsior* type, *Salix* | *Asphodelus, Artemisia, Butomus umbellatus,* Cyperaceae, *Scirpus* type, *Stachys sylvatica* type, *Scilla* type, *Hordeum* group, Poaceae wild grass group, *Sparganium emersum* type |
| 6280–-6230 | Sect.3 archaeological phase 1 | PDLE2 | 125–118 | 23<br>32 | *Abies*, *Alnus*, *Fagus sylvatica*, *Corylus avellana*, *Fraxinus excelsior* type, *Acer campestre* type | Chenopodiaceae/Amaranthaceae, *Peucedanum palustre* type, *Brassica* type, Cyperaceae, *Scirpus* type, *Mentha* type, *Stachys sylvatica* type, *Scilla* type, *Hordeum* group, Poaceae wild grass group, *Ranunculus* type, *Filipendula, Sparganium emersum* type |
| 6190–-6140 | Sect.3 archaeological phase 1 | PDLE3a | 114–106 | 33 | *Alnus, Corylus avellana, Ostrya carpinifolia/Carpinus orientalis* type, deciduous *Quercus, Tilia platyphyllos* type, *Acer campestre* type, *Ulmus, Hedera Helix, Prunus, Vitis vinifera* | Chenopodiaceae/Amaranthaceae, Apiaceae, *Artemisia, Aster* type, *Centaurea nigra* type, *Brassica* type, *Avena/Triticum* group, *Hordeum* group, *Mentha* type, *Stachys sylvatica* type, *Ranunculus* type, *Thalictrum flavum* type, *Filipendula, Sparganium emersum* type |
| 6140–-6080 | Sect.3 archaeological phase 2 | PDLE3b | 101–98 | 30 | *Alnus, Corylus avellana, Ostrya carpinifolia/Carpinus orientalis* type, deciduous *Quercus, Acer campestre* type, *Ulmus, Hedera helix* | Chenopodiaceae/Amaranthaceae, Apiaceae, *Artemisia, Aster* type, *Centaurea nigra* type, *Brassica* type, *Avena/Triticum* group, *Hordeum* group, Poaceae wild grass group, *Mentha* type, *Stachys sylvatica* type, *Ranunculus* type, *Thalictrum flavum* type, *Filipendula, Plantago, Sparganium emersum* type |
| 6220–6020 | Sect.3 archaeological phase 3 | PDLW2a | 112–104 | 14 | *Abies, Pinus, Fagus sylvatica, Alnus, Salix, Acer campestre* type, deciduous *Quercus, Ulmus, Hedera helix, Vitis vinifera* | Apiaceae, *Artemisia, Aster* type, *Avena/Triticum* group, *Brassica* type, *Centaurea nigra* type, *Hordeum* group, *Hypericum perforatum* type, *Lamium* type, *Phragmites australis,* Poaceae wild grass group, *Potamogeton, Rhinanthus* type, *Scirpus* type, *Filipendula, Galium* type, *Solanum dulcamara, Urtica dioica* type. |
| 5980–-5830 | Sect.3 archaeological phase 3 | PDLE4a | 85–81 | 20 | *Salix, Carpinus betulus, Corylus avellana,* deciduous *Quercus, Fraxinus excelsior* type, *Acer campestre* type, *Prunus, Vitis vinifera* | Chenopodiaceae/Amaranthaceae, Apiaceae, *Artemisia, Aster* type, *Centaurea nigra* type, *Brassica* type, *Sinapis* type, Caryophyllaceae, Cyperaceae, *Scirpus* type, *Mentha* type, *Stachys sylvatica* type, *Scilla* type, *Avena/Triticum* group, *Hordeum* group, Poaceae wild grass group, *Ranunculus* type, *Thalictrum flavum* type, *Filipendula, Solanum nigrum* type |
| 6020–5750 | Sect.3 archaeological phase 4<br>Sect.3 archaeological phase 5a | PDLW2b | 100–84 | 13/12<br>11 | *Abies, Pinus, Fagus sylvatica, Acer campestre* type, deciduous *Quercus, Ulmus, Ostrya carpinifolia/Carpinus orientalis* type, *Carpinus betulus, Cornus mas, Hedera helix, Vitis vinifera, Quercus ilex* type, *Fraxinus ornus* | Apiaceae, *Artemisia, Aster* type, *Avena/Triticum* group, *Panicum, Brassica* type, *Centaurea nigra* type, *Hordeum* group, *Hypericum perforatum* type, *Lamium* type, *Phragmites australis,* Poaceae wild grass group, *Potamogeton, Rhinanthus* type, *Scirpus* type, *Solanum dulcamara, Urtica dioica* type. |
| 5830–5670 | Sect.3 archaeological phase 5 b<br>Post–settlement | PDLE4b | 79–73 | 8<br>6 | *Fagus sylvatica, Alnus, Populus, Salix, Corylus avellana, Tilia platyphyllos* type, *Ulmus, Cistus, Castanea sativa, Prunus, Vitis vinifera* | Chenopodiaceae/Amaranthaceae, Apiaceae, *Artemisia, Aster* type, *Centaurea nigra* type, *Mentha* type, *Stachys sylvatica* type, *Scilla* type, *Hordeum* group, Poaceae wild grass group, *Ranunculus* type, *Filipendula, Sparganium emersum* type, *Typha latifolia* type |
| 5740–4930 | Sect.3 archaeological phase 5 b<br>Post-settlement | PDLW3 | 76–67 | 7<br>6 | *Abies, Picea abies, Pinus, Alnus, Salix, Corylus avellana, Ulmus, Hedera helix, Rosa, Vitis vinifera* | Apiaceae, *Artemisia, Aster* type, *Avena/Triticum* group, *Brassica* type, *Cannabis sativa,* Chenopodiaceae/Amaranthaceae, *Hordeum* group, *Hornungia* type, *Lamium* type, *Panicum,* Poaceae wild grass group, *Potamogeton, Scilla* type, *Scripus* type, *Stachys sylvatica* type, *Solanum nigrum* type, *Urtica dioica* type |
| 4850–-2870 | Post-–settlement | PDLW4a | 63–50 | 6<br>4<br>3 | *Abies, Picea abies, Pinus, Fagus sylvatica, Betula, Alnus, Populus, Salix, Acer campestre* type, *Carpinus betulus, Tilia platyphyllos* type, *Ulmus, Juglans regia, Quercus ilex* type, *Vitis vinifera* | Apiaceae, *Centaurea nigra* type, Chenopodiaceae/Amaranthaceae, Cyperaceae, *Galium* type, *Hordeum* group, *Hornungia* type, *Myriophyllum, Plantago, Ranunculus acris* type, *Scirpus* type, *Solanum dulcamara, Sparganium emersum* type |
| 4850–-2870 | Post-–settlement | PDLW4b | 45–38 | 3 | *Pinus, Betula, Fagus sylvatica, Alnus, Salix, Carpinus betulus, Fraxinus excelsior* type, *Ulmus, Juglans regia, Prunus, Quercus ilex* type | Apiaceae, *Artemisia, Aster* type, Cichorieae, Chenopodiaceae/Amaranthaceae, Cyperaceae, *Galium* type, *Hornungia* type, *Lythrum, Myriophyllum, Phragmites australis, Ranunculus acris* type, *Scirpus* type, *Solanum dulcamara, Trifolium repens* type, *Urtica dioica* type |

oakwoods increasing. Hygrophilous woods are also present, indicating locally wet conditions, consistent with broader reconstructions of a humid Early Holocene (Jalut et al., 2000; Walker et al., 2012) and with local evidence from Lake Ledro (Magny et al., 2012; Vannière et al., 2013). The presence of wet-meadow herbs and hygro-hydrophilous species further support this interpretation. In general, a sparse hygrophilous wood was present together with a developed reed and sedge bed, with deeper and stagnant waters. In PAL3 pollen zone (9060 – 8200 cal yr BP; Fig. 6), several changes are evident: in the first part of the zone (PAL3a – from ca. 9060 to 8820 cal yr BP), the environment is dominated by upland and conifer forests, with mesophilous woods at lower altitudes and patches of steppe vegetation, reflecting persistently cold and steppic conditions. A distinctive feature of this zone is the appearance of *Linnaea borealis,* that probably lived under conifer canopies that were widely distributed, on acid soils and under cold climatic conditions (Zappa et al., 2025a, 2025b). The microcharcoal record highlights in this zone a peak in small sized particles, suggesting the presence of regional fires. In the second part of the zone (PAL3b – from ca. 8820 to 8200 cal yr BP), conifer and upland forests begin to decline, while hygrophilous taxa (both trees than herbs) increase. In the mixed oakwood forest, *Corylus avellana* increases compared to the previous subzone, following the trend of expansion of this species documented across the Alps and in central and northern Europe (e.g., Finsinger et al., 2006; Valsecchi et al., 2008).

At the local scale, the on-site record for the same time interval (PaluON2–PDLE1; Fig. 5) indicates the presence of woodland surrounding the site, dominated by mixed oakwood and upland forest, consistent with the off-site sequence. Hygrophilous habitats are also documented, in agreement with the basin-scale evidence, including wet meadows and hydrophyte communities. Human presence is weak, consistently with Pini (2004), who observed that a human imprint in the Palù di Livenza basin is not clearly attested before the Late Neolithic, i.e. the final phase of the prehistoric occupation documented at the site. Although sporadic traces of human activity are recorded within the basin, evidence of late and final Epigravettian settlements presence in the Carnic Prealps is attested on the Cansiglio Plateau at Palughetto (Peresani et al., 2009; Peresani et al., 2011), Bus de la Lum (Peresani et al., 1999–2000) and Pian di Landro (Visentin et al., 2018), at Piancavallo (Guerreschi, 1975; Duches et al., 2007) and on the Pradis Plateau, at the Grotta Clusantin (Peresani et al., 2008; Romandini et al., 2012) and Grotte Verdi (Gurioli et al., 2011; Naudinot et al., 2014; Lugli et al., 2022 ). Knowledge of this period in the Palù di Livenza basin itself remains scarce and based only on few lithic materials, underscoring the need for further investigation to shed light on the earliest human presence in the site and along the piedmont zone.

### 4.1.2. Land use and the Neolithic occupation (8200 – 5600 cal yr BP)

Combined palaeoenvironmental and archaeological evidence indicates that the basin began to be colonised during Neolithic. The Neolithic occupation of the basin includes two main phases, spanning ca. 6300–5450 cal yr BP. The earliest phases recorded in the on-site sequence PaluON2 correspond to the earliest pile-dwelling occupation attributed to the SMP culture–phase 3. The subsequent phase is featured by Late Neolithic Alpine Groups layers at the site. During this period, the pollen diagrams are characterised by: (i) a decline in the AP curve, (ii) high concentrations of microcharcoals, (iii) an increase in API, and (iv) a significant presence of coprophilous fungi.

At local scale (Fig. 5), in PDLE2 we see a slight change in woodland composition is observed, which may suggest the onset of wood management at the site. Some human related plants are present, although their abundances remain low. In PDLE3, however, the presence of these human-related taxa increases, becoming more evident. Not only API increase but so do other possibly cultivable trees or fodder species (e.g., *Hedera helix*; used as winter forage for cattle – Karg, 1998; Pini, 2004) as well as other synanthropic plants. In particular, the presence of pastoral indicators supports the hypothesis of some pasture activities at the site. Moreover, the presence of microcharcoals has been documented, suggesting both regional and local fire events. Small to medium-sized microcharcoals, which can be transported over long distances from their source, indicate regional fires, whereas larger microcharcoal particles, which are less easily dispersed, point to local fires (Conedera et al., 2018; Mercuri et al., 2019b). Local fires during this phase (Fig. 5) are likely linked to combustion events within the site: archaeological investigations in this area (Micheli et al., 2022, 2023) indicate that the size and features of the various structures reflect an alternation of functions between residential spaces and ancillary buildings, such as grain storage structures. In at least two episodes, such structures were destroyed by fire, one of which occurred during this phase, leading to the collapse of both the structures and their contents. As a result, all cereal grains – including *Triticum dicoccum*, *T. monococcum*, *T. aestivum*, and *Hordeum vulgare* – were charred and preserved in the layers (Micheli et al., 2022, 2023).

Even if the population is likely to have significantly expanded, no drastic decrease in AP is recorded. This evidence suggests that deforestation linked to Neolithic settlement at the site was relatively modest, both in terms of intensity and spatial extent. Human activities during the Neolithic therefore had a limited impact on the surrounding forested landscape. This situation contrasts sharply with the alluvial plains of northern Italy during the Bronze Age, where forest clearance was far more extensive and intensive, likely reflecting higher population densities, developed agricultural practices, and a strong degree of landscape management (e.g., sites of the Terramare culture and in the Friuli plain; Cremaschi et al., 2016; Fontana et al., 2024). However, it should be also considered that tree cover does not always decline in response to increased human influence, because some species were actively preserved by population as they exploit their fruits rather than their wood (e.g., cultivated trees such as *Corylus avellana*, *Juglans regia*; Roberts et al., 2019). In general, the marked change and increase in floristic diversity can be largely attributed to anthropogenic activities, which fragmented the local natural environment creating new niches suitable for some new species (e.g, nitrophilous plants; Garcés-Pastor et al., 2025). The local economy was based on cultivation (mainly cereals) but also on exploitation of cultivable trees and on animal husbandry/pastoral activities, that favoured the spreading of synanthropic plants and contributed to local fires occurrence. The multiple land use activities (combining crops, pastures and gathering) were in use at the Palù di Livenza site, as documented at numerous other Neolithic sites in Italy (Mercuri et al., 2019a).

At basin scale, in PAL4 (which also encompasses the Neolithic period; Fig. 6), some anthropogenic indicators are detectable (e.g., API, nitrophilous plants) although in relatively low abundances. Notably, a slight decrease in mixed oakwood is observed during PAL4b, mainly due to a reduction in *Fraxinus excelsior* type, *Ulmus*, and *Tilia*. This pattern may reflect a contraction of wetland areas, consistent with the decline of other wetland indicator species, and could also indicate the utilisation of these species as building material and tools construction. The microcharcoal record shows a peak in small and medium-sized particles, suggesting regional fires in the area. These fires may be linked to human activities at nearby Neolithic sites, which not only caused burning but also promoted the introduction of nitrophilous and synanthropic plants, which thrive in more arid conditions. However, this vegetation change may also reflect broader climatic trends, as records indicate a shift toward drier and colder conditions from around 5500 cal yr BP (the so-called Middle Holocene; Jalut et al., 2000; Walker et al., 2012; Roberts et al., 2019). *Fagus sylvatica* also shows a minor decline in this phase. At Lake Ledro, similar patterns have been recorded (Joannin et al., 2013). The temporary slowdown in *Fagus* growth has been attributed to general climatic instabilities in Europe between 6000 and 5000 cal yr BP, which led to rapid climate changes (RCC; Mayewski et al., 2004). Locally, in this part of the Alps, these instabilities caused lake level rises, as evidenced by climatic records, which in turn inhibited *Fagus* development between approximately 5800 and 5300 cal yr BP at

Lake Ledro. A comparable scenario appears to have occurred during this phase in the Palù di Livenza basin.

#### *4.1.3. The natural regeneration of the environment (5600–1500 cal yr BP)*

At some point, the settlement was abandoned, as indicated by both archaeological and palaeoenvironmental evidence. Key lines of evidence include the onset of general forest recovery from ~5600 cal yr BP (recorded on-site in PDLE4b and off-site in PAL5 and PAL6; Figs. 5 and 6) and a marked decline in anthropogenic plants, implying reduced human pressure. Concurrently, hygrophilous communities gradually expanded, ultimately leading to the complete colonisation/rewilding of the area. The hygrophilous arboreal component is mainly represented by *Alnus*, whereas hygro- and hydrophilous herbs reflect the establishment of a swamp together with the hygrophilous woodland. Among NPPs, increased values of the cyanobacterium *Rivularia* type — suggesting enhanced nutrient inputs to the bog under persistently wet conditions and the direct presence of standing water (Clò and Florenzano, 2022) — further support the expansion of the wetland.

Considering the chronology and comparing this record (PaluON2) with PaluON1 (Zappa et al., 2023), the swamping of the area (started with the accumulation of mud deposits) appears to have affected the eastern sector of the pile-dwelling earlier (PDLE4b; 5790–5710 cal yr BP), and subsequently the western sector, where mud deposition is dated to ~5400 cal yr BP (Fig. 9). Swamp conditions became stable from ~4400 cal yr BP onwards.

Off-site (Fig. 9), a brief decrease in wetland indicators occurs in the early part of the zone (PAL5a; 4840–4050 cal yr BP). This interval corresponds to a phase of abrupt lake-level rise documented at Lake Ledro around ~4500 cal yr BP, followed by persistently high-water tables in subsequent periods (Magny et al., 2012; Joannin et al., 2013). Bini et al. (2019) reported that between 4.3 and 3.8 cal kyr BP the Mediterranean basin experienced climatic and environmental changes, although some oscillations cannot be interpreted unequivocally. Many records indicate a major shift in the hydrological regime towards more arid conditions (the so-called 4.2 ka event); however, local responses can be contradictory, reflecting different regional expressions (Bini et al., 2019). In the Palù di Livenza basin, following a colder and possibly drier phase, a more humid interval developed. Hydro-to hygrophilous herbs expanded at the expense of trees, and new taxa entered the record (e.g., *Allium* type, *Aristolochia*, *Myriophyllum spicatum* type, *Lythrum*) around ~4800 cal yr BP. This shift suggests a reorganisation of the wetland plant assemblage, consistent with deeper waters and a hygrophilous woodland accompanied by more developed reed and sedge beds and the presence of open water. *Rivularia* type also increased under these altered hydrological conditions. In addition, fern spores — relatively abundant during this phase but absent in the preceding one — indicate forest opening and/or thinning.

This phase precedes and overlaps with the last on-site phases (PDLW4 and PDLE5), during which widespread swamping is recorded. On-site, this process is documented first by the formation of mud deposits between 5700 and 4400 cal yr BP (pollen zones PDLE4a–b), and later by the definitive establishment of swamp conditions from ~4400 cal yr BP onwards (from the middle of PDLW4a). Off-site, comparable wetland expansion appears to have begun earlier, with the spread of hydro-to hygrophilous grasses from ~7500 cal yr BP (pollen zone PAL4a) and a later increase in hygrophilous trees (at ~3900 cal yr BP). A plausible interpretation is that local communities actively limited the expansion of wet conditions on-site in order to maintain habitability within the village. This management may have persisted for centuries, until it was no longer maintained, coinciding with the abandonment of the area and the subsequent predominance of natural wetland dynamics.

The last period recorded in the off-site record (PAL6 – 2890–1500 cal yr BP) represents the phase following the infilling in of the wetland that developed in a forest bog. Wetlands formed during phases of constant water flow and inputs, promoting the spread of hygrophilous herbs along watercourses. When the flow slows down, riverbanks became colonized by hygrophilous woody plants. This pattern is in accordance with steps of bog formation: initially, the emergence of wetland context occurs in lowlands along rivers, in most cases on alluvial and periodically flooded floodplains. This promotes the growth of species that can tolerate high groundwater table (such as *Alnus*) in areas that were previously occupied by meadows or deciduous forests, ultimately leading to the formation of a peat or mire. Generally, the first phase is characterised by the emergence of a free water layer on a dry surface. Here, organic matter begins to accumulate, initially composed mainly by algae and benthic organisms. Typically, floating rooted plants dominate in deep water, growing upward until they reach the surface (Mitsch and Gosselink, 2015). After this first phase, semi-terrestrial

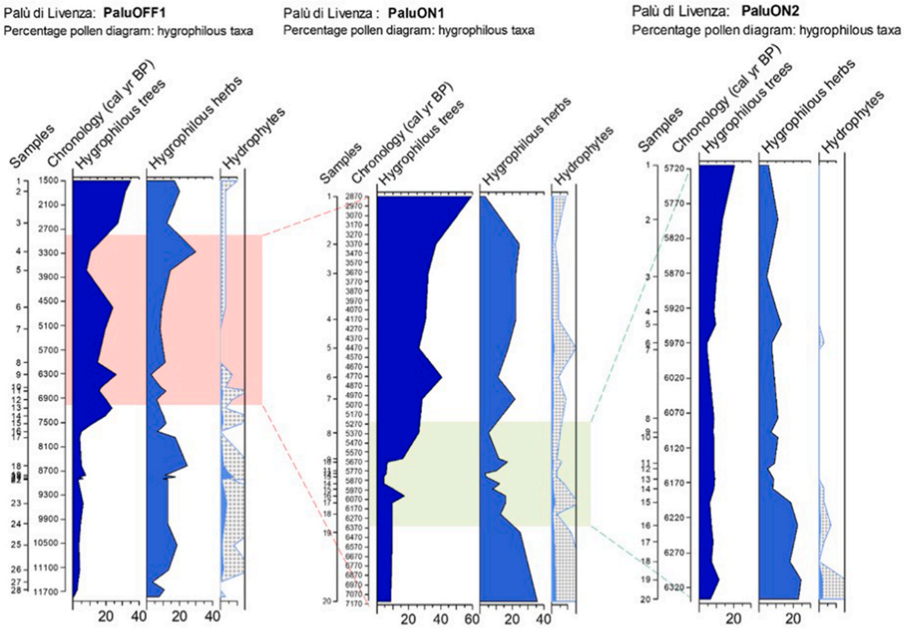

**Fig. 9.** Comparison among the curve related to hygrophilous taxa (hygrophilous trees, hygrophilous herbs and hydrophytes) for the three sequences studied at Palù di Livenza (PaluOFF1: off-site record, PaluON1 and PaluON2: on-site records).

plants begin to establish, with the spreading of hygrophilous species rooting above the water surface. When a peat is dominated by woody vegetation, it is classified as a swamp, as observed at Palù di Livenza. The high abundance of wetlands species in pollen spectra, together with NPPs highlighting high concentrations of spores of ferns and algae, confirms the formation of a swamp in the basin, with no evidence of continued human occupation.

Finally, it was during 19th century that this area was exploited, again due to land reclamation, urbanisation works, and water management and exploitation for the surrounding area. In recent years, a new interest in wetlands has emerged, driven by recognition of their high ecological value, the abundance of ecosystem services they provide, and their suitability as habitats for endemic and threatened species.

Within this present-day ecological framework and as a final complementary perspective to the palaeoenvironmental discussion, the comparison between the fossil record and the modern pollen rain derived from the three moss samples (Fig. S7) reveals a vegetation history marked by both persistence and change in the Palù di Livenza basin. While the continuity of arboreal taxa such as *Alnus*, *Quercus*, and *Fraxinus* suggests the long-term resilience of key woodland components, the prominence of *Platanus*, often linked to managed/ornamental planting, and the occurrence of ruderal or nitrophilous herbaceous types are consistent with more recent landscape modification driven by land-use change and intensified disturbance regimes in the post-Medieval and contemporary period. These changes correspond to trends commonly observed in pollen records from the last millennium, where deforestation, agriculture, and landscape fragmentation contribute to the rise of disturbance-adapted species and secondary vegetation structures (Sadori et al., 2016; Roberts et al., 2018).

Generally, the Palù di Livenza record can be framed within a broader geographical context that documents Holocene environmental dynamics in northern Italy and in the Mediterranean basin. A useful comparison is provided by Lake Ledro (Magny et al., 2012), even if it represents a southern Alpine lacustrine system rather than a lowland spring-fed wetland. Nevertheless, both records show early Holocene temperate forest expansion, while the increasing wetland conditions observed at Palù after ca. 5000 cal yr BP appears consistent with the shift toward wetter late-Holocene conditions documented at Ledro after ca. 4500 cal yr BP (Magny et al., 2012). However, this signal in the Palù basin was probably affected by local geomorphological, hydrological, and anthropogenic factors detected in the records.

At Mediterranean scale, this pattern should not be interpreted as uniform. As the Mediterranean basin appears to be a mosaic landscape with different features and response to climatic and anthropogenic events (Servera-Vives et al., 2018; Roberts et al., 2019). Holocene hydroclimatic trends were regionally differentiated, with northern Mediterranean records often showing wetter conditions during the late-Holocene, while southern Mediterranean areas frequently experienced increasing aridity (Peyron et al., 2013). In this framework, Palù di Livenza may be interpreted as a local expression of broader northern Mediterranean climatic tendencies, filtered through site-specific wetland dynamics and increasing human influence.

### 4.2. Statistical comparison among on-site and off-site sequences

A Principal Component Analysis (PCA) was performed to compare the three studied sequences (PaluON1, PaluON2 and PaluOFF1; Fig. 10). The first component (F1) distinguishes between natural and anthropogenic environment, while the second (F2) separates different types of land uses. In particular, the first quadrant includes plants mostly related to an anthropogenic context in which pasture indicators (Ranunculaceae, Brassicaceae including *Hornungia* type) and cereals (*Hordeum* group) are well attested together with indicators of open meadows (Apiaceae, Poaceae wild grass group). Here are represented only samples of the PaluON2 sequence (all except the three most ancient ones), which chronology is related to the Neolithic period when the village was settled and activities were ongoing. The second quadrant includes mainly arboreal plants representing for the most part the mixed oakwood (*Fraxinus excelsior* type, *Tilia platyphyllos* type, deciduous *Quercus*, *Corylus avellana*) and some upland forest (*Abies*, *Fagus sylvatica*). Samples included in quadrant II are mostly belonging to the PaluOFF1 record, meaning that – as expected – off-site environment was less impacted by human activities. This quadrant also includes some of the most ancient PaluON2 samples, referring to the pre-settlement phase or at its very onset, when human impact on the territory was minimal. Quadrant III comprises indicators of wet environments (*Sparganium emersum* type, *Ulmus*, Cyperaceae, *Alnus*, *Potamogeton*) and includes some samples from the PaluOFF1 core, as well as the most recent (ON1-1/7) and the most ancient (ON1–19/20) samples from the PaluON1 sequence, referring to a period following and preceding the Neolithic settlement, when the territory was thus less affected by human influence. Finally, the fourth quadrant identifies plants related to anthropogenic environment (*Potentilla* type, Asteraceae, Fabaceae, Chenopodiaceae/Amaranthaceae, *Avena/Triticum* group, *Vitis vinifera*, *Trifolium* type, *Urtica*, *Plantago*).

In general, since F1 and F2 explain <30% of the total variance, the multivariate structure is highly dispersed across higher-order components. This indicates that the simple separation into anthropogenic vs. non-anthropogenic and forested vs. wet assemblages does not fully capture the environmental complexity.

### 4.3. Land cover reconstruction: interpretation of results and methodological limitations

Quantitative reconstructions of past vegetation based on the REVEALS algorithm require an accurate understanding of pollen-vegetation relationships (Davis et al., 2020) and have been widely applied across diverse environmental and archaeological settings (e.g., Behre, 1981; Bunting, 2002; Mazier et al., 2006; Lopez-Saez et al., 2010; Fernandez Freire et al., 2012). Despite recent methodological advances (Githumbi et al., 2021; Serge et al., 2023; Kern et al., 2024), their application remains challenging in Mediterranean landscapes, where high biodiversity and long-term human land use create complex mosaic patterns that are not fully covered by parameters developed for Northern Europe (Mercuri and Sadori, 2014; Roberts et al., 2019; Servera-Vives et al., 2018). For example, the exclusion of entomophilous taxa with limited pollen dispersal restricts the representation of open landscapes and fruit-tree crops (e.g., *Malus, Pyrus, Prunus, Vitis*), so only a subset of the palynological record could be used for GIS-based processing. Additional limitations arise from the GIS modelling itself, largely due to the small number of base maps used. Vegetation patterns can be controlled by a wide range of environmental and disturbance variables (e.g., herbivore pressure, trampling, landscape openness, soil type, mean decadal rainfall, slope, fire disturbance, altitude, aspect, nitrophilous conditions; (Servera-Vives et al., 2022). While acknowledging that many of these drivers were not included, the use of three base maps was prioritised to reduce overfitting and potential collinearity, which would have been difficult to assess and mitigate for. This basic model provided a reasonable first-order approximation and a practical starting point for future improvements. Finally, the decision rules implemented in the model rely on expert knowledge and did not consider stochastic variability in land cover allocation. Future developments could integrate statistical, non-deterministic approaches to reduce subjectivity and enhance precision, building on land use modelling approaches widely applied in land system science (Verburg et al., 2019).

As far, in these elaborations (Fig. 11), the selected parameters have proven appropriate and sufficient to highlight the main spatio-temporal changes, consistent with the PaluOFF1 palynological record. Overall, the elaboration highlights major shifts in vegetation and landscape composition from the Late Glacial to the Mid-Late Holocene, showing alternating phases of forest expansion, wetland development, and

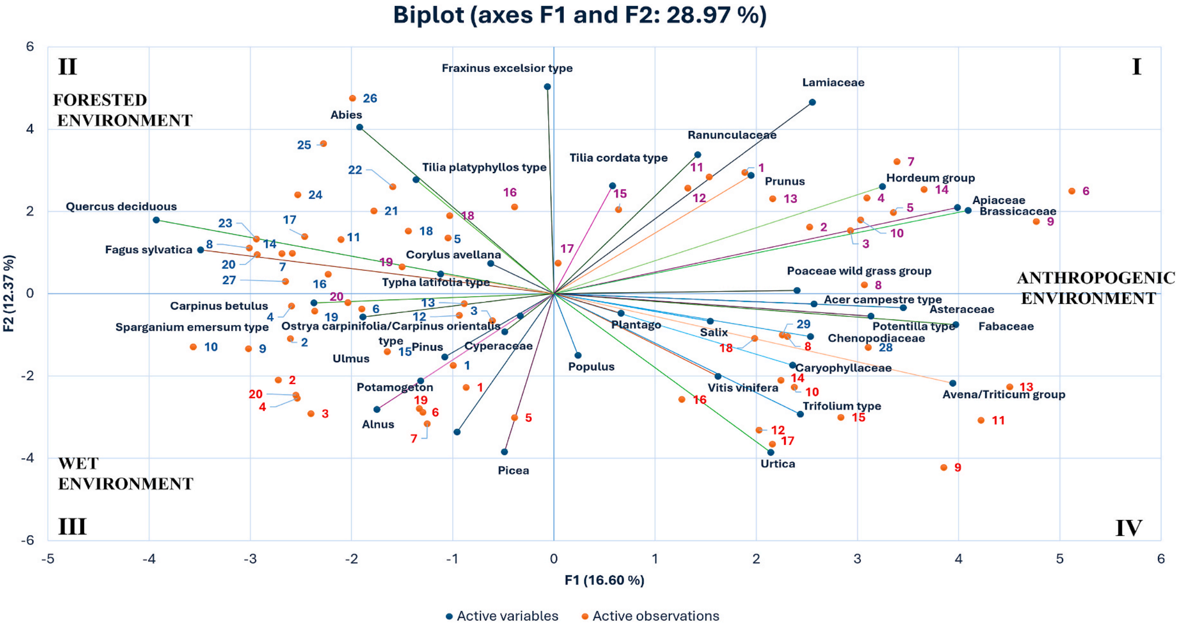

**Fig. 10.** PCA applied to the three pollen sequences at Palù di Livenza. Samples from the PaluOFF1 core are shown in blue, PaluON1 in red, and PaluON2 in violet. The first component F1 separates more natural environment (left) from anthropogenic environment (right), while the component F2 separated among different types of land uses.

changes in open and human-influenced environments. PAL1 reflects a predominantly cold and forested landscape, while PAL2 marks the expansion of temperate deciduous forests and wet environments. In PAL3 and PAL4, wetlands and human-related environments become increasingly prominent; PAL5 records a decline in mixed oakwood in favour of meadows and wetlands, whereas PAL6 is characterised by wetland dominance and a reduction in both mixed oakwood and human-related environments. Notably, the oldest pollen zone (PAL1) shows a high proportion of taxa grouped as “anthropogenic environments”, despite the absence of archaeological evidence for human presence at this time. This pattern is driven by the occurrence of *Artemisia*, which here is interpreted not as an anthropogenic indicator, but as a

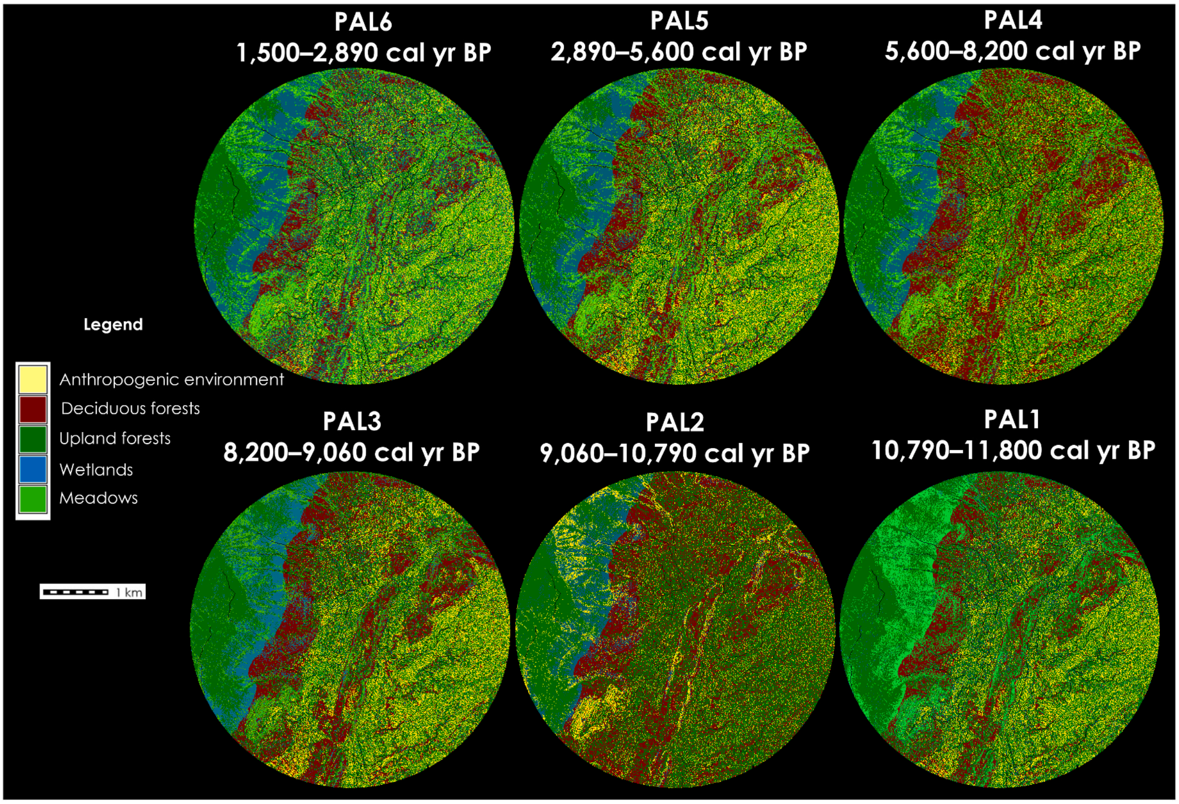

**Fig. 11.** Maps showing the distribution of the land cover types across the six LPAZ recognised in the PaluOFF1 core from 11,800 cal yr BP (PAL1) to 1500 cal yr BP (PAL6). Elaborations performed in GRASS GIS environment.

component of dry steppe vegetation together with Poaceae and Chenopodiaceae, reflecting the colder, more open conditions prevailing during this phase (see Discussion).

The workflow, applied for the first time in this study, performed well in translating REVEALS-derived regional pollen proportions into spatially explicit maps. This approach therefore appears robust for producing comparable, map-based reconstructions of past vegetation cover, offering a promising framework for integrating palynological data with GIS-based landscape analyses and supporting further palaeoenvironmental interpretation at the regional scale.

## 5. Conclusions

The palynological records from Palù di Livenza provide a detailed and nuanced reconstruction of past biodiversity and vegetation dynamics, offering insights into both natural and anthropogenic processes. A key strength of this study lies in the explicit comparison between on-site and off-site records, which allows us to disentangle local, human-driven ecosystem transformations from broader, climate-driven environmental changes. The on-site sequence from the pile-dwelling settlement captures the immediate ecological imprint of Neolithic activities (including multi-functional land use practices based on agriculture, pastoralism, and woodland exploitation) expressed through clear anthropogenic signals. In contrast, the off-site record provides a more spatially integrated perspective, where human impact is generally diluted but still detectable, and where vegetation changes can be interpreted within a regional climatic and landscape context. Together, these two archives offer complementary information: the on-site record documents how and where human communities reshaped the wetland environment, while the off-site sequence reveals to what extent these effects propagated across the basin and how they interacted with wider climatic shifts over time.

The combined use of REVEALS modelling and GIS mapping has been instrumental in translating palynological signals into spatial reconstructions, enabling a more comprehensive understanding of vegetation change across the landscape. The quantitative and spatial approach applied to palynological data is new not only at local scale but also at regional scale for northeastern Italy, where such reconstructions have so far been rare. Implemented here for the first time, the methodology demonstrates strong reconstructive potential and directly supports conservation science, because it expresses long-term vegetation dynamics in a spatial format and terminology aligned with conservation ecology (e.g., land-cover proportions and habitat-relevant patterns), thus enabling clearer comparison with modern baselines and management targets.

Ultimately, this study underscores the value of an integrated, multiscalar approach to interpreting human-environment interactions over time, offering important implications for both archaeological research and environmental studies.

## Author contribution

Jessica Zappa: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – original draft, Writing – review and editing. Anna Maria Mercuri: Conceptualization, Methodology, Supervision, Writing – review and editing. Giacomo Vinci: Investigation, Validation, Writing – review and editing. Alessandro Fontana: Validation, Visualization, Writing – review and editing. Francesco Carrer: Investigation, Software, Writing – review and editing. Roberto Micheli: Writing – review and editing. Assunta Florenzano: Conceptualization, Methodology, Supervision, Writing – review and editing.

## 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.quascirev.2026.110075.

## Data availability

A link to the data and/or code is provided as part of this submission.

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