

Modern palynological assemblages from nearby Mediterranean coastal lagoons: implications for palaeoecological interpretation

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ABSTRACT

Site-specific modern pollen assemblages are essential for interpreting fossil records, yet their links to local conditions and surrounding landscapes are often poorly understood. This study presents a modern palynological dataset from subsurface sediments of the shallow Burano and Orbetello lagoons in Tuscany, Italy. This dataset is part of a broader project which includes fossil sediment cores from the same basins. Spatially distributed samples were analyzed for grain-size, pollen, non-pollen palynomorphs, and sieved charcoal, with water physico-chemical parameters measured at each site. Terrestrial pollen assemblages mainly reflect regional wind-pollinated vegetation but show strong distortions, with forests overrepresented and open areas—especially cereal crops and vineyards—underrepresented. Modern calibration of *Pinus* and *Olea* pollen registrations is particularly informative given their key role in local human-driven landscape change. Sieved charcoal (> 125 µm), a proxy for local fire, is unevenly distributed and correlated with *Glomus* chlamydospores, indicating additional transport via runoff. At Burano, intra-basin pollen deposition is largely controlled by morphometric and sedimentological factors which explain 58.1% of the observed variance. In contrast, at the Orbetello lagoon, these factors explain only 26.7% of the variance, reflecting more complex hydrodynamic controls on sediment and pollen redistribution. Among aquatic groups, brackish macrophytes dominate across broad salinity ranges, primarily controlled by water depth, salinity, and associated with dissolved oxygen. Microalgal groups respond to temperature and nutrient availability, with high concentrations of harmful algae (*Alexandrium* spp.) indicating ecological stress. Overall, this modern spatial dataset provides a site-specific framework for interpreting fossil records and reconstructing past environmental changes. It also demonstrates the potential of combining palaeoecological research with modern data to translate scientific knowledge into practical applications for biodiversity conservation.

1. Introduction

Modern to recent palynological assemblages are widely used in palaeoecological studies. They comprise thousands of surface samples, typically collected from diverse environmental contexts and broadly distributed across space (e.g., Davis et al., 2020). Most often, modern pollen data are obtained from moss polsters or anaerobic contexts such as the surface layers of lake, bog and fluviomarine sediments which collect pollen in slightly different ways (Lisitsyna et al., 2012). Several authors have highlighted the importance of analyzing modern pollen

from water-basin surface sediments, given that lake sediments represent the primary source of fossil pollen in palaeoecological research (Seppä et al., 2004; Qin et al., 2015).

The use of site-specific datasets—surface samples collected from the same basin as the fossil record (e.g., Castro-Parada and Sobrino, 2022; Wang et al., 2025) is particularly valuable for characterizing local factors that influence pollen dispersal patterns, including transmission mode and distance from parent plants (Matthias and Giesecke, 2014; He et al., 2024), as well as pollen transport, deposition, and preservation within basins (e.g., García-Moreiras et al., 2015; Frazer et al., 2020).

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Pollen percentages do not directly reflect vegetation cover, as they are influenced by factors such as pollen production and the size and type of the sedimentation basin (Jacobson and Bradshaw, 1981; Sugita, 1994; Hicks et al., 2001). Consequently, several theoretical models have been developed to estimate pollen source areas in small, enclosed basins (e.g., Sugita, 2007a, 2007b), although these typically consider only wind as the primary pollen transport mechanism. However, in many real-world settings, such models are not easily applicable, as conditions diverge markedly from the ideal environments for which they were designed. This is particularly true in heavily transformed areas and contexts with strong hydrological connectivity, where these factors can influence pollen input, dispersal, and deposition.

Among waterlogged depositional settings, Mediterranean coastal lagoons represent a particularly challenging environment for palynological reconstruction (Santos et al., 2001; Marco-Barba et al., 2013; Niccolini et al., 2025). These basins lie along a steep ecotonal gradient extending from terrestrial sclerophyll forests, through scrub and macchia communities, to hygrophilous, fully aquatic, including coastal marine environments. As a result, they receive multiple pollen inputs transported by both wind and water, influenced simultaneously by

continental drainage dynamics and marine inflow. In these shallow basins, aquatic taxa represent major primary producers and play a key role in maintaining the functioning of aquatic ecosystems (Obrador and Pretus, 2012; Thomaz, 2023). Because they are closely connected to terrestrial processes, aquatic ecosystems can capture disturbances occurring at both local and extralocal scales (Dinis et al., 2020; Soria et al., 2022). In Mediterranean lagoons, such disturbances may lead to the loss of specialized species and the proliferation of more generalist taxa (Pasqualini et al., 2017), as well as frequent algal blooms and recurrent episodes of oxygen depletion (Newton et al., 2018). In recent decades, an increasing number of reports have documented shifts towards dinoflagellates dominance in phytoplankton communities, particularly involving potentially toxic species such as *Prorocentrum* spp. and *Alexandrium* spp., which are known to cause harmful algal blooms (HABs) (Xiao et al., 2018; Fischer et al., 2020). Modeling aquatic pollen-vegetation relationships is even more challenging due to the limited availability of underwater vegetation data and the dynamism of aquatic environments. Furthermore, pollen dispersal can be significantly impacted by lake mixing and diffusion processes, potentially reducing its effectiveness as an indicator of the spatial distribution of aquatic

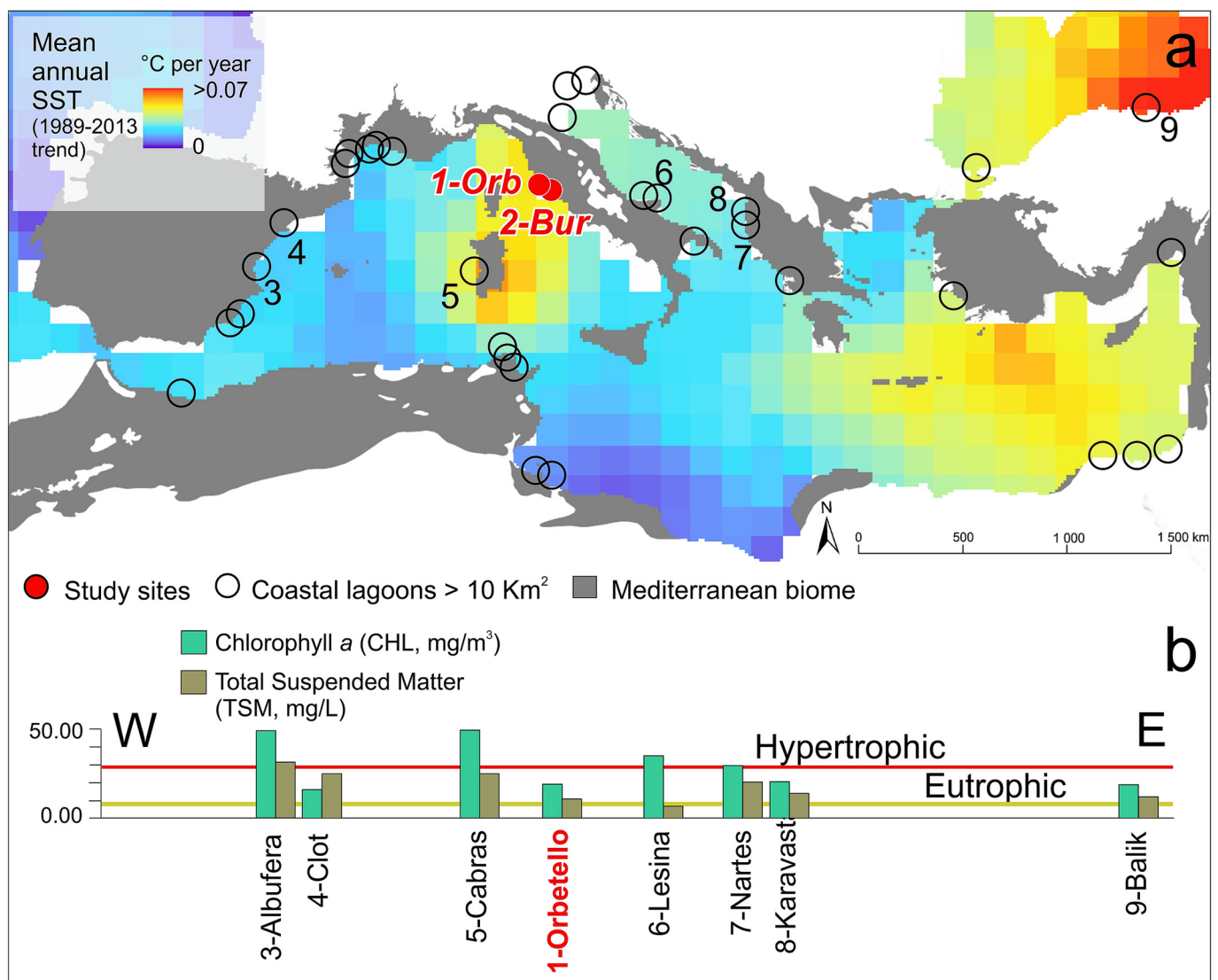


Fig. 1. Geographical context: a) Mediterranean Basin including the mean annual Sea Surface Temperature trend over the 1989–2013 interval (HadISST - Global sea ice and Sea Surface Temperature analyses). The location of coastal lagoons >10 km² is shown. Key to abbreviations: 1-Orb (Orbetello) and 2-Bur (Burano) lagoons (this study); b) West–east transect of lagoons with an area of less than 55 km² and a depth of less than 3 m (i.e., similar to the Orbetello lagoon) was used to compare the trophic status by means of chlorophyll a concentration in summer 2020 and total suspended matter concentration values (modified from Soria et al., 2022).

plants (Xu et al., 2016). Nevertheless, modern aquatic pollen data remain valuable for providing an overview of communities colonizing different shoreline and lake-bottom habitats along chemical and physical gradients (e.g., Medeanic et al., 2016).

In this paper, we present two case studies from the Mediterranean region: the non-tidal shallow lagoons of Burano and Orbetello (WWF Oases, Tuscany, Italy; Fig. 1). In both basins, spatially distributed surface sediments were collected to analyze sedimentological, palynological, and micro- and macroscopic charcoal particles across physico-chemical gradients. This study is part of a broader project that also includes the analysis of fossil sediment cores from the same basins, specifically the OLP11-B core in western Orbetello and the LB5B core in the Burano basin (Fig. 2). The resulting dataset provides a site-specific calibration of local to extralocal palynological signals, serving as a valuable basis for the interpretation of fossil records. Ultimately, this study demonstrates the potential of integrating palynological data to inform biodiversity conservation and guide the design of targeted management strategies.

2. Study area

The study area encompasses the coastal lagoons of Orbetello and Burano (Tuscany, Italy), which are located in the central Mediterranean region. The two basins are separated from the sea by a beach-dune system which developed between about 8 and 4 ka BP (D'Orefice et al., 2022), recently further investigated (Brocard et al., 2024). Today, the sea-lagoon connections are maintained by artificial canals (Fig. 2). The two lagoons face the Tyrrhenian Sea, which has experienced recent sea surface temperature increases of up to 0.077 °C/year between 2010 and 2019 (García-Monteiro et al., 2022). From a bioclimatic perspective, the area is classified as mesomediterranean, with a subhumid ombroclimate (Biondi and Baldoni, 1994). Aquatic ecosystems are dominated by *Ruppia* spp. which form dense and often monospecific meadows that

play a key role in the functioning of the ecosystem (Obrador and Pretus, 2012). Marsh vegetation, e.g., *Phragmites australis*, grows on shores of both lagoons together with halophytic communities on hypersaline to long-term flooded soils (see SI-1 for further details). Coastal dunes support psammophilous species, while surrounding areas host Mediterranean scrub and sclerophyllous plants, including *Quercus ilex* woodlands. In more humid areas, the holm oak grows alongside deciduous trees, bordering broadleaved forests dominated by *Quercus pubescens* and *Quercus cerris* (see SI-1). Long-standing anthropogenic pressures, from ancient land use to modern agriculture, pollution, and tourism, have profoundly altered the landscape and ecological conditions (e.g., Corsi and Focardi, 2002; Mancini et al., 2022).

2.1. Anthropogenic pressure

The Tyrrhenian coast, where the lagoons of Orbetello and Burano are located, has undergone major anthropogenic transformations since the Etruscan-Roman period (Perkins, 2010; De Giorgi, 2023). In recent centuries, land reclamation, agricultural practices and deforestation have had a major impact on the geomorphological evolution of the basins and the surrounding landscape (Gabbriellini, 1995; Bellarosa et al., 1996; see IGM maps: e.g., IGM 135 II, 1941), also in terms of changes in biodiversity and the spread of invasive plants (Angiolini et al., 2002; Selvi, 2010). The Orbetello lagoon is classified as a “national reclamation site” by the Italian legislation (Decree 26 November 2007- Italian Ministry of the Environment) due to the prolonged presence of mining activities since Roman times and the highly polluting factories since the late 1800s. Studies on sediment geochemistry and benthic foraminifera identify the sediments of the Orbetello lagoon as strongly contaminated by Cd, Cu, Ni, Pb, Zn, and Hg, whereas benthic foraminifera showed a high number of abnormal specimens attributable to elevated metal concentrations (Frontalini et al., 2010; Romano et al., 2015; Mancini et al., 2022). Moreover, the lagoon has been affected by sewage effluents

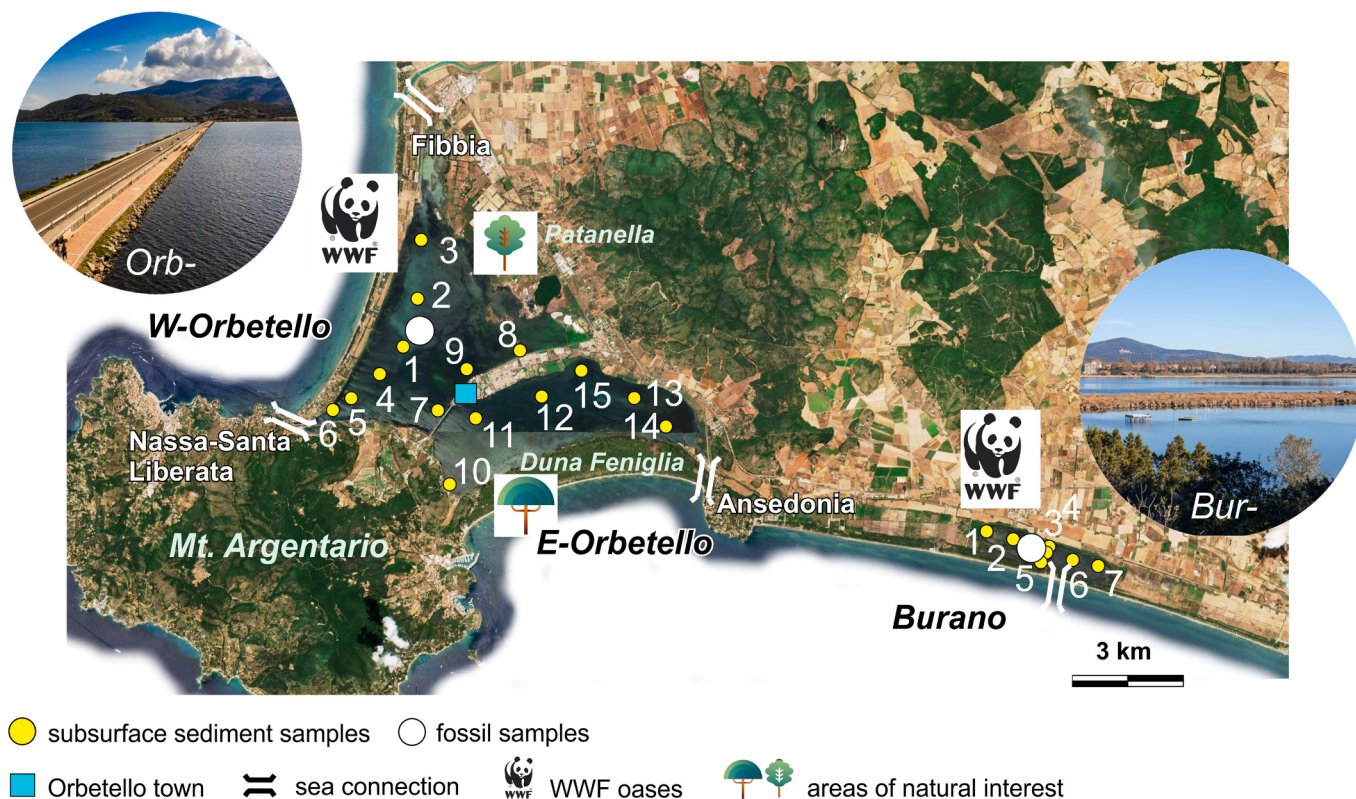


Fig. 2. Focus on the study area including the coastal lagoons of Orbetello and Burano (Tuscany, Italy). The location of subsurface sediment samples and fossil cores (OLP11-B in western Orbetello and LB5B in Burano basins) are highlighted in yellow and white, respectively.

from the Orbetello town, and wastewater from agriculture and aquaculture, which increased considerably in the second half of the 20th century (Lenzi et al., 2003). Since the beginning of the 1980s, the flat area behind the Burano lagoon has been converted from pasture to arable land (mainly crops), woody cultivations (e.g., olive groves, vineyards, peach orchards) and intensive forage production (e.g., Rilievo dell'Uso del Suolo da fotointerpretazione del volo regionale, 1978, 1:25.000 <https://tinyurl.com/y8kw8flr>). The anthropic pressure on the whole area is exacerbated by the massive presence of tourists, which causes an increase in urban wastewater, especially during the spring and summer seasons (Corsi and Focardi, 2002).

3. Material and methods

3.1. Sampling

In late June 2022, subsurface sediments from 22 sites in the Burano and Orbetello lagoons were collected and analyzed for grain-size, palynology and sieved charcoal content (Fig. 2). Sampling locations were selected based on spatial representativeness and recorded via GPS (± 20 m accuracy). Subsurface sediments up to 10 cm depth were collected with a Van Veen grab (capacity 0.5 l, sampled surface approx. 126 cm²) from water columns ranging between 72 and 178 cm in Orbetello and 64–140 cm in Burano. The locations of two fossil sequences collected using gravity corers—LB5B in Burano and OLP11-B in Orbetello—are also shown in Fig. 2. The palynological analysis of these fossil sequences is not addressed in this paper.

3.2. Grain-size analysis

Granulometric analysis of subsurface sediment samples from both lagoons was carried out at the OMEAA platform (Archéorient, Université Lumière Lyon 2/CNRS). About 2 g of sediment per sample underwent sequential treatment with pure H₂O₂, 20% HCl, 0.1 M and 0.02 M KCl, followed by rinsing with 40 °C water. Samples were centrifuged at 3500 rpm for 10 min, then dispersed in (NaPO₃)₆ and mixed for 5 h. Grain-size distribution was measured via laser diffraction using a Fritsch Analysette 22 Next granulometer.

3.3. Palynological analyses

Sub-samples of 1.4–2.9 g of sediment were processed for palynological analysis using standard chemical treatments: 7% HCl, 38% HF, 7% HCl, (NaPO₃)₆, 10% KOH, and sieving at 10 µm in an ultrasonic bath. *Lycopodium clavatum* tablets were added as spore tracers for concentration calculations. Pollen identification was performed at up to 1000× magnification using reference atlases (Reille, 1992, 1998; Beug, 2004), pollen monographs (e.g. Punt and Hoen, 2009) and the pollen reference collection available at the Department of Earth Sciences (University of Florence). Oak pollen was identified into major groups: the *Quercus robur* group (including *Q. robur*, *Q. petraea*, and *Q. pubescens*), the *Quercus ilex/coccifera* type, and the species *Q. cerris* and *Q. suber*, following Smit (1973), Van Benthem et al. (1984) and Wronńska-Pilarek et al. (2016). Poaceae pollen was classified by grain and annulus size, with larger grains ($D > 47$ µm, $d > 11$ µm) attributed to cereals (e.g., cultivated *Avena* and *Triticum*). “Anthropogenic taxa” included pollen from cultivated, ornamental, and synanthropic plants. Microcharcoal particles (10–62 µm) were also quantified alongside pollen (Clark, 1988). Diagrams were produced with Tilia 3.0.1 and refined graphically with Corel Draw X8. Pollen sums for percentage and concentration calculations included trees, shrubs, and upland herbs, excluding helophytes, halophytes, aquatics, and wetland species.

3.4. Sieved charcoal particles analyses

Sub-samples of approximately 2.5 g, with the exception of sample

ORB-8 (42 g) which differs from the others due to a dominant sandy fraction, were analyzed for charcoal particles using standard sieving techniques (Whitlock and Larsen, 2002). Samples were disaggregated in a 50/50 solution of 10% sodium hexametaphosphate and sodium hypochlorite for 24 h, then wet-sieved through 62, 125, and 500 µm meshes. The sieved fractions were counted on a gridded platform using a stereomicroscope. Macroscopic charcoal particles (> 125 µm) are interpreted as indicators of high-severity fires occurring within a few kilometers of the study area (Whitlock and Larsen, 2002; Higuera et al., 2011).

3.5. Physico-chemical water parameters

The following physico-chemical water parameters: T (°C), pH, conductivity (ms/cm), salinity (ppt), dissolved oxygen (ODO, mg/L) and water column depth (m) were measured at each sampling site in June 2022, as part of this study. Data collection in the Orbetello lagoon was integrated with another spatially distributed dataset coming from the monitoring activities of the Department of Environmental, Earth and Physical Sciences of the University of Siena within the “Interreg Marittimo IT-FR Retralags” project. In addition to the parameters listed above, the monitoring plan included: turbidity (NTU), oxidation–reduction potential (ORP, mV), chlorophyll-*a* (Chl-*a*, µg/L), phycoerythrin (BGA-PE, µg/L). From this dataset, we considered the measurements collected in June–July 2020, selecting those located within a 500 m radius of each sampling site.

3.6. Compilation of vegetation and fire data

Vegetation data were extracted from the “Italian Map of Nature” (IMN) open data base of the habitats of Italy at a scale of 1:50,000 (Amadei et al., 2004; Biondi et al., 2009). Vegetation classification was simplified by merging macrohabitat classes in GIS environment, being more comparable with pollen data. To obtain detailed information on the vegetation near the sampling sites, vegetation data were extracted within 500 m, 5 km and 15 km buffers surrounding the basin shores. This procedure was adopted because the Orbetello and Burano basins are not round in shape, and this approach more accurately reflects the vegetation gradient around the basins (Matthias and Giesecke, 2014).

Qualitative local vegetation surveys were also considered (Angiolini et al., 2002; Pedrotti et al., 1979). Fire data were extracted from the Regione Toscana - Banca dati incendi boschivi repository (<https://www502.regione.toscana.it/geoscopio/incendiboschivi.html>) within a 15 km buffer and processed in a GIS environment.

3.7. Numerical analyses

Pollen samples were classified into groups using unconstrained incremental sum of squares cluster analysis (Cavalli Sforza's chord distance as dissimilarity coefficient) (Edwards and Cavalli-Sforza, 1965). Clustering was restricted to terrestrial taxa whose pollen reached over 2%. On the same dataset, ordination techniques were used to identify relationships between terrestrial pollen data and explanatory variables: grain-size, water depth and shore distance. Data were Hellinger-transformed to stabilize variances and optimize the signal-to-noise ratio of the data set (Legendre and Gallagher, 2001). Given the short gradient lengths: 0.54 for Orbetello and 0.87 for Burano, a linear ordination method—redundancy analysis (RDA)—was deemed appropriate for our data (ter Braak and Prentice, 1988). The statistical significance of the RDA models was evaluated using Monte Carlo permutation tests with 999 unrestricted permutations. Calculation of correlation coefficients and *p*-values on selected data was done in R using the function `rcorr` (package “Hmisc”) (Harrell and Harrell, 2013) and the function `corrplot` (package “corrplot”) (Wei et al., 2017) to plot the correlation matrices.

4. Results

4.1. Sample overview and preservation

Twenty-two subsurface sediment samples were analyzed: 15 from the Orbetello lagoon and 7 from the Burano lagoon (Fig. 2). Preservation of pollen and Non-Pollen Palynomorphs (NPPs) was generally good. We identified 154 pollen taxa and 58 NPP types. Total pollen concentrations ranged between 14,058 and 74,623 grains/g, except for sample ORB-8, which was nearly pollen-barren due to its high sand content (98%). Sediments predominantly consist of fine sandy to silty-clayey matrices (Fig. 3).

4.1.1. Aquatic and hygrophilous vegetation signal

Sixteen pollen taxa were identified from local aquatic and hygrophilous plant communities. *Ruppia* spp. was present at nearly all sites, reaching up to 6.6% and 1430 grains/g, especially in marginal lagoon areas (Fig. S1). *Lemna* pollen appeared sporadically in both

lagoons, while *Myriophyllum spicatum* was mainly recorded in Burano (Fig. 3). *Chara* gyrogonites, not previously reported at Orbetello, were found at sites ORB-8, 13, and 14. Poaceae (including cf. *Phragmites* sensu Clark and Patterson III, 1985) and Amaranthaceae were abundant at Burano sites, likely due to their closer proximity to the shoreline. Helophyte pollen from *Sparganium erectum*, *S. emersum*, *Alisma* sp., *Thalictrum*, and Cyperaceae was frequent, while riparian taxa like *Alnus glutinosa* and *Salix* were consistently recorded but remained below 4% (Fig. 3). Overall, the assemblages reflect typical wetland and marginal aquatic vegetation surrounding the lagoons.

4.1.2. Non-pollen palynomorphs and algal indicators

Two morphotypes of dinoflagellate cysts attributed to the potentially harmful genus *Alexandrium* were identified (SI-2 and Fig. S2), though species-level determination was not possible due to the absence of vegetative cells which are required for reliable morphological discrimination (Bravo et al., 2008). High cyst concentrations were found both in Burano (17,690 cells/g, morphotype-1) and East Orbetello (19,569

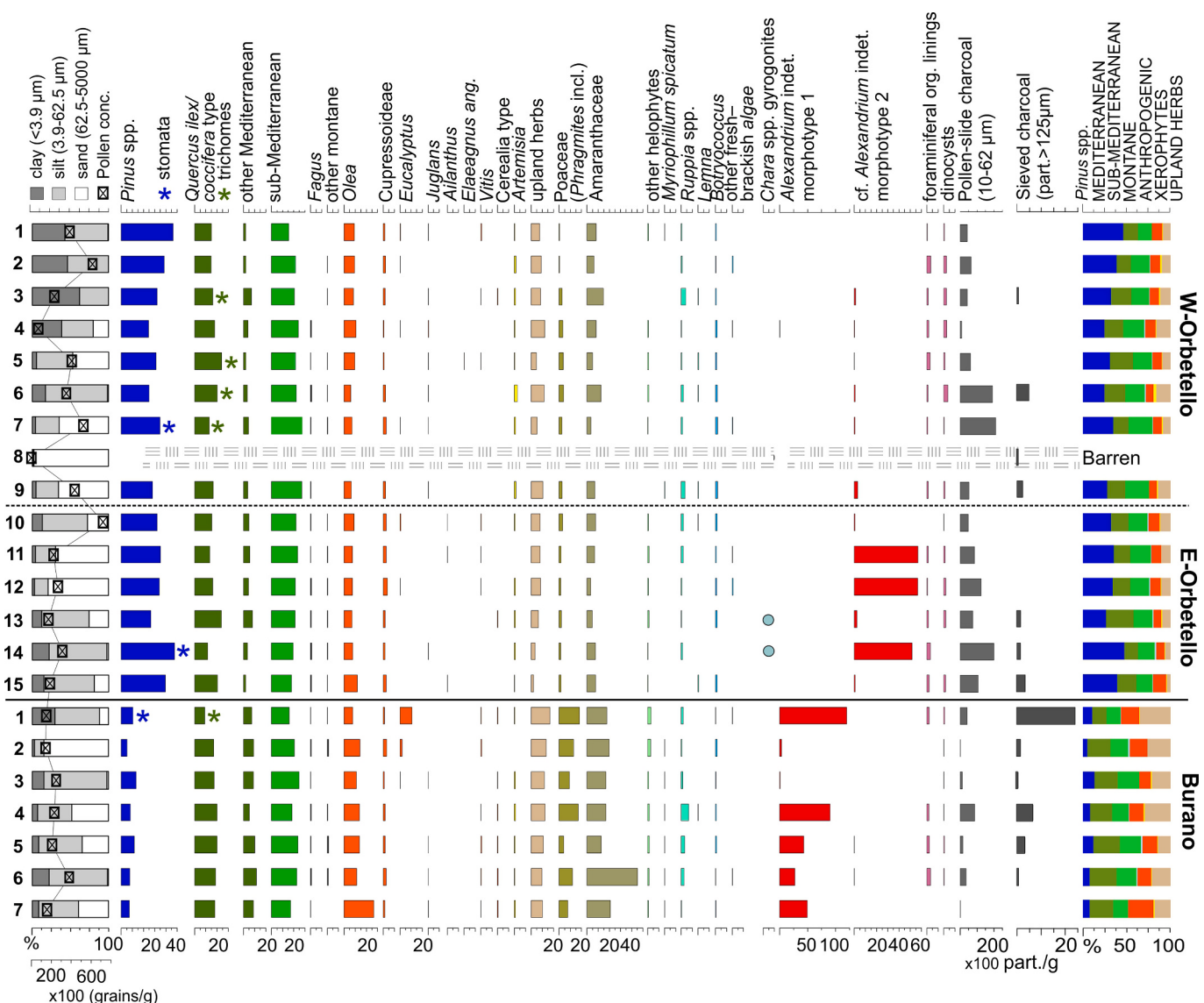


Fig. 3. Selected palynological, macrobotanical and sieved charcoal data from Orbetello and Burano subsurface sediment samples: ORB-1 to 15 and BUR-1 to 7, respectively. Key to pollen and non pollen palynomorphs sums: other Mediterranean (*Phillyrea*, *Ligustrum*, *Pistacia*, *Myrtus* sp., *Buxus*, *Rhamnus*, *Tamarix*, *Juniperus*); sub-Mediterranean (*Q. suber*, *Corylus*, *Carpinus orientalis*/*Ostrya carpinifolia*, *C. betulus*, *Q. robur* group, *Q. cerris*, *Ulmus*, *Celtis*, *Acer*, *Tilia*, *Fraxinus excelsior* type, *F. ornus* type, *Viburnum*, *Sambucus*); other montane (*Betula*, *Abies*, *Picea*); other helophytes (*Typha* sp., *Alisma* sp., *Sagittaria* sp., *Sparganium erectum* and *S. emersum*, *Lythrum* cf. *salicaria*, Cyperaceae); other Fresh/fresh-brackish algae (*Pseudoschizaea*, Zygnemataceae, Cyanophyta, *Spirogyra*, *Cosmarium* sp.).

cells/g, morphotype-2) (Figs. 3, and S1). The colonial green alga *Botryococcus* appeared at all sites except ORB-14, reaching up to 1140 particles/g (Figs. 3 and S1). Scattered occurrences of *Cosmarium* (freshwater Desmidiaceae) (BUR-1), *Spirogyra* zygospores (BUR-1 and ORB-4), other Zygnemataceae, and Cyanophyta were also recorded. The dinoflagellate cysts like *Spiniferites* spp., *Polykrikos schwartzii*, and *Hexasterias* sp., as well as foraminiferal organic linings, were present in very low percentages, with higher concentrations near lagoon canals of Nassa-Santa Liberata and Fibbia (ORB-2,3,5,6; Figs. 2 and S1).

4.1.3. Terrestrial pollen signal

A total of 137 terrestrial pollen taxa were identified, reflecting diverse vegetation communities. In Orbetello, *Pinus* spp. is the most abundant taxon (~35% compared to ~10% at Burano, Fig. 3). Apart from *Pinus*, *Quercus ilex/coccifera* type represents the main taxon in both lagoons (~26% at Orbetello and ~19% at Burano), while other Mediterranean sclerophylls are present in lower abundances (e.g., *Pistacia*, *Phillyrea*, *Myrtus*) (Figs. 3 and S1). Deciduous oaks, particularly *Quercus robur* group, including *Q. pubescens* (according to Van Benthem et al., 1984), *Q. cerris*, and *Q. suber*, are especially abundant at Orbetello, with the highest concentrations in the western basin (Figs. 2 and S1). *Quercus suber* shows the highest percentages and concentrations at Burano, reaching up to 9% and 1670 grains g⁻¹, respectively (Figs. 3 and S1). Anthropogenic taxa such as *Olea* (up to 26.3% at BUR-7) and introduced species like *Eucalyptus* and Cupressaceae are also prominent, exhibiting uneven spatial distributions (Figs. 3 and S1). Other anthropogenic and synanthropic taxa are also present: *Cedrus*, *Juglans*, *Vitis*, *Elaeagnus angustifolia*, *Ailanthus*, *Ambrosia artemisiifolia* type, Cerealia type (sensu Joly et al., 2007), the latter mostly recorded in the Burano sites (Fig. 3). *Plantago lanceolata* (~1%) occurs in all sites, especially near Orbetello town and Mt. Argentario shoreline, except ORB-15 (Fig. 2). Upland and steppic taxa, including *Artemisia* and *Ephedra*, are present throughout. *Fagus* is present at all sites except ORB1–2–3, with percentages up to 2% (Fig. 3).

4.1.4. Pollen-slide and sieved charcoals

Pollen-slide and sieved charcoal particles concentrations are shown in Fig. 3 and S1. Pollen-slide charcoal (10–62 µm fraction) is documented at all sites. At Orbetello, the highest concentrations are found near the Ansedonia and Nassa-Santa Liberata canals (>20,000 part./g, ORB14-6-7, Fig. S1), while at Burano, the highest concentrations are detected in the central lagoon near its connection with the sea (BUR-4, Fig. S1). Concentrations of sieved charcoal particles (62–125 µm) vary markedly across samples, with the highest values recorded in the western Orbetello and Burano basins (Fig. S1). Concentrations of particles larger than 125 µm vary between 0 and 24 particles/g at Burano and 0 to 4.5 particles/g at Orbetello (Fig. 3). Charcoal particles >500 µm are only present at ORB-6.

4.2. Grain-size

Grain-size ranges from clay to fine sand, with particle sizes between 3.9 and 500 µm (Fig. 3). Samples from the western Orbetello basin are predominantly clayey-silty, except for ORB-7, ORB-8, and ORB-9, which are dominated by the fine-sand fraction, with ORB-8 exhibiting the coarsest grain-size distribution (Fig. 3). A similar pattern is observed in samples ORB-11 and ORB-12 from the eastern lagoon (Fig. 3). All these samples are located close to the peninsula on which the town of Orbetello is situated. At Burano, the coarsest grain-size fraction characterizes site BUR-2, whereas the other sampling sites are dominated by a clayey-silty matrix (Fig. 3).

4.3. Physico-chemical water parameters

Physico-chemical water parameters measured at Orbetello (June 2020 and 2022) and Burano (July 2022) are shown in Fig. 5.

Measurements were conducted during the same season to minimize seasonal variability and to capture spatial gradients across the study sites. Burano shows higher average temperature (29.7 °C) and oxygenation (12.3 mg/L O₂) but lower salinity (26.8 ppt) than Orbetello, where salinity exceeds 42 ppt in both basins. pH was generally >8.3 at Burano (except BUR-3), while Orbetello values ranged from 7.5 to 8.1. In Orbetello, the eastern basin exhibited the highest turbidity (up to 567.5 NTU) and chlorophyll-a (11.1 µg/L), along with strong variability in redox potential and phycoerythrin (Fig. 4).

4.4. Vegetation and fire spatial data analyses

At all spatial scales considered, i.e., 500 m, 5 km, and 15 km buffers, “crops and arable lands” represent the main vegetation category (Fig. 5). From the 500 m to the 15 km buffers, vegetation classes are more stable at Orbetello, with an increase of only 2 categories, compared to 11 at Burano (Fig. 5). The most widespread classes (i.e. covering >8% of the surface area) are illustrated below. Within the 500-m buffer at Burano these classes are: “crops and arable lands” (50%), “Mediterranean maquis, juniper groves, and coastal dune bushes” (27%), and “urban areas and infrastructures” (12%). (Fig. 5). Olive groves (0.2%) and vineyards (2%) are present in much lower proportions (Fig. 5). At Orbetello, the most represented classes within the 500-m buffer are “crops and arable lands” (20%), “urban areas and infrastructures” (16%), “Mediterranean maquis, juniper groves, and coastal dune bushes” (15%), and “pine woodlands” (14%), while “*Quercus ilex* woodlands” account for 5.7% of the area (Fig. 5). “Olive groves” are present in higher proportions than at Burano (3.6%), whereas vineyards occur at lower proportions (0.6%) (Fig. 5). Within the 5-km buffer, crops and arable lands cover 63% of the area at Burano and 27% at Orbetello (Fig. 5). Forest cover is dominated by *Quercus ilex* woodlands at Orbetello (24%), compared to only 2.3% at Burano. Olive groves account for 7% of the area at Burano and 5% at Orbetello. At the 15-km buffer, the two sites display much more comparable vegetation patterns (Fig. 5). The total burned area within this buffer—representing a relevant source area for wood charcoal particles >125 µm dispersed into the lagoons (Vachula and Rehn, 2023)—was estimated at 238 ha within the watershed draining into the Orbetello basin and 27.3 ha within the watershed draining into the Burano basin (Fig. 6).

4.5. Clustering and redundancy analysis (RDA)

Cluster analysis of terrestrial taxa reveals two main clades corresponding to samples from the Orbetello and Burano basins (Fig. S3). At Burano, sample BUR-1 (cluster D; Fig. 7a) shows the highest intrabasin divergence, clearly separating from all other samples, which group within cluster C (Fig. 7a). Within the Orbetello basin, secondary sub-clades broadly distinguish samples from the western and eastern sectors (Fig. 7b). Notable exceptions occur: for example, samples ORB-13 and ORB-15 (cluster B), although collected in the eastern sector, cluster more closely with samples from the western sector (Fig. 7b). RDA triplots indicate that the first two axes explain 58.1% of the total variance at Burano and 26.7% at Orbetello (Fig. 7a–b). At Burano, RDA Axis 1 explains 43.1% of the total variance and clearly separates BUR-1 from all other samples (Fig. 7a). BUR-1 is primarily associated with grain-size variables, particularly clay content, and with distance from the shoreline, whereas the remaining samples are mainly related to water depth. Among terrestrial taxa, *Eucalyptus* and *Olea* plot away from the main sample group, loading in the second and fourth quadrants of the ordination space (Fig. 7a). At Orbetello, RDA Axis 1 explains 17.5% of the variance and broadly differentiates samples from the western (cluster B) and eastern (cluster A) sub-basins (Fig. 7b). Samples from the western basin are influenced by multiple environmental variables, with distance from the shoreline emerging as the most important. In contrast, samples from the eastern basin are primarily associated with grain-size parameters, particularly the fine-sand fraction (Fig. 7b). Among terrestrial

Physico-chemical water parameters

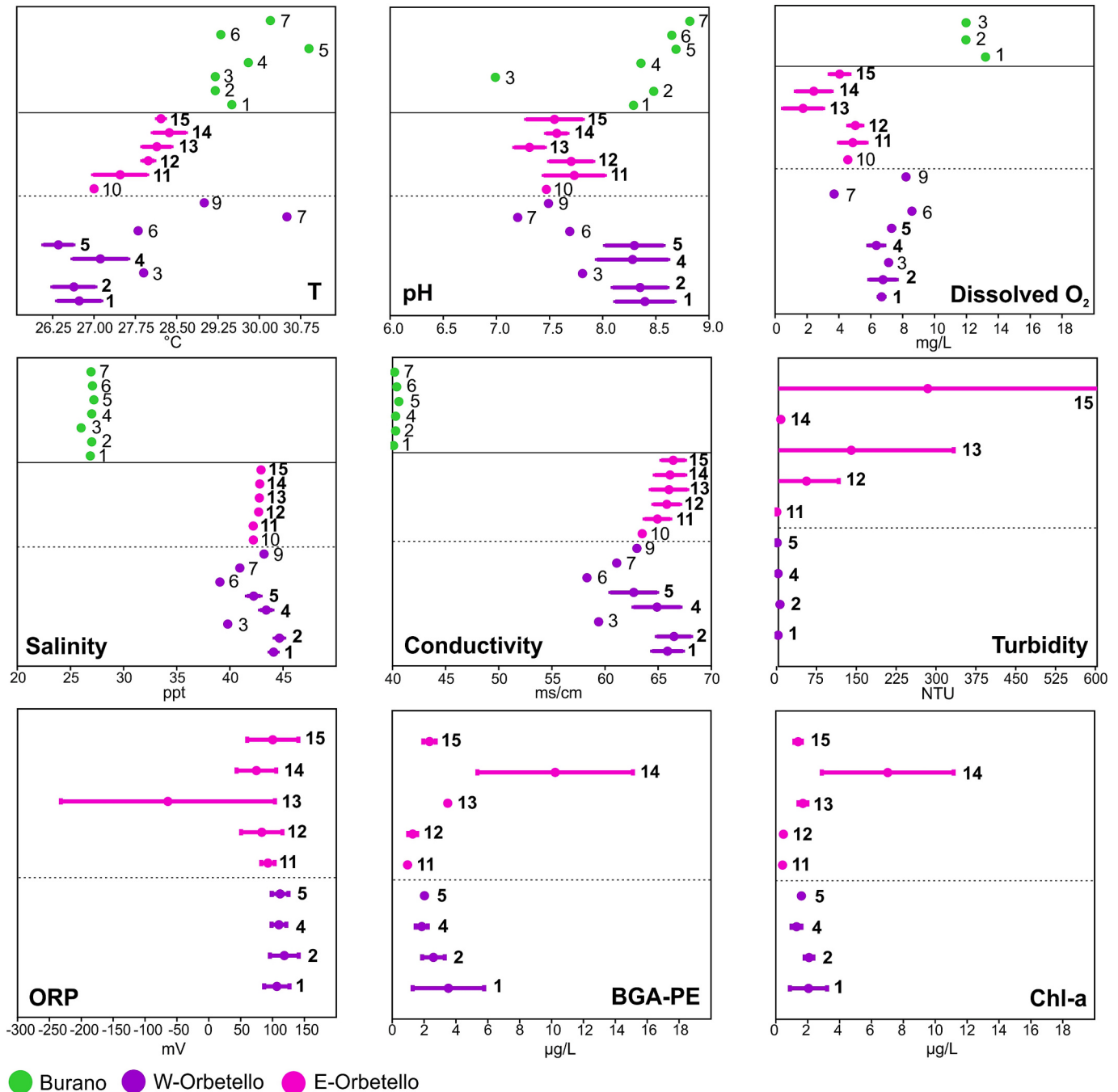


Fig. 4. Physico-chemical water parameters measured at the Burano and Orbetello sampling sites in June 2022 and June–July 2020. Repeated measurements are shown in bold, whereas single measurements are shown in regular type. Key to abbreviations: T (Temperature), ORP (oxidation–reduction potential), BGA-PE (phycoerythrin) and Chl-a (chlorophyll-a).

taxa, *Quercus robur* group, *Quercus ilex/coccifera* type and *Quercus suber* plot away from the main sample group in the second and fourth quadrants of the ordination space (Fig. 7b).

5. Discussion

5.1. Source of pollen from main wind-pollinated tree species

Comparing terrestrial pollen input in the Orbetello and Burano basins with vegetation distribution and local wind patterns provides valuable insights into pollen atmospheric transport in the lagoons. The

terrestrial pollen input in both lagoons roughly reflects the local to regional dominant vegetation formations displaced within 15 km (Fig. 5). A background vegetation signal is also registered, as indicated by the occurrence of *Fagus* pollen, whose source populations are located approximately 60 km from the sampling area (Sabbatini et al., 2011). The terrestrial pollen assemblages are generally comparable between the two investigated basins, with the most notable difference observed in the *Pinus* signal, which is three times higher at Orbetello than at Burano (Fig. 3). The uneven distribution of *Pinus* pollen likely reflects windblown inputs from the “pine woodland” vegetation class, which covers 14% of the 500 m buffer around the Orbetello basin (≈474 ha)

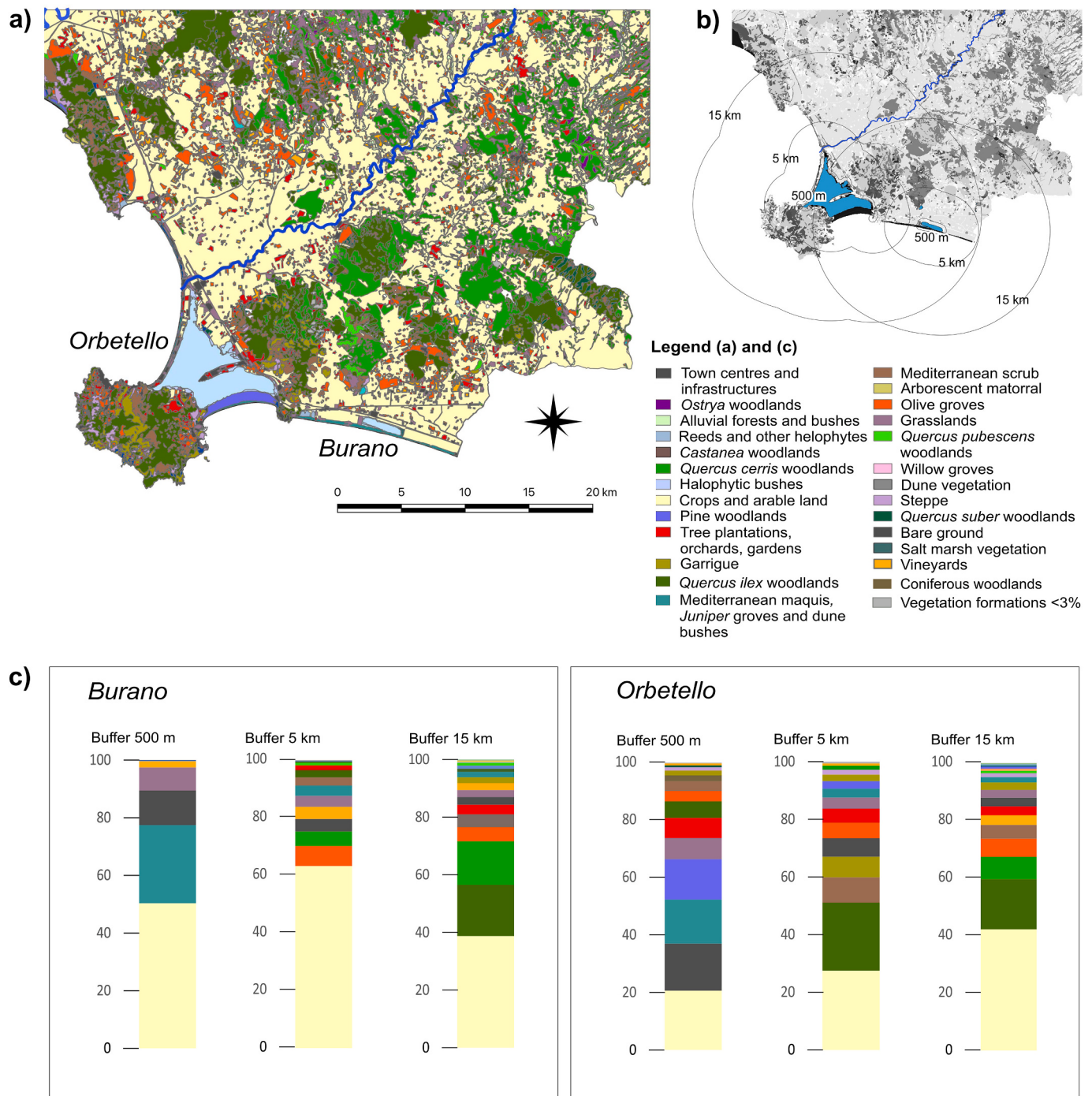


Fig. 5. a) Vegetation map modified from the Italian Map of Nature (IMN) at 1:50,000 scale (Amadei et al., 2004); b) Scheme illustrating vegetation extraction within buffer zones (500 m, 5 km, 15 km) calculated from the shoreline of each basin; c) Comparison of vegetation classes expressed as percentages of buffer area (see text for details).

and is dominated by *P. pinea*, *P. halepensis*, and *P. pinaster* along the Feniglia tombolo (Figs. 2, 5c). This area underwent severe deforestation between 1700 and 1900 due to intensive human exploitation. Rehabilitation began in the early 1900s with dune stabilization and the planting of Mediterranean pines, a process completed in the 1950s, followed by further forest expansion between 1955 and 1985 (from 273 to 334 ha) (Bellarosa et al., 1996). This pattern is likely enhanced by local wind circulation, which creates two distinct clusters: a dominant south-east–northwest flow over the Orbetello lagoon (mean speed $\approx 4 \text{ m s}^{-1}$) and a northeast flow over the Burano basin (mean speed $\approx 2.5 \text{ m s}^{-1}$; 2012–2022 data from Orbetello and Burano stations, Servizio Idrologico

Regione Toscana) (Fig. 6), modulating the dispersal of *Pinus* pollen (Fernández-González et al., 2021). As observed elsewhere, at local scales, pollen depositional patterns are strongly influenced by wind direction relative to the spatial distribution of pollen sources (Silva et al., 2000; Damialis et al., 2005; Rojo et al., 2015).

Among Mediterranean taxa, the “*Quercus ilex* woodlands” pollen signal is dominant, reaching 18% at Burano and 16% at Orbetello (Fig. S4). This pattern reflects the widespread distribution of these forests within the 15 km buffers around the Burano and Orbetello basins, covering 17.8% and 18% of the area, respectively (Fig. 5). At Orbetello, they form a dense belt near the shoreline, covering 5.7% of the 500 m

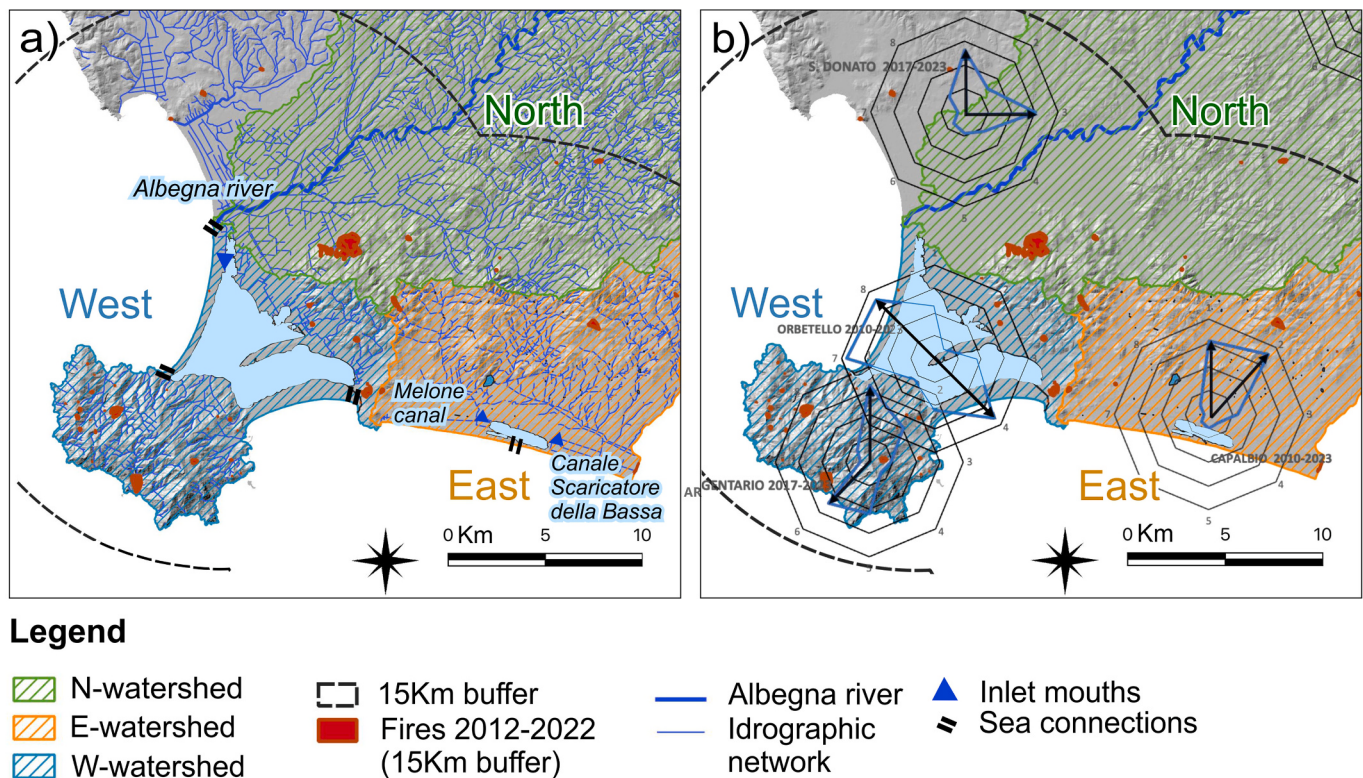


Fig. 6. a) Map showing the hydrographic network of the three watersheds draining into the lagoons (North, East and West) and areas of burned vegetation (2012–2022) relevant for the sieved charcoal registration in both lagoons; b) Map showing dominant wind directions and areas of burned vegetation (2012–2022) within 15 km of the sampling sites.

buffer and 23% of the 5 km buffer areas (Fig. 5). This results in a *Q. ilex/coccifera* pollen concentration roughly twice that at Burano (6300 vs. 3200 grains g^{-1} , mean values; Fig. S1). The presence of *Quercus* trichomes in the western Orbetello basin further indicates the proximity of parent plants (Hardin, 1976; Fig. 3). The *Quercus ilex* and *Quercus rotundifolia* forests on Mount Argentario (Viciani et al., 2018) likely represent one of the main pollen sources for the Orbetello lagoon with pollen dispersal further enhanced by the prevailing south–north wind regime (Servizio Idrologico Regione Toscana; Fig. 6). Among other Mediterranean taxa, pollen indicators of the “Mediterranean maquis, *Juniper* groves, and dune bushes” vegetation class reach 8.7% at Burano, roughly double the 4.4% at Orbetello, reflecting the greater vegetation cover of the 500 m buffers: 27% vs. 15%, respectively (Fig. 5). This is expressed as a dense belt of maquis and dune shrublands along the lido (barrier island) separating the Burano Lagoon from the sea (Fig. 5; Pedrotti et al., 1979; Angiolini et al., 2002).

Among anthropogenic taxa, pollen indicators of the “Crops and arable land” vegetation class show a discrepancy between pollen percentages—reaching only 0.7% at Burano and 0.3% at Orbetello—and the current vegetation cover, which is dominant at both sites across the three buffers (20–63%; Fig. S4 and Table S1). This mismatch is consistent with previous studies showing that *Cerealia* type pollen is produced in relatively low amounts and undergoes limited long-distance transport (Lambert et al., 2017). However, a certain overrepresentation of this vegetation class in cartographic data (Fig. 5) cannot be ruled out, possibly due to recently abandoned fields recolonized by vegetation belonging to other classes. Among anthropogenic taxa, the pollen signal of “olive groves” is dominant, with mean values of 15% at Burano and 8% at Orbetello (Fig. S4). Pollen of *Olea* originates from olive groves surrounding the sites, which cover 4.9% of the 15-km buffer at Burano and 6.4% at Orbetello (Fig. 5). This landscape configuration results from a long-standing tradition of olive cultivation in the region. Historical records document a major expansion after the 1950s agrarian reform in

the Tuscan Maremma, when the number of cultivated trees increased from ~35,000 to over 90,000 between 1951 and 1954 (Belotti, 1960). This intensification—supported by the widespread use of organic and chemical fertilizers, as well as urban discharges and aquaculture—contributed to increased nutrient loading in coastal lagoons. During the 1990s, fertilizer application alone was estimated to supply ~45,000 kg of nitrogen and 1500 kg of phosphorus per year to the Burano basin (Ministero dell'Ambiente, 1993). The pollen signal from vineyards, though present near the basins—covering 2.1% of the 500 m buffer at Burano and 0.6% at Orbetello—is more evenly recorded throughout the Burano basin (0.3%, mean value) and only sporadically detected at Orbetello (0.2%, mean value) (Figs. 5 and S3). Stemflow transport and the exponential decline of *Vitis* pollen with distance from vineyards help explain these low values (Turner and Brown, 2004), and smaller basin size also appears to favor its detection (Fig. S1). Among the non-native invasive species, the pollen signal of *Ailanthus altissima* (Mill.) Swingle (Simaroubaceae) is recorded in samples close to the Terre Rosse mining area and the town of Orbetello (Fig. 2). As demonstrated in other locations (Motti et al., 2021), the spread of this species is linked to highly fragmented and degraded areas. Native to eastern China and northern Vietnam, *Ailanthus altissima* was first introduced to Europe as an ornamental plant in the 1740s and is now regarded as one of the most problematic invasive species on the continent (DAISIE - Inventory of alien invasive species in Europe, 2023). Due to its historically documented human-mediated spread, the detection of its pollen can also serve as a chronological marker in palaeoecological studies.

Overall, this framework reveals a pronounced distortion, with forests overestimated and open areas underestimated in both basins, and a particularly clear under-representation of cereal crops. Differences in the representation of vegetation classes arise from a complex interplay between regional pollen inputs and local environmental controls, primarily driven by the proximity of source vegetation and local wind patterns, underscoring the importance of considering these factors when

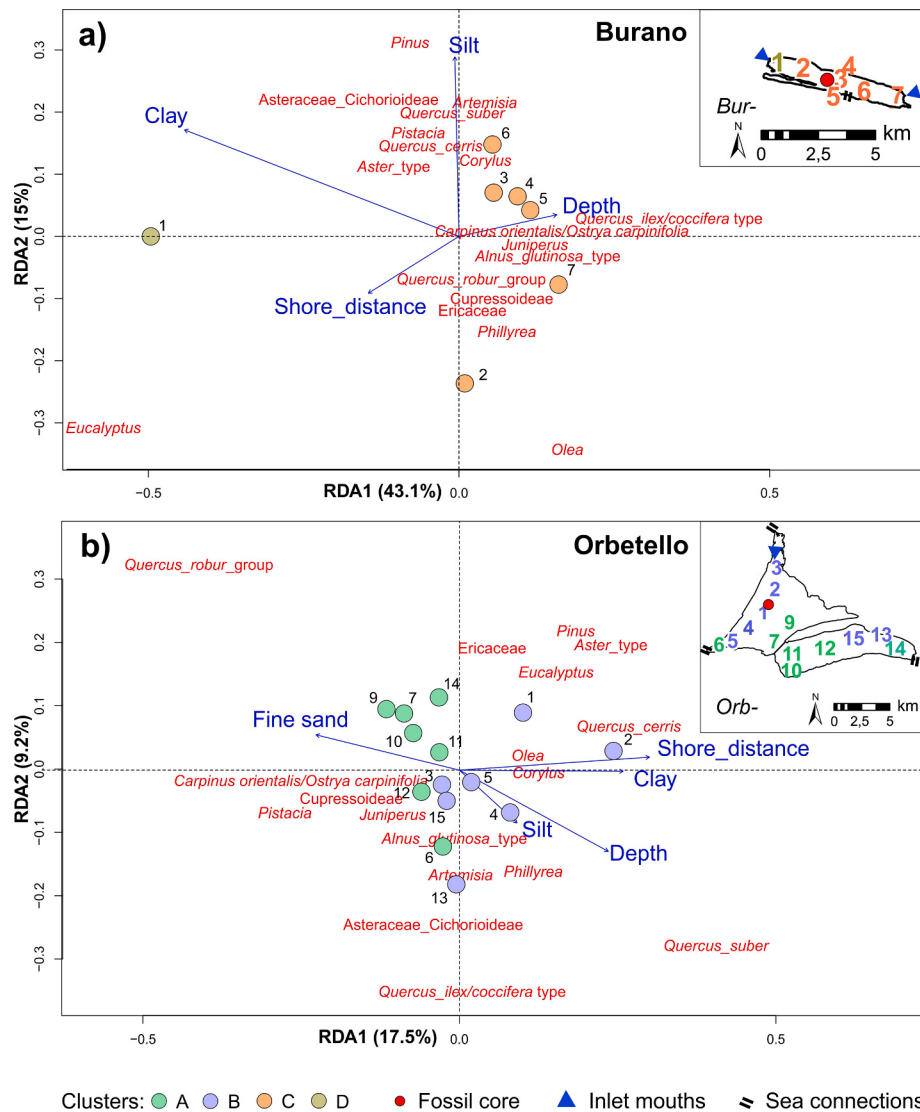


Fig. 7. a) and b) Redundancy Analyses (RDA) triplots: distribution of the explanatory variables as vectors, the dominant wind-pollinated terrestrial taxa as response variables and sampling sites for the Orbetello and Burano datasets. Clusters refer to the clustering analysis shown in Fig. S3.

interpreting fossil pollen records.

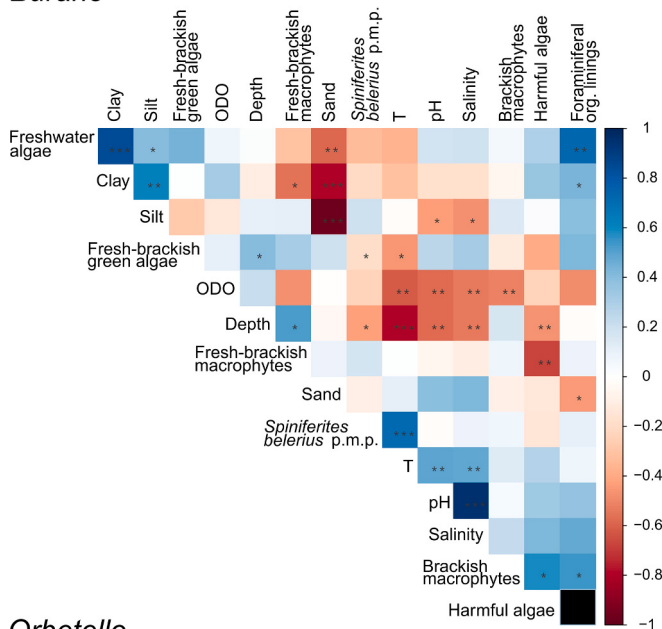
5.2. Intra-basin variability of terrestrial pollen concentrations

The Orbetello and Burano lagoons, being shallow basins with hydrological connectivity, receive both freshwater inflow from local streams and periodic water exchange with the sea. Consequently, in addition to atmospheric transport, hydrological and sedimentological processes can play a role in shaping the depositional patterns of terrestrial pollen (Matthias and Giesecke, 2014; Wang et al., 2025). Grain-size affects pollen concentrations at Burano, where silt is positively correlated with both total and terrestrial pollen ($r = 0.65$ and $r = 0.74$, respectively; $p < 0.1$), while fine sand shows a negative correlation with total pollen ($r = -0.60$; $p < 0.1$). At Orbetello, pollen concentrations are generally higher in the western basin, dominated by clay-rich sediments, than in areas near Orbetello town, where fine sandy deposits prevail (Fig. S5), although no significant correlations with pollen concentration are observed (Fig. S5). Pollen concentrations are also largely unaffected by water depth ($r = 0.48$ at Burano, $r = -0.39$ at Orbetello; Fig. S5). This is consistent with observations from other basins with extremely flat bottoms, where sediment focusing and resuspension from shallow to deeper areas are limited (Giesecke and Fontana, 2008).

At Burano, morphometric, hydrological, and sedimentological factors explain 58.1% of the variance in terrestrial pollen concentrations, with 43.1% and 15.0% accounted for by the first and second RDA axes, respectively (Fig. 7). Along the first axis, sample 1 (Cluster D, Figs. 8a and S5) diverges, correlating with *Eucalyptus* pollen and reflecting depositional conditions influenced by the shoreline and clay-rich sediments (Fig. 7a). This pattern likely reflects inputs from the westernmost inlet (Melone canal; Fig. 6), which adds pollen from *Eucalyptus resinifer* plants growing within ~500 m of the shoreline (Angiolini et al., 2002). Other samples (Cluster C; Figs. S5 and 8a) form a more homogeneous group, except for samples BUR-2 and BUR-7, which correlate with *Olea* (Fig. 7a). The proximity of these sites to the shoreline and canal mouths Melone and Canale Scaricatore della Bassa (Fig. 6), suggests that waterflow enhances the contribution of olive pollen in these sectors of the basin.

At Orbetello, morphometric and sedimentological variables together explain only 26.7% of the total variance in terrestrial pollen concentrations (17.5% along Axis 1 and 9.2% along Axis 2; Fig. 7). Axis 1 broadly separates pollen Clusters A and B, which roughly correspond to samples originating from eastern and western basin, respectively (Fig. 7b). In the westernmost basin, where the fossil sequence is located, samples are primarily influenced by their distance from the shoreline

Burano



Orbetello

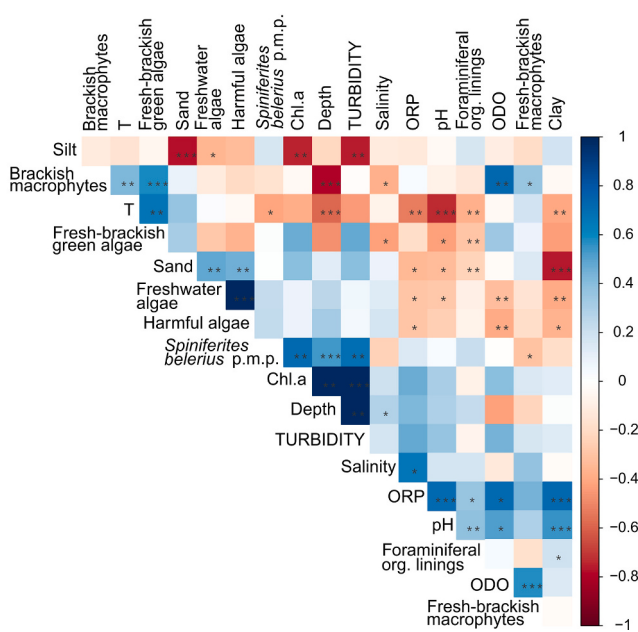


Fig. 8. Correlation matrices computed for each lagoon for key aquatic groups (see Table 1), sedimentological, chemical and physical water variables. Pearson correlation coefficients are indicated (* 0.10 ** 0.05 *** 0.01).

(Fig. 7b). In particular, sample ORB-2 stands out from the rest of the group due to its higher *Quercus cerris* pollen concentrations (Figs. 8b and S1). The “*Quercus cerris* woodlands” vegetation class is absent from the immediate basin surroundings (i.e., the 500 m buffer) but occurs within the 15 km buffer, covering 7.8% of the area (Fig. 5). These forests are widespread across the Albegna river watershed, which likely facilitates fluvial transport of this pollen type, influencing the assemblage of samples near the Albegna river mouth (i.e. Fibbia canal, Fig. 2 and Fig. 6). However, in the Orbetello basin, the low explanatory power of the considered variables suggests the influence of additional hydrodynamic processes, likely related to efficient sea–lagoon water exchange through pumping stations since the nineteenth century, up to the modern configuration via the Fibbia and Nassa-Santa Liberata canals (Antonelli, 1870; Cappietti et al., 2020). This exchange helps maintain a

constant water flow throughout the basin—particularly during summer—thereby preventing the upward spread of bottom-water anoxia (Simonetti et al., 2024). Such artificial circulation likely enhances water mixing and diffusion processes, complementing the effects of wind and substantially influencing pollen redistribution and deposition within the basins. In contrast, in the Burano basin, the more limited water exchange with the sea and the resulting lower hydrodynamicity reduce intra-basin pollen mixing.

5.3. Fire signal and intra-basin variability of charcoal concentrations

In coastal Mediterranean ecosystems, fire is a key disturbance factor (Keeley et al., 2011), also through its secondary effects on soil erosion and nutrient transfer to aquatic systems (Neves and Santos, 2022). Here, spatial relationships between fire activity and charcoal particles in the Orbetello and Burano lagoons are examined (Figs. 6 and S1). Charcoal fragments > 125 µm, a proxy for local fire events (Higuera et al., 2011), are unevenly distributed in both basins, with mean concentrations about five times higher at Burano (5 ± 8.6 part./g) than at Orbetello (0.8 ± 1.4 part./g). Concentrations of charcoal fragments > 125 µm are strongly correlated with *Glomus* chlamydospores ($r = 0.77$, $p < 0.01$), which is a proxy for soil erosion (van Geel et al., 1989; Kołaczek et al., 2013), suggesting runoff as an additional transport mechanism (Anderson, 2014) potentially enhanced by post-fire soil denudation (Mastrolonardo et al., 2024). The source area of the observed charcoal concentrations likely corresponds to vegetation burned within 15 km of the lagoons (Vachula and Rehn, 2023), which is estimated approximately 146.6 ha at Orbetello (West and South watersheds, Fig. 6) and 27.3 ha at Burano (East watershed, Fig. 6) between 2012 and 2022 (Regione Toscana – Banca Dati Incendi Boschivi), although remobilization of older particles cannot be excluded. Discrepancies between Burano and Orbetello may reflect the differences in basin size (2.3 km² versus 27 km²), which influence the deposition and redistribution of sieved charcoal particles, while site-specific transport processes beyond wind-driven dispersal also play a role.

This pattern is apparent at Burano, where sieved charcoal particle concentrations in both the 62–125 µm and >125 µm size classes peak near the Melone canal mouth (BUR-2; Figs. 1 and S1), indicating an additional inlet contribution (Fig. S1). At Orbetello, sieved charcoal shows a more complex spatial pattern, with the 62–125 µm fraction concentrated in the western basin, highlighting a preferential contribution from the Albegna River via the Fibbia canal (Figs. 2 and S1). In contrast, the occurrence of charcoal particles in the >125 µm class, and particularly those >500 µm at ORB-6, appears to be more related to short-distance transport from small fires (<26 ha) documented within 1 km of the shoreline (Fig. 6).

By contrast, the smallest charcoal size class (10–62 µm) exhibits a markedly different spatial pattern in both lagoons, being abundant in samples near the sea connections (ORB-6, ORB-14, and BUR-4; Figs. 3 and 6). This suggests a dominant sea-mediated transport of charred particles, deriving from a background signal not directly linked to local fire activity.

The observed patterns of different charcoal size classes, in relation to the burned source area and transport processes, provide key insights for interpreting past fire activity in the fossil records of these two transitional environments.

5.4. Aquatic palynological signal and its indicative significances

Aquatic and hygrophilous groups, identified through diagnostic pollen and non-pollen palynomorph (NPP) types are summarized in Table 1. Salt marshes and amphibious plant communities show a similar spatial pattern, dominating the pollen signal among shoreline taxa. Salt marshes are less abundant in the eastern Orbetello basin (Fig. 3), where samples are characterized by lower pH (mean 7.4) and dissolved oxygen

Table 1

Key vegetation/aquatic groups based on diagnostic pollen, non-pollen palynomorph types and macroremains registered in Burano and Orbetello modern samples. Grouping is primarily based on the FloraVeg.EU database, which contains information on European vegetation, habitats and flora (Chytrý et al., 2024).

Vegetation type (physiognomic or phytosociological information) / aquatic group description	Diagnostic types	Orbetello and Burano registration	Groups
Shoreline - pollen indicators			
Wet terrestrial herb communities (Molinio-Arrhenatheretea)	<i>Thalictrum</i>	Sporadic at Orbetello and Burano	Wet-terrestrial communities
Wet terrestrial riparian forest (<i>Alnetea glutinosae</i>)	<i>Alnus glutinosa</i> and <i>Salix</i>	Recorded at all sites	Riparian forests
Flooded or waterlogged amphibious helophyte-dominated vegetation (<i>Phragmitetalia</i> , Small-helophyte bed, Tall-helophyte bed)	<i>Typha</i> sp., <i>Alisma</i> sp., <i>Sagittaria</i> sp., <i>Sparganium erectum</i> and <i>S. emersum</i> , <i>Lythrum</i> cf. <i>salicaria</i> , Poaceae including the pollen type cf. <i>Phragmites</i> , Cyperaceae	Recorded at all sites	Flooded amphibious helophytes
Flooded succulent plant communities forming salt marsh belts (<i>Thero-Salicornietea</i>)	Amarathaceae, including halophyte communities colonizing the flooded banks, <i>Limonium</i>	Recorded at all sites	Salt marshes communities
Water body - pollen and macroremain indicators			
Vegetation of rooted floating or submerged macrophytes (<i>Potamogetonetea</i>)	<i>Myriophyllum</i> spp., <i>Myriophyllum spicatum</i>	Sporadic at Orbetello, recorded at Burano, except BUR-1	Fresh-brackish macrophytes
Submerged rooted herbaceous vegetation of brackish waters (<i>Ruppiaetea maritima</i>)	<i>Ruppia</i> spp., <i>Lemna</i>	Recorded at all sites	Brackish macrophytes
Submerged macroalgal stonewort swards in neutral to alkaline and lime-rich waters (<i>Charetea intermediae</i>)	<i>Chara</i> spp. (gyrogonites)	Orbetello: ORB-8,13,14	
Water body - Non Pollen Palynomorphs (NPP) indicators			
Phytoplankton: potential harmful dinoflagellates	<i>Alexandrium</i> morphotype 1, cf. <i>A.</i> morphotype 2	<i>A.</i> morph. 1 abundant at Burano, cf. <i>A.</i> morph. 2 Abundant at eastern Orbetello sites: ORB-11,12,14	Harmful Algae (<i>Alexandrium</i> spp.)
Fresh-brackish green algae	<i>Botryococcus</i> , <i>Pseudoschizaea</i>	Recorded at Orbetello, Sporadic at Burano	Fresh-brackish green algae
Prevalent freshwater filamentous and unicellular algae	Zygnemataceae, Cyanophyta, <i>Spirogyra</i> , Desmidiaceae: <i>Cosmarium</i> sp.	Sporadic at Orbetello and Burano	Freshwater algae
Phytoplankton: dinoflagellates (mesotrophic to eutrophic environments)	<i>Spiniferites</i> spp., <i>S. belerius</i> , <i>S. ramosus</i> , <i>Polykrikos schwartzii</i> , <i>Brigantediunium</i> sp., cf. <i>Quinquecupis</i> sp.	Sporadic at Orbetello and Burano	<i>Spiniferites belerius</i> p.m.p.
Rotaliid benthic foraminifera	Foraminiferal organic linings (<i>Ammonia tepida</i> , <i>A. ammoniformis</i>)	Sporadic at Orbetello and Burano	Foraminiferal organic linings

(mean 4.4 mg L⁻¹) compared to the western basin (Fig. 4). Although the coupled and highly variable behavior of these parameters on flooded shoreline vegetation remain poorly understood (Baumann et al., 2015), monitoring them is essential, as such conditions are expected to intensify under future climate-change scenarios (Cai et al., 2011). Along the Feniglia Tombolo, these habitats—mainly *Sarcocornia fruticosa* and the annual *Salicornietum emerici* association—formed a narrow belt in 2004 (Andreucci, 2004). Their current patchy distribution likely reflects, among other factors, sensitivity to fluctuations in physico-chemical conditions and to eutrophication processes (Moreno et al., 2020). Brackish macrophytes dominate across both water bodies over a wide salinity range (26–44.6 ppt; Fig. 4). In particular, *Ruppia* is widespread among aquatic macrophytes due to its tolerance to osmotic stress (Mannino and Sara, 2006). At Burano, this signal is unevenly distributed (Fig. S1) across a salinity range of 26–27.2 ppt (Fig. 4). In this basin, *Ruppia* progressively replaced *Potamogeton* from the 1980s onward, eventually covering the lagoon floor by 1984 (Lenzi and Angelini, 1985). Since then, its distribution has fluctuated in response to environmental stress, particularly during periodic dystrophic events. The most recent event, occurred in 2021, caused the complete detachment of *Ruppia spiralis* fronds and stems (Lenzi and Cianchi, 2022). The unevenness of the modern signal likely reflects the influence of these recent ecological disturbances. At Orbetello, the spatial distribution of brackish macrophytes is negatively correlated with water depth ($r = -0.79$, $p < 0.01$) and salinity ($r = -0.38$, $p < 0.10$) and positively correlated with dissolved oxygen ($r = 0.73$, $p < 0.05$) (Fig. 8). The reduced pollen concentrations observed at several sites may be associated with elevated chlorophyll-a, BGA, and turbidity levels (e.g., ORB-14, ORB-15; Figs. S1 and 3), reflecting the high sensitivity of *Ruppia* to nitrogen loading (Giusti and Marsili-Libelli, 2005), although no statistically significant correlation is detected (Fig. 8). Other aquatic plants, such as fresh-brackish macrophytes (e.g., *Myriophyllum* spp. and *M. spicatum*), remain subordinate and show a scattered distribution (Fig. 3). The discovery of

fertilized *Chara* spp. gyrogonites—previously unreported at Orbetello—is ecologically noteworthy, as these taxa constitute EU priority habitats (Habitats Directive 92/43/EEC). In this basin, fresh-brackish green algae (*Botryococcus* p.m.p.) show a positive correlation with temperature ($r = 0.67$; $p < 0.05$; Fig. 8). This highlights the role of high temperatures in driving blooms, as demonstrated in experimental studies showing the highest biomass productivity of *Botryococcus* sp. at 33 °C (Gani et al., 2021) and the high tolerance of these green microalgae to temperature extremes (Demura et al., 2014). In these coastal systems, dinocysts (*Spiniferites belerius* p.m.p.; see Table 1), although sporadic, show positive correlations with turbidity and chlorophyll-a at Orbetello, where *S. belerius* and *S. ramosus* dominate ($r = 0.69$, $p < 0.05$ and $r = 0.71$, $p < 0.05$, respectively; Fig. 8), and with temperature at Burano (*S. belerius* dominates; $r = 0.71$, $p < 0.01$), suggesting environment-specific drivers in each system.

Overall, relationships between the abundance and spatial distribution of these aquatic groups and physico-chemical variables provide a local calibration for interpreting their variability in fossil sequences.

5.5. The occurrence of *Alexandrium* dinocysts

Among microalgae, the extremely high concentrations of potentially harmful resting cysts attributed to the *Alexandrium* genus in Burano basin underscore a significant ecological risk, as this genus is well known for triggering red tides in the Mediterranean Sea (Vila et al., 2001). At Burano cysts of *Alexandrium* morphotype 1 (Fig. 3 and SI-2), were detected with concentration higher than 7000 cells/g in all samples except BUR2 and 3 (Fig. S1). In November 2021 this genus was already identified at Burano during a dystrophic crisis which evolved gradually from Cyanobacteria, in August, to the Dinophyta *Alexandrium tamarense*, in September, and Bacillariophyta (Lenzi and Cianchi, 2022). The *A. tamarense* species complex appears to be one of the most widely dispersed and occurs in many locations worldwide, covering all ocean

basins and many regional seas, including the Mediterranean (Lilly et al., 2007; Penna et al., 2007). It is likely that the cysts we observed mostly derive from the bloom that occurred the year before sampling, although the absence of vegetative cells in our material prevents identification at the species level (SI-2).

In the Orbetello Lagoon, cf. *Alexandrium* morphotype 2 dinocysts (SI-2) were detected, reaching peak abundances of approximately 19,500 cells/g in the eastern basin (site ORB11; Figs. 3 and S1). *Alexandrium* species were not detected at Orbetello during the recurrent eutrophication events documented between 1995 and 2001, which were characterized by dynamic phytoplankton blooms dominated by diatoms, other dinoflagellates, and other flagellates (Nuccio et al., 2003). However, in July 2005, the occurrence of *Alexandrium insuetum* and *Alexandrium* sp. was documented in the lagoon (Facca and Sfriso, 2009), suggesting a relatively recent colonization of the genus in this area. *Alexandrium insuetum* has been recorded at several Mediterranean sites, including the French coast (Guillou et al., 2002), the Amvrakikos Gulf in western Greece (Nikolaidis et al., 2005), and the Aegean Sea (Spatharis et al., 2007). However, information on its historical distribution and occurrences in the Mediterranean over recent decades remains largely unknown. The cf. *Alexandrium* morphotype 2 displays morphological affinities with *A. insuetum* (see SI-2; Shin et al., 2014), although its taxonomic assignment remains tentative.

Elevated cyst concentrations in the sediments may act as a long-term inoculum for future harmful algal blooms (HABs). Their presence therefore warrants careful monitoring, and sediment-disturbing activities—such as dredging—should be managed cautiously to avoid cyst resuspension and the potential triggering of new blooms.

6. Conclusions and final remarks

This study presents a site-specific modern palynological dataset from subsurface sediments of the Burano and Orbetello lagoons (Tuscany, Italy), providing insights into pollen representativeness, transport and deposition processes, and the influence of local environmental variables. One of the main implications concerns the use of this local calibration set for the study of two fossil records—the OLP11-B core from western Orbetello and the LB5B core from the Burano basin—aimed at reconstructing ecological trajectories over the past 200 years (Badino et al., in press). The principal aspects emerging relate to the following points:

- 1) The hydrological network and the “shore distance effect” locally influence pollen and sieved charcoal deposition, particularly in samples located near inlet mouths in both lagoons.
- 2) Intra-basin pollen deposition is more strongly explained by morphometric and sedimentological factors at Burano, which account for 58.1% of the observed variance, compared to 26.7% at Orbetello. This reflects the more complex hydrodynamics of Orbetello, influenced by the periodic opening and closure of canals connecting the lagoon to the sea, which promote greater pollen mixing and partially obscure local depositional patterns. Interpreting the fossil records therefore requires consideration of historical lagoon–sea connectivity.
- 3) Natural sediment redistribution is negligible in both basins due to their shallow depths and flat bottoms. However, especially in Orbetello, localized bioturbation or redepositional processes—possibly linked to anthropogenic disturbances—may have occurred and could explain the lack in the attenuation of ^{137}Cs and ^{210}Pb activity profiles in several cores (Romano et al., 2015). In contrast, the presence of distinct ^{137}Cs fallout peaks in the Burano sediments suggests little or no redeposition (Pili, PhD thesis; unpublished results).
- 4) Vegetation–pollen relationships show pronounced distortions in the pollen signal, with forests overrepresented and open areas, particularly cereal crops and vineyards, underrepresented in both basins. Modern calibration of *Pinus* and *Olea* signals is especially valuable for

interpreting fossil records, given their dominant role in current and historical landscape transformations, such as the early 20th-century afforestation of the Feniglia tombolo and the 1950s agrarian reform. Correlating these events to the fossil pollen record can provide additional tie-points to refine the recent chronology.

- 5) Different charcoal size classes reveal distinct source and transport pathways. Sieved charcoal (>125 μm) reflects runoff- and water-mediated transport of particles from documented fires within the lagoon watersheds, whereas pollen-slide charcoal (10–62 μm) is mainly associated with sea-mediated transport.
- 6) Modern relationships between aquatic groups, inferred from diagnostic pollen and non-pollen palynomorphs (NPPs) and water physico-chemical gradients, serve as references for interpreting variability in fossil sequences.
- 7) High concentrations of *Alexandrium* spp. cysts in modern sediments underscore the need to assess their presence in the fossil records, as they are associated with harmful algal blooms (HABs) and little is known about their historical distribution in the Mediterranean.

Finally, this study, contributes to the integration of palaeoecological research with ongoing monitoring and high-impact communication activities, ultimately translating scientific knowledge into practical tools for biodiversity conservation and the sustainable management of Mediterranean coastal wetlands.

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.2026.105502>.

Data availability

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

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