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Non-pollen palynomorph assemblages in mid- to late Holocene wetland deposits and their palaeoenvironments of deposition: Microfossil signatures in sediment sequences of the Yangtze Delta coastal lowlands, East China

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ABSTRACT

Fluvial processes such as sediment deposition within drainage channels and seasonal overbank flooding, and fluvial events such as occasional high intensity floods all leave particular sedimentary signatures in terms of their lithology and also in their contained microfossil assemblages, which represent different environments of deposition. Over several thousand years the Yangtze River in eastern China has developed a coastal lowland plain around its delta that is mainly composed of stacked fluvial sediment facies, but also includes many marine or estuarine layers in some areas, as well as deposits of limnic and semi-terrestrial pool, marsh and mire origin, some of which are highly organic. The fluvial facies are dominantly clastic sequences of sands, silts and clays that reflect a range of deposition from quiet water to high energy conditions and in varying water depths, mainly governed by fluvial input from the Yangtze and the many other, smaller, rivers and streams of the deltaic lowland. The limnic and marshland sediments reflect autochthonous deposition in a range of freshwater wetland types of varying water depth, from lake through marsh/fen to surface peatland. Allied to lithological and pollen data, non-pollen palynomorph spore assemblages and abundances within these complex sedimentary sequences, particularly from algal communities, provide signatures of floodplain wetland depositional history and hydrodynamic patterns. We have used groupings of these microfossil data to characterise the sedimentary facies of the lower Yangtze coastal plain and to reconstruct hydrological history across the area at a range of spatial scales. Fluctuations in the relative taxa abundances are good indicators of changes in water levels at the site scale from surface waterlogging through reedswamp and fen to deeper open water. While some changes seem to be site specific, the data show flooding and increased water depths that correlate with known phases of climatic deterioration.

1. Introduction

The sedimentary record in the Yangtze Delta area to the west of Shanghai in eastern China has been the subject of considerable geological and palaeoenvironmental research, including the infill of the incised Yangtze river valley itself (Zhao et al., 2018; Jiang et al., 2021; Gao et al., 2022), which lies beneath and to the north of the modern river Yangtze, but also the sediments within the valleys of the other rivers that cross the low-lying floodplain between the Yangtze and Hangzhou Bay to the south. This research has often been performed as part of studies into the history of sea-level change that has affected this coast during much of the mid- and late Holocene (Chen and Stanley, 1998; Zhu et al., 2003; Zong, 2004; Wang et al., 2013). Much of the sedimentary sequences preserved in the often migrating (Schneiderman et al., 2003) river channels and the overall coastal floodplain of the Yangtze Delta's southern flank are fluvial, as might be expected. These fluvial facies include overbank flood deposits and are mainly sequences of sands, silts and clays (Li and Wang, 1998) that reflect a range of deposition from quiet water to high energy conditions and in varying water depths. As well as fluvial, there are also significant marine and estuarine deposits in the Yangtze palaeochannel and in those of some of the other major rivers of the area (Li et al., 2002), such as the Qiantang (Zhang and Li, 1998; Lin et al., 2005; Zhang et al., 2014; Jin et al., 2019; Liu et al., 2021), the Tiaoxi (Liu et al., 2015; Chen et al., 2018; Zhang et al., 2020a; Yan et al.,

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2020) and the now buried Taihu (Liu et al., 2018a; Fu et al., 2023), as well as within the still prograding (Zhang et al., 2015a; Yang et al., 2021; Zhao et al., 2021) delta front that lies to the east of a series of shell and gravel chenier ridges (Wu et al., 2022). These ridges have formed at intervals during the mid- and late Holocene (Liu and Walker, 1989; Yan et al., 1989) as a result of major storm events (Xu, 1997) and have formed barriers against sea-level rise and marine inundation since the early mid-Holocene. The delta began forming about 7000 years ago as a result of postglacial sea-level readjustment (Hori and Saito, 2007; Hori et al., 2002; Song et al., 2013), before which marine conditions had penetrated well to the west of the area, including west of current Lake Tai at Luotuodun (Li et al., 2009). Since its formation the deltaic lowland has been prograding eastwards (Chen, 1996; Hori et al., 2001) and the delta east of the chenier ridges has only formed in recent millennia (Chen and Zong, 1998). These chenier barrier ridges have allowed the development to their westward of a stable area of very low-lying freshwater marshland and small lakes, which has accumulated autogenic organic limnic, detrital and semi-terrestrial sediments of various kinds as hydroseral succession has progressed since the mid-Holocene, in addition to the regular input of clastic facies from overbank Yangtze and other river flooding (Wang et al., 2006; Zhang et al., 2015b). Sites immediately behind the ridges, like Beiganshan (Zong et al., 2011) and ZX-1 (Chen et al., 2005; Tao et al., 2006; Wang et al., 2006) remained influenced by brackish conditions for longer. The coastal lowlands of the southern flank of the Yangtze River Delta have therefore had a complex Holocene sedimentary history (Fan et al., 2017) with a mosaic of several contrasting wetland depositional environments, governed by a wide range of fluvial, aquatic, terrestrial, estuarine and marine influences, which have deposited a varied sediment suite across the area between the very large lake Tai (Taihu) at their western edge and the Delta's sea coast to the east. Previous papers (e.g., Li et al., 2000; Wang et al., 2012; Chen et al., 2018), have correlated records of sedimentary sequences from across these deltaic lowlands and have interpreted them in terms of the changing palaeo-distribution of wetland environments through time, including freshwater. The relative importance of these sediment inputs varied spatially at any one time, at the scale of the overall lowland, but also at the individual site scale as they were subjected to contrasting and fluctuating depositional regimes. As a result, the Yangtze Delta coastal lowlands comprise deep sediment piles with complex successions of different lithological units (Huang et al., 1999), analogous to those in adjacent coastal lowlands such as the Ningshao Plain to the south of Hangzhou Bay (Liu et al., 2016, 2018b; Ouyang et al., 2019), which provide useful comparable stratigraphies.

Some sedimentary facies can themselves provide information regarding their palaeoenvironment of deposition (Li et al., 1986; Ling et al., 2021), such as in clastic deposits laid down under marine and estuarine conditions (Wu et al., 2022), or more organic saltmarsh sediments (Yang, 1999; Lyu et al., 2021, 2022), both of which can be supplemented by diatom, foraminifera and ostracod analyses to indicate palaeosalinity (e.g., Zong et al., 2011; Chen et al., 2018; Dai et al., 2018; Jin et al., 2019; Jiang et al., 2021; Wu et al., 2022; Fu et al., 2023). However, factors such as water depth and quality in freshwater limnic or detrital facies are harder to determine, although a switch from peat to lacustrine gyttja would suggest increased water depth, for example. Generally, however, the type of freshwater wetland environment and plant community (Rodwell, 1995; Keddy, 2010) in which such sediments were deposited is more difficult to ascertain. While the freshwater wetland, and therefore largely organic, sediment sequences in the Taihu coastal lowlands contain pollen, pollen analysis is a poor tool for reconstructing site-specific environments, as pollen assemblages are composite and contain pollen from several source areas and vegetational communities (Bunting, 2008), some of which were growing at the site but with others perhaps a significant distance from the wetland point of deposition and so not representative of conditions there.

In a recent paper Innes and Zong (2021) evaluated the possible role of non-pollen palynomorphs (NPPs) in reconstructing water depth and quality of mid- to late Holocene aquatic systems at four sites in the Taihu coastal lowlands. Frequencies of algal spores in particular (Mao et al., 2011), but also of some fungal spores, should reflect very local conditions (Tang et al., 2013) in the way that pollen data cannot, as NPPs are not transported far but are deposited close to their point of origin (Ingold, 1971; van Geel, 2001), unless carried by flood events and freshwater flux (Zong et al., 2006). Studies of contemporary surface algal assemblages, some in the study area, can assist in the reconstruction of past environments (Wang et al., 1982; Yang et al., 2008; Xiang et al., 2021). Innes and Zong (2021) were able to recognise fluvial impacts in the wetland sediments that were not apparent in the site lithostratigraphy. Such reconstructions need not be confined to flooding horizons, however. The abundances of algae, or phytoplankton, that live in the water column at aquatic sites and that have differing tolerances to various aquatic conditions and controlling factors (Ortega-Mayagoitia et al., 2003; Stivrins et al., 2015, 2018), such as temperature, light availability and eutrophication (van Geel et al., 1994; Cheng and Li, 2010; Zhang et al., 2018) as well as water depth, should reflect hydrological conditions at a site (Hu and Wei, 2006; Medeanic, 2006; Ouyang et al., 2019; McCarthy et al., 2021). Freshwater algae are sensitive to perturbations such as water level changes (Medeanic, 2006; Medeanic et al., 2010) and so they should allow interpretation as being mainly a particular kind of wetland, with changes throughout its Holocene history. Studies of algal reponses to environmental change in floodplain wetlands are relatively few, but some are available to add to the findings of Innes and Zong (2021). For example, Junk et al. (1989) and Lemke et al. (2017) emphasised the importance of the flood pulse in governing algal communities in floodplain wetlands, Medeanic et al. (2010) noted the relation between algal communities and water-level changes in palaeolagoonal wetlands, Stoyneva (2003) studied algal assemblages under disturbance or equilibrium in floodplain wetlands, while Izaguirre et al. (2004) investigated algal variability across shallow floodplain wetlands. All studies stress the sensitivity of algal communities to flood perturbations and water depth and quality.

In this paper we have extended NPP analyses to five more sites in the area, to see if they can help to clarify the spatial variability, which was probably considerable (Liu et al., 2006; An et al., 2007), of wetland types and vegetation communities in the mid- to late Holocene within the Taihu lowlands, and also to test the viability of NPP assemblages as a proxy for reconstructing wetland type and history of development. Following Zong et al. (2011), on the basis of floodplain geomorphology and distance from marine influence we have divided the Taihu plain (southern Yangtze Delta) into four regions: the area seaward of the chenier ridges, the land immediately to the westward of the ridges, the central lowland area and the area around the many lakes, including Taihu (Qu et al., 2000; Wang et al., 2001), in its western part. The latter two areas are differentiated because the lake area contains many deep depressions, smaller versions of the Lake Tai basin itself, in which lakes formed and which might well preserve more fully aquatic sequences than the central lowland area, which has a generally flatter topography and is more likely to have supported semi-terrestrial reedswamp and fen in very shallow to surface floodplain wetlands. Topography rather than height above sea level seems to have been the controlling factor regulating sedimentation in the two areas, hence their separation. Although mainly lying to the east of the Lake Tai lake district, the central lowland area also extends to the south of Lake Tai, towards the Qiantang River. The locations of the nine analysed profiles used in this paper are shown in Fig. 1, together with selected previously published sites which assist interpretation of past palaeoenvironments in the four regions, as listed in Table 1. We have concentrated upon the freshwater sequences of the central lowland and the lake district areas' environments as they will have supported freshwater since the inception of the delta, largely unaffected by marine or estuarine sedimentation from the mid-Holocene onwards.

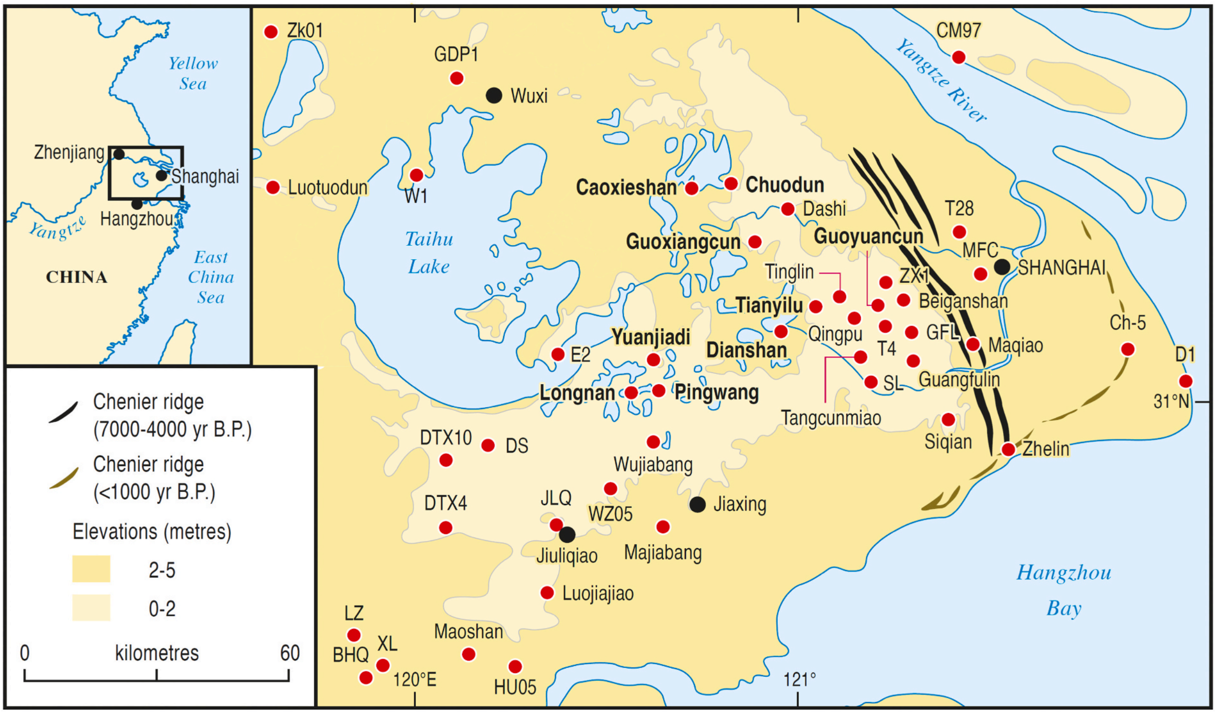

Fig. 1. Locations of the nine profiles presented in this paper, shown in bold, and of selected previously published profiles used to assist palaeoenvironmental reconstruction. The 'Lake District' area (LD in the text) lies immediately to the east of Lake Tai, and the 'Central Wetlands' area (CW) lies farther to the east and south. Site references are: Chuodun, Zong et al., 2012, Long et al., 2014; Dashi, Gong et al., 2007; Qingpu, Atahan et al., 2007; Itzstein-Davey et al., 2007; Tinglin and Tangcunmiao, Zong et al., 2011; Pingwang, Innes et al., 2014; Guangfulin, Atahan et al., 2008; Zk01, Shu et al., 2007; Luotuodun, Li et al., 2009, Lu et al., 2015, Deng et al., 2023; D1, Li et al., 1986; XL, Liu et al., 2015, 2018a; Zhelin, Wu et al., 2022; GDP, Qiu et al., 2020; ZX-1, Stanley et al., 1999 Chen et al., 2005 Tao et al., 2006, Wang et al., 2006; SL, Wang et al., 2013; Jiang et al., 2021; W1 and E2, Wang et al., 2001; JLQ and DS, Hong, 1991; T4 and T28, Li et al., 2000; GFL, Wang et al., 2012, 2013; DTX, Chen et al., 2018; Majiabang, Long et al., 2014; Wujiabang and Luojiajiao, Qin et al., 2011; Ch5, Qin et al., 1987; CM97, Yi et al., 2003, 2006; MFC, Zhao et al., 2008, Wang et al., 2012; WZ05, Fu et al., 2023; Maoshan, Zhuang et al., 2014, Jin et al., 2019; BHQ, Zhang et al., 2020a; LZ, Liu et al., 2015, He et al., 2021.

2. Methods

Standard laboratory techniques (Moore et al., 1991) were used to prepare the palynological samples. Alkali digestion with NaOH disaggregated the sediment and removed humic acids after which it was sieved at 180 μm. Mineral material was dissolved with hydrofluoric and hydrochloric acids, and then acetolysis was used to remove lignin and cellulose. The residue was stained with safranin before mounting on microscope slides in silicone fluid. Almost all non-pollen microfossils, including algal and fungal spores, survive this laboratory preparation well (Clarke, 1994), and so can be counted on the same slides as pollen grains, for which the procedure was designed. At least 200 land pollen grains were identified at each counted level, using the key of Moore et al. (1991), supplemented by the reference keys of Wang et al. (1995) and Zhang et al. (1990). All aquatic pollen and pteridophyte and bryophyte spores were also counted, although were excluded from the counting sum following established protocols (Moore et al., 1991) as they are very local and can be greatly over-represented. As the focus of this paper is on the reconstruction of very local, site-specific wetland environments and depositional changes, full pollen data are not presented here. The taphonomy of most pollen grains means that they derive from several different and sometimes distant source areas and are therefore less well suited to strictly local site studies of site hydrology but reflect the wider wetland mosaic, although some contemporary assemblage studies can be useful (Wang et al., 1982; Sun and Wu, 1988). Obligate aquatic pollen types including *Myriophyllum*, *Potamogeton* and *Typha latifolia*, are shown on this paper's diagrams, however, as they will help reconstruction of water depth at the site. *Typha angustifolia*, an important indicator of marshland (Keddy, 2010) and present in substantial frequencies in many pollen diagrams from the area (e.g., Zong et al., 2007; Li et al., 2012; Innes et al., 2014; Tang et al., 2019; Zhang et al., 2020b; Ye et al., 2022) is also included. As in other studies (Ke et al., 2023), a curve for Poaceae pollen grains of less than 40 μm size is also shown, as they almost certainly represent *Phragmites* growing in reedswamp and early succession marsh vegetation communities (Wang et al., 1995). Full pollen data or summary curves for some of the sites used in this paper have been shown elsewhere (Innes et al., 2014; Zong et al., 2011, 2012; Innes and Zong, 2021).

To reconstruct local hydrological evolution through time in different areas of the Taihu coastal plain we present selected non-pollen palynomorph (NPP) records (Cook et al., 2011; Shumilovskikh and van Geel, 2020) for those algal and fungal spores that are likely to have been produced and deposited close to in situ (Ingold, 1971), unless introduced with sediment via flooding events (Dai and Lu, 2010; Liu et al., 2020a, 2020b). These will therefore allow the reconstruction of site-specific hydrological conditions, including factors such as water depth and quality, which can be interpreted in terms of wetland environments and plant communities. Algal and fungal spores were counted until the land pollen sum was achieved, resulting in at least 100 being identified at each level, by reference to the illustrations and descriptions of NPPs in the range of published papers listed by Miola (2012), e.g., van Geel (1978, 1986, 2001) and van Geel and Aptroot (2006), and in subsequent publications (Shumilovskikh and van Geel, 2020; Shumilovskikh et al., 2021, 2022). Many NPPs have not yet been taxonomically identified and remain known only by their Type (HdV) number in the Hugo de Vries Laboratory catalogue in Amsterdam (van Hoeve and Hendrikse, 1998), but their palaeoecology can be inferred by their previously recorded depositional environment and associations in the microfossil assemblage. Where taxa can be identified, their HdV numbers are shown on the microfossil diagrams and with the first mention of the NPP type in

Table 1
Selected sites in the four main areas of the Taihu lowlands which have provided data for the reconstruction of wetland type, water depth and quality since the establishment of the deltaic lowland about 7000 years ago. Four broad categories of Open Water, Marsh/Fen, Reedswamp and Semi-terrestrial Wetlands (which includes 'other' general types) are defined and the non-pollen palynomorphs (NPPs) that are characteristic of those categories, and which are shown as such on the microfossil diagrams, are listed. NPP ecology is derived from several published papers (see text). NPPs are numbered following the Hugo de Vries (HdV) catalogue at the University of Amsterdam.

Time cal yr BP	Around Taihu and smaller lakes	In the central wetlands	Close to the chenier ridges	Deltaic plain seaward of ridges
	Pingwang, E2, Longnan, Yuanjiadi, Caoxieshan, Dianshan, Chuodun, GDP1, Wujiabang	Guoxiancun, Tinglin, T1, T4, Tangcunmiao, Tianyilu, Qingpu, Guoyuancun, JLQ, Dashi, DX, DTX, Luojiajiao, SL	Beiganshan, GFL, ZX-1	T28, Ch-5, D1, Zhelin, CM97, MFC, Maqiao
1000			Freshwater marsh	Low-salinity marsh
2000				Saltmarsh
3000		Freshwater marsh/ lake	Saltmarsh	
4000				
5000	Freshwater marsh/lake		Brackish water (lagoonal)	
6000		Low-salinity marsh		
7000	Brackish water	Brackish water	Brackish water	Brackish water (estuarine)

Freshwater wetland NPPs			
Open water	Marsh/fen	Reedswamp	Semi-terrestrial wetland
Closterium (60)	*Herpotrichiella* (22)	306	*Anthostomella fuegiana* (4A)
119	*Clasterosporium* (25)	708	*Coniochaeta xylariispora* (6)
120 121	*Zygnema* (58)		*Chaetomium* (7A)
Volvocaceae (128)	65		11
Spirogyra (130)	*Persociospora* (124)		*Kretzschmaria deusta* (44)
Gloeotrichia (146)	*Valsaria variospora* (140)		*Byssothecium circinans* (16C)
Tetraedon (371)	200		18
Pediastrum (760)	*Mougeotia* (313)		*Glomus* (207)
Botryococcus (766)	*Gyrotrix hermaphroditus* (353)		*Sordariaceae* (55A)
	715		*Sordariaceae* (55B)
	733		90
			92
			Cercophora (112)
			Coniochaeta cf. ligniaria (172)
			Podospora (368)
			731

the text. In this paper microfossil diagrams for each site show frequencies for selected individual NPP taxa that are present in substantial frequencies and are sensitive to water level, calculated as percentages of the total land pollen sum. These taxa provide an indication of water table changes, with rises in fully aquatic algal spore frequencies showing increased water depth whereas fungal spore taxa and marsh algae represent more stable semi-terrestrial or shallow marsh conditions. Four broad categories of Open Water, Marsh/Fen, Reedswamp and Semi-terrestrial Wetlands (which includes 'other' general types) are defined and the non-pollen palynomorphs (NPPs) that are characteristic of those hydrological categories, and which are shown as such on the microfossil diagrams, listed in Table 1.

Radiocarbon (AMS) dates are from Beta-Analytic, Miami, on organic sediment or on pollen (organic) residues. The latter have produced consistent results (Itzstein-Davey et al., 2007; Atahan et al., 2008) and are reliable. Alluvial sediment samples are avoided as these can produce anomalous dates (Stanley and Chen, 2000). Dating produced mostly unreliable dates at two sites, Guoxiangcun and Longnan, probably caused by old carbon effects. Dates are calibrated using OxCal4.4 and IntCal20 (Reimer et al., 2020) and calibrated age ranges are shown on the microfossil diagrams. Full details of the dates are shown in Table 2. The sites chosen for analysis are those that the authors used in previous studies of floodplain wetland history, salinity and human activity (Zong et al., 2011, 2012; Innes et al., 2014, 2019), and to which these new proxies have been applied. Together they cover the full range of wetland types in the study area. The full lithostratigraphies of the sites are shown in full in Supplementary Table S1, and those sections that correspond to the palynomorph data are numbered on each diagram and explained in the figure captions. Microfossil diagrams were constructed using TILIA (Grimm (2004).

3. Results

As explained above, the individual site results are divided into two regions: the central lowland wetlands (CW), including the area to the south of Lake Tai, and the western lake district (LD) nearer to Taihu, where many lakes of various sizes still exist despite modern reclamation (Chen et al. 2008; Cui et al., 2013; Xie et al., 2017; Hou et al., 2020). Sites in these regions are shown on Table 1. On the microfossil diagrams the selected taxa are grouped into the four wetland palaeoenvironmental categories defined in the Methods section. Although it is acknowledged that taxa might occur in more than one category, each will have a favoured aquatic niche into which they can be placed. More of the analysed sites occur in the lake district region. The locations of the nine sites are shown on Fig. 1. Although chronological control at Guoxiangcun and Longnan is very poor, the sites are still included as the main aim of this paper is to test the viability of the wetland NPP methodology for reconstructing water level movements and so the records from these two sites remain valuable.

3.1. Guoyuancun (CW) 121°14′00″E 31°12′03″N

The Guoyuancun profile (Fig. 2) is located in the centre of the central lowlands to the east of Taihu, midway between the chenier ridges to the east and the 'lake district' to the west. Its ground altitude is 1.7 m YSD (Yellow Sea Datum: Yang and Min, 2023). Its lithology unit 1 is a green-grey clayey mud with occasional plant roots, and through most of the unit the microfossil curves are very uniform, with almost no fluctuations in frequency. There are virtually no records for semi-terrestrial NPPs and open water algae dominate the assemblage, although shallower water marsh-reedswamp taxa are also present in substantial frequencies, mainly *Zygnema* (HdV-58) and HdV-708 (van Geel, 1976; van Geel and Grenfell, 1996; Medeanic, 2006). There seems to have been little variability in water depth during this stable phase. Later in this lower unit there is some change, with first *Pediastrum* (HdV-760) and then *Gloeotrichia* (HdV-146) fading from the assemblage, while *Typha* pollen

Table 2
Details of radiocarbon dating from the Taihu lowland sites that are used in this paper. Calibrated age ranges are shown on the microfossil diagrams. Dates were calibrated using OxCal4.4 and IntCal20 (Reimer et al., 2020).

Site	Mean depth (cm)	Lab code	^{14}C date (BP)	Age range (2δ cal. BP)	Mean age (cal. BP)
Guoyuancun	70	Beta-266429	3440 ± 40	3576–3775	3675 ± 99
Guoyuancun	110	Beta-266430	3520 ± 40	3690–3901	3795 ± 105
Tianyilu	121	Beta-266436	2330 ± 40	2178–2470	2324 ± 146
Tianyilu	161	Beta-266434	2390 ± 40	2339–2695	2517 ± 178
Tianyilu	201	Beta-266439	3680 ± 40	3896–4146	4021 ± 125
Chuodun	91	Beta-245327	2000 ± 40	1827–2045	1936 ± 109
Chuodun	121	Beta-243206	3160 ± 40	3352–3446	3399 ± 47
Caoxieshan	51	Beta-245328	2960 ± 40	2994–3238	4727 ± 115
Caoxieshan	73	Beta-243338	4190 ± 40	4612–4843	3116 ± 122
Dianshan	145	Beta-443478	890 ± 30	728–906	817 ± 89
Dianshan	185	Beta-443477	1260 ± 30	1076–1282	1179 ± 103
Dianshan	245	Beta-228441	1680 ± 40	1417–1699	1558 ± 141
Dianshan	300	Beta-504811	2170 ± 30	2052–2308	2180 ± 128
Pingwang	160	Beta-255432	2700 ± 40	2749–2871	2810 ± 61
Pingwang	186	Beta-266433	4430 ± 40	4870–5280	5075 ± 205
Pingwang	226	Beta-243208	4720 ± 40	5323–5580	5451 ± 128
Pingwang	376	Beta-228442	6290 ± 50	7021–7320	7170 ± 150
Yuanjiadi	72.5	Beta-253347	3570 ± 40	3722–3979	3851 ± 129
Yuanjiadi	100	Beta-243209	5600 ± 40	6299–6481	6390 ± 91
Longnan	102.5	Beta-245330	530 ± 40	673–794	733 ± 60

increases markedly. This could be because of a fall in water level but could also have resulted from a reduction in water clarity, both algae preferring higher light levels (van Geel et al., 1989; Chmura et al., 2006). A fall in water level seems likely however, as at the start of lithology unit 2, a black-grey clayey mud, the semi-terrestrial NPPs Sordariaceae (HdV-55) and *Coniochaeta* cf. *ligniaria* (HdV-172) appear in low frequencies and *Typha* falls, although frequencies of the aquatic algal types are little changed. At the start of lithology unit 3, a brownish-grey clayey mud with plant roots, these semi-terrestrial NPPs are no longer recorded and a moderate increase in water depth is inferred, with *Zygnema* increasing most and the floating aquatic *Myriophyllum* appearing. An increase in fen-reedswamp environments seems probable, as HdV-306 appears and the small Poaceae curve rises sharply. Another fall in water level occurred in the upper part of unit 3, with semi-terrestrial NPPs returning to the assemblage. Overall, however, aquatic algae dominate the assemblage and high but fluctuating water levels seem to have characterised the profile throughout its history. Unfortunately, radiocarbon dates are not available for this profile, so these water level changes remain undated.

3.2. *Tianyilu (CW) 121°06′40″E 31°11′54″N*

The Tianyilu profile (Fig. 3) is located several kilometers to the east of Lake Dianshan. Its ground altitude is 1.9 m YSD. Its lower lithology unit is a green-grey clayey mud that indicates limnic and detrital deposition in a water body that was quite shallow, as the reedswamp NPP HdV-708 occurs and frequencies of the marsh/fen and open water types are relatively low. The shallowness is supported by the high percentages of the semi-terrestrial taxon Sordariaceae, a general decomposer of plant material, and *Coniochaeta* cf. *ligniaria*, indicating wet surface conditions just above water level close by. The black-grey sediment of lithology unit 2 suggests an increased organic input, but the microfossils indicate an increase in water depth, as the near-surface semi-terrestrial and reedswamp taxa decline sharply to be almost absent, replaced by increases in fen taxa *Zygnema* and *Mougeotia* (HdV-313) and an expansion of the open water types Volvocaceae (HdV-128), *Spirogyra* (HdV-130) and the blue-green alga *Gloeotrichia*. This rise in water depth began around 4000 cal. BP (Table 2) and continued into early lithology unit 3, a brown-grey clay, *Typha* frequencies gradually falling to low values at about 2500 cal. BP, until stable aquatic conditions are established in mid-unit 3 before about 2300 cal. BP (Table 2). A decrease in water depth occurs in the upper part of unit 3, as semi-terrestrial wetland NPPs Sordariaceae, *Coniochaeta* cf. *ligniaria* and *Cercophora* (HdV-112) return to the assemblage, the sediment becomes more organic and plant roots are present. The deeper water aquatic NPPs are reduced in frequency as the more terrestrial types rise, although the continued presence of open water taxa suggests the persistence of deeper pools at the site as part of a complex wetland topography. This late fall in water depth is unfortunately not directly dated but occurred well after c.2300 cal. BP.

3.3. *Guoxiangcun (CW) 120°49′20″E 31°15′36″N*

The Guoxiangcun profile (Fig. 4) is located in the central wetland area to the northeast of Lake Cheng Hu to the east of Lake Tai. Its ground altitude is 2.7 m YSD. A sample from 270 cm in mid-profile was dated but its age at the start of the Holocene is considered much too early, before the floodplain was established, because of hard water error, and so is discounted. The sampled profile consists of a single lithology unit 1, a blueish-grey clayey mud. In the lower part of this unit the microfossil curves vary little and it seems that a stable water level existed that was quite low, as NPPs Sordariaceae, *Cercophora* and *Coniochaeta* cf. *ligniaria* are the most abundant grouping. A waterlogged ground surface a little above water level seems likely with those taxa growing on the wetland herbaceous vegetation. That a wide range of reedswamp, marsh and open water microfossils are recorded in low frequencies, however,

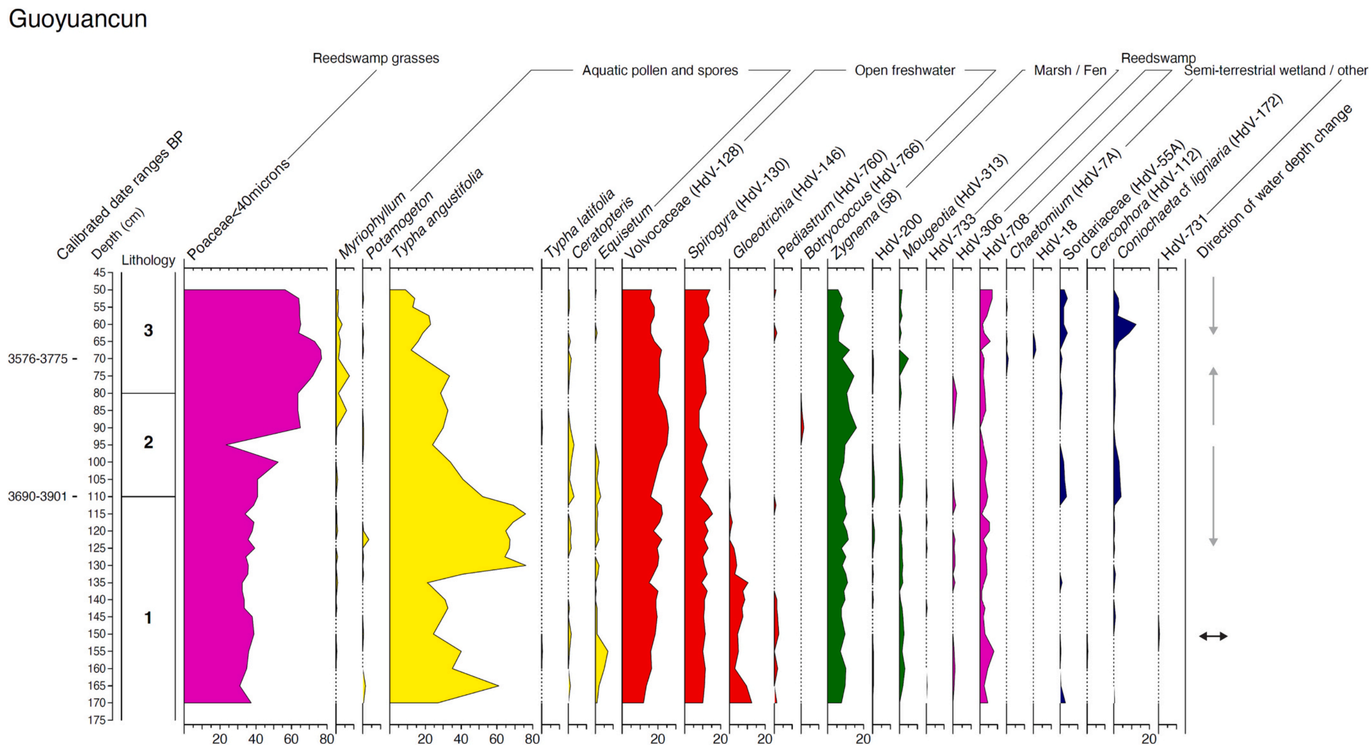

Fig. 2. Aquatic pollen, spore and NPP percentages from Guoyancun. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey clay mud with plant roots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

indicates the complex suite of aquatic environments existing at the site. A decline of *Cercophora* and increases in *Mougeotia* and *Pediastrum* indicate a modest rise in water levels to bring this stable phase to an end, with small Poaceae (*Phragmites*) and *Typha* also increasing slightly, taxa shown by observation and by DCA analysis (Zhang et al., 2019) to be often associated. Stability at this slightly higher level was re-established in mid-profile as all microfossil curves occur in moderate frequencies that do not fluctuate. Near the top of the sampled profile a renewed slow increase in water depth occurs, as the marsh taxon *Mougeotia* declines, along with *Typha*, while *Myriophyllum* is recorded and open water aquatic algae *Gloeotrichia* and *Botryococcus* (HdV-766) increase. A slight deepening of aquatic habitats seems to be recorded, although the continued presence of the full range of wetland microfossil groups suggests that changes to the wetland landscape at this site were very subtle. Diatom data (Zong et al., 2011) indicate brackish influence in the lower profile but freshwater conditions for most of it, as indicated by the algal evidence. Unfortunately, no reliable radiocarbon dates are available for this profile and the wetland history remains undated, although pollen data (Zong et al., 2011) suggests early to mid-Holocene.

3.4. Chuodun (LD) 120°50′37″E 31°24′16″N

The Chuodun profile (Fig. 5) is located at the southeastern shore of Lake Yangchen Hu to the northeast of Lake Tai. Its ground altitude is 2.5 m YSD. The lower lithology unit 1 comprises a greenish-grey clayey mud which is typical of sedimentation within a limnic-detrital depositional regime. The microfossil data support this, as there are very few records of semi-terrestrial NPP taxa, only HdV-731 and Sordariaceae being present, and then in very low percentages. A range of reedswamp, marsh and open water types dominate, with HdV-708, HdV-306, *Zygnema*, *Mougeotia*, *Spirogyra* and Volvocaceae representing these environmental groups. Conditions were very stable during this phase with water depth unchanging, as the curves for these taxa, as well as those for *Typha* and small Poaceae, hardly fluctuate. This wetland stability lasted until the start of lithology unit 2, at about 3400 cal. BP, when the deposit changes to a blackish-grey clayey mud. After this date there is a progressive fall in water depth, as open water taxa fade from the assemblage and frequencies for semi-terrestrial taxa increase greatly, mainly for Sordariaceae and *Coniochaeta* cf. *ligniaria*. A waterlogged peaty surface sediment seems likely, as *Sphagnum* spores are recorded briefly. Reedswamp, shown by high values for HdV-708, HdV-306 and small Poaceae, was the main wetland type, with some shallow marsh conditions, with *Zygnema*. A stable wetland phase with these conditions maintained occurs at the end of lithology unit 2. At about 1940 cal. BP in early lithology unit 3, a greenish-grey clayey mud, a major increase in water depth occurs, as frequencies for open water taxa Volovocaceae and *Spirogyra* rise sharply and semi-terrestrial wetland taxa fall to very low values. Reedswamp and marsh taxa percentages change little, except that HdV-306 becomes absent from the assemblage. This taxon might represent shallower areas of reedswamp, and so was adversely affected by the water depth increase, which continues to the top of the counted profile.

3.5. Caoxieshan (LD) 120°47′30″E 31°22′44″N

The Caoxieshan profile (Fig. 6) is located near the southwestern shore of Lake Yangchen Hu to the northeast of Lake Tai. Its ground altitude is 2.6 m YSD. The lower lithology unit 1 is a green-grey clayey mud that is typically of limnic-detrital origin, and it contains a range of aquatic algal microfossils. Of these, types indicative of shallow marsh-reedswamp dominate, in particular *Zygnema*, *Mougeotia* and HdV-708, supported by strong *Typha* and small Poaceae curves. Taxa likely to represent rather deeper water, Volvocaceae and *Spirogyra*, are present but only in moderate frequencies, while semi-terrestrial NPP types are almost absent. The assemblage hardly changes, suggesting the shallow water marsh-reedswamp was very stable. That wooden piles for wetland dwellings occur in this type of sediment at this site (Zong et al., 2012) indicates that people were able to live and subsist in this long-term

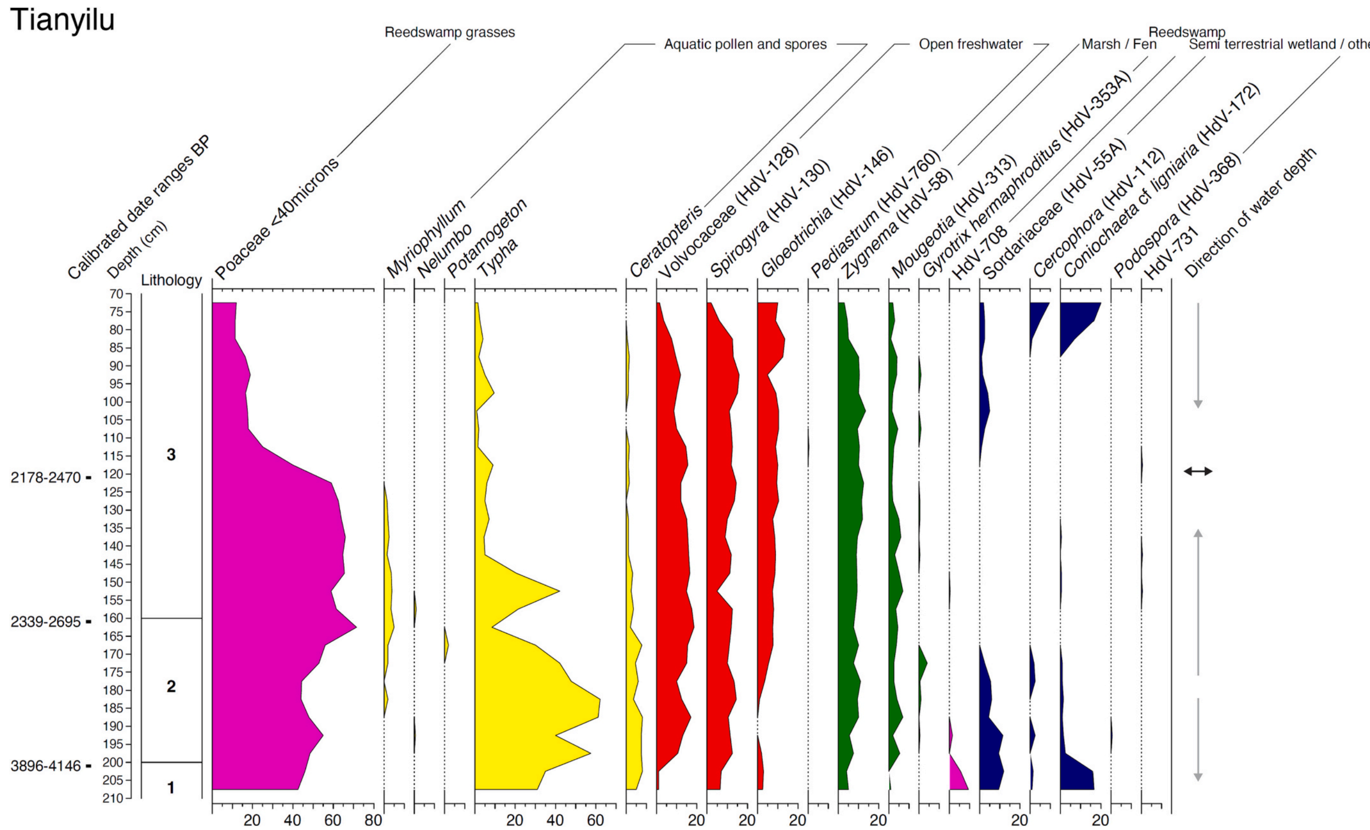

Fig. 3. Aquatic pollen, spore and NPP percentages from Tianyilu. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey silty clay mud 2. Black-grey silty clay mud 3. Brown-grey organic silty clay mud with plant roots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stable shallow wetland. At about 4700 cal. BP (Table 2) at the start of lithology unit 2 the shallow marsh indicators *Zygnema*, small Poaceae and HdV-708 decline, as does *Spirogyra*, replaced by semi-terrestrial NPPs, primarily *Coniochaeta* cf. *ligniaria* but also Sordariaceae. The aquatic *Typha* also fades from the pollen record. The lithology changes to a much more organic black clayey mud and all these indicators together indicate a fall in water depth and the emergence of a surface waterlogged organic wetland soil. At a time that can be estimated at about 4200 cal. BP (Table 2) towards the end of lithology unit 2 there was a sudden increase in water depth, as frequencies of semi-terrestrial NPPs are greatly reduced and those of the deeper water aquatic algae Volvocaceae and *Spirogyra* sharply rise. Fen-reedswamp types are still present, but a clear reversal in the direction of water depth took place. It is probable that semi-terrestrial areas were converted to fen and reedswamp while areas already under shallow water became much deeper. The switch in lithology unit 3 to a green-grey clayey mud supports this change to a much more limnic depositional environment.

3.6. Dianshan (LD) 120°59′00″E 31°05′35″N

The Dianshan profile (Fig. 7) is located at the eastern shore of Lake Dianshan. Its ground altitude is 2.0 m YSD. Full microfossil data were published by Innes et al. (2019), but NPP data are included here to inform the wider discussion. Lithology unit 1 is a grey clayey mud that transitions to a greenish-grey clayey mud in lithology unit 2. Both sediments are of limnic origin. The NPP assemblage in unit 1 is very mixed, with all ecological groupings well represented, and reflects a stable wetland environment with little change in water depth. Although the open water taxa Volvocaceae, *Gloeotrichia* and *Pediastrum* are present in high frequencies, marsh and reedswamp types *Zygnema* and HdV-708 are also common and semi-terrestrial taxa Sordariaceae and *Coniochaeta* cf. *ligniaria* are also present in high percentages. An aquatic but ecologically mixed wetland environment is indicated, presumably with local topographic highs that allowed semi-terrestrial areas to exist. After about 2200 cal. BP a gradual increase in water depth occurred and open water taxa increase, particularly *Gloeotrichia*, with HdV-121 and *Pediastrum* percentages also rising. An increase in the proportion of clear open water at the site occurred, with shallow marsh types in particular declining. Semi-terrestrial NPPs also are much reduced in this phase, with only Sordariaceae still significant under quite stable wetland conditions. In lithology unit 3, the sediment changes to a peaty mud and then to a black peat, formed at the water surface under waterlogged conditions. In this phase *Gloeotrichia* declines sharply, perhaps because of peatier, less clear water, and semi-terrestrial taxa rise, primarily Sordariaceae and HdV-92. Reedswamp taxa are the main aquatic types recorded, plus *Mougeotia* which can be common in shallow water (van Geel et al., 1981, 1989). A reversal of the former gradual increase in water depth occurred, with the water table falling and allowing organic accumulation and peat formation at the waterlogged sediment surface. A renewed increase in water depth characterises lithology unit 4, a greenish-grey limnic mud indicative of aquatic sedimentation, starting at about 1550 cal. BP. HdV-119, Volvocaceae and *Gloeotrichia* increase, as well as *Potamogeton* pollen, followed by sharp peaks in frequencies for *Botryococcus* and the blue-green alga *Aphanizomenon* (HdV-600), both likely caused by algal blooms caused by eutrophication of the aquatic environment (van Geel et al., 1994; Batten and Grenfell, 1996; Qin et al., 2013). Marsh and fen taxa also increase. Eutrophication might well have been caused by local human activity (McCarthy et al., 2018) during units 4 and 5, as Innes et al. (2019) recorded intensive rice cultivation with associated weed floras during this period between c.1550 and c.1200 cal. BP. Peaks in semi-terrestrial NPP taxa, including *Podospora* (HdV-368) and the soil erosion indicator *Glomus* (HdV-207) probably reflect

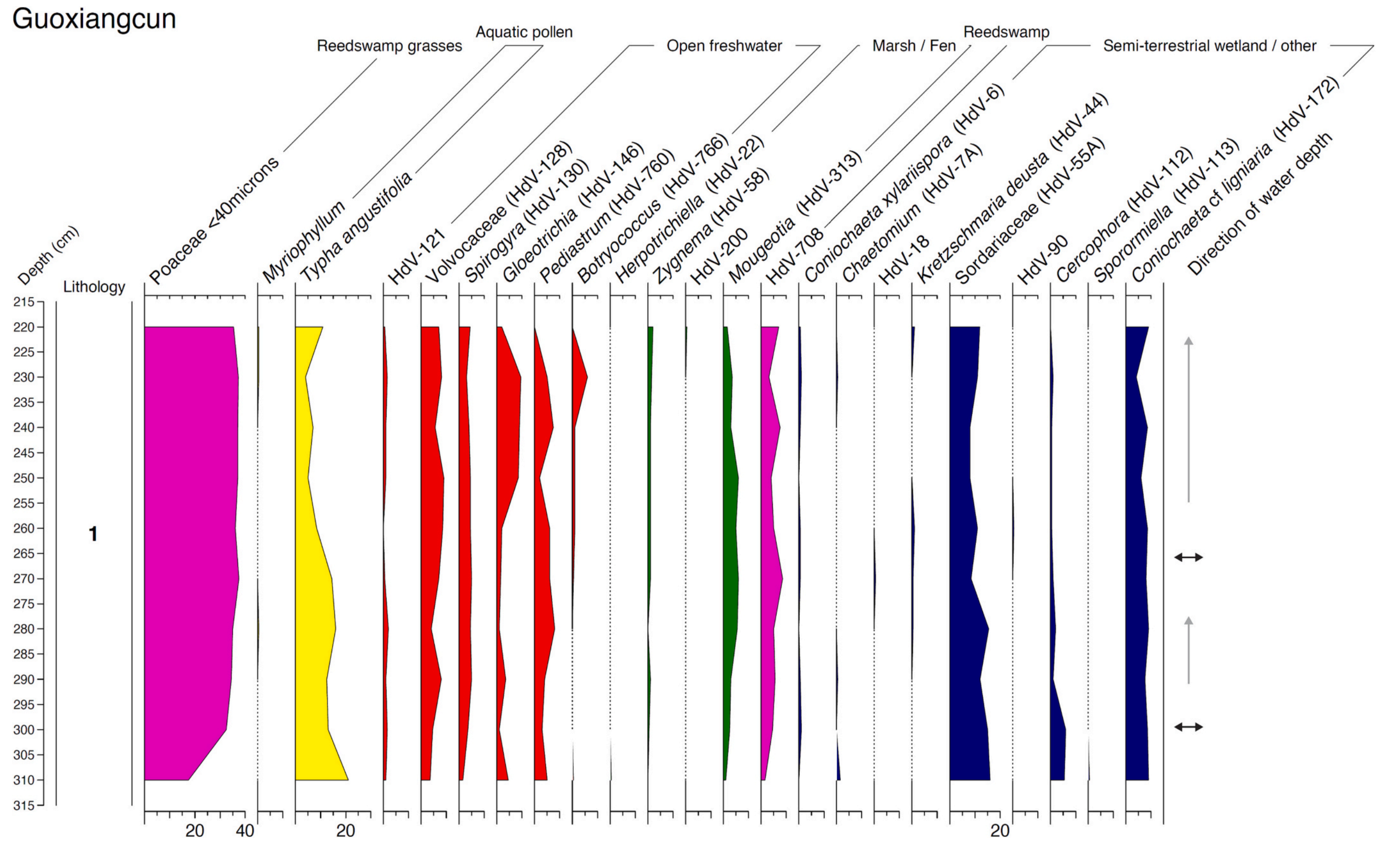

Fig. 4. Aquatic pollen, spore and NPP percentages from Guoxiangcun. NPPs are grouped according to their most probable wetland type. Litho-stratigraphic units are numbered. 1. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

the effects, including hydrological, of this human activity at Dianshan. Lithology unit 6, starting at about 1200 cal. BP, is a dark grey clayey mud and records limnic deposition and the end of the phase of human activity and cultivation, as semi-terrestrial NPPs fade from the assemblage except for Sordariaceae. Reedswamp taxa also decline later in the unit, with marsh taxa rising and then also declining. Open water algae, primarily Volvocaceae, become dominant, indicating a gradual deepening of the water at the site during unit 6.

3.7. Pingwang (LD) 120°38′25″E 30°57′30″N

The Pingwang profile (Fig. 8) is located at the southern edge of Lake Yingdou to the southeast of Lake Tai. Its ground altitude is 1.6 m YSD. Full microfossil data were published by Innes et al. (2014), but NPP data are included here to inform the wider discussion. The lowest lithology unit 1 is a blackish-brown peat, which indicates a waterlogged surface organic soil above any aquatic environments with low water levels. Semi-terrestrial NPPs, Sordariaceae, *Coniochaeta* cf. *ligniaria* and HdV-11, are present in high frequencies, probably originating on plants growing on the peat surface. Wetland NPPs are present, particularly reedswamp and shallow marsh types including HdV-708, *Zygnema* and *Mougeotia*, as well as *Typha*, indicating slightly deeper water nearby. Open water aquatic algae, however, are poorly represented. Conditions seem stable during this phase as all curves are relatively consistent. Lithology unit 2 comprises a greenish-grey clayey mud, a sediment that implies deposition in limnic-detrital conditions and deeper water. Starting at about 7200 cal. BP there was a gradual increase in water depth, as all semi-terrestrial NPPs' frequencies fall except for Sordariaceae, and those for Volvocaceae, *Spirogyra* and *Gloeotrichia* all rise. Increasingly aquatic conditions are also shown by *Potamogeton* replacing *Typha*. This deepening water trend continues and at the start of lithology unit 3, a grey organic-rich clayey mud, *Pediastrum* joins the algal assemblage, probably indicating enhanced trophic conditions (Jankovská and Komárek, 2000) and the shallow water marsh and semi-terrestrial types continue to decline. Stable wetland conditions seem to have been established in mid-unit 3, with open water taxa dominant and all curves fluctuating little. Towards the end of unit 3, at about 5450 cal. BP, *Gloeotrichia* becomes abundant, probably indicating eutrophication of the water and high light levels (van Geel et al., 1996; van Geel, 2001; Chmura et al., 2006). These conditions continued through lithology unit 4, a brownish-grey organic clayey mud, when a deep water pool and stable aquatic conditions persisted. These were maintained through lithology unit 5, a limnic greenish-grey clayey mud as might be expected under this lacustrine environment, which began about 5000 cal. BP. There are some slight indications of reducing water depth in unit 5 from about 2800 cal. BP with *Typha* and marsh and reedswamp NPPs *Zygnema*, *Mougeotia* and HdV-708 increasing, but only marginally. *Gloeotrichia* declines, perhaps because of reduced light levels in the water, to be replaced by Volvocaceae. The site was within a lacustrine environment for most of the profile, and in the mid-Holocene could perhaps have been within one of the large, shallow lakes near Taihu, which were expanding at this time (Wang et al., 2001; Wu et al., 2014).

3.8. Yuanjiadi (LD) 120°35′31″E 30°59′45″N

The Yuanjiadi profile (Fig. 9) is located southeast of Taihu amid a cluster of small shallow lakes. The lowest lithology unit 1 is a greenish-grey clayey mud that, as at many other sites, indicates limnic deposition in an aquatic environment. This is supported by the high frequencies for the open water taxa Volvocaceae and *Spirogyra*. Other wetland niche taxa do occur, including HdV-708 and *Zygnema*, usually indicating shallower water, along with *Typha* pollen and *Ceratopteris* spores, that have a similar ecology. Semi-terrestrial taxa are almost completely absent, indicating the site was covered by surface water during most of unit

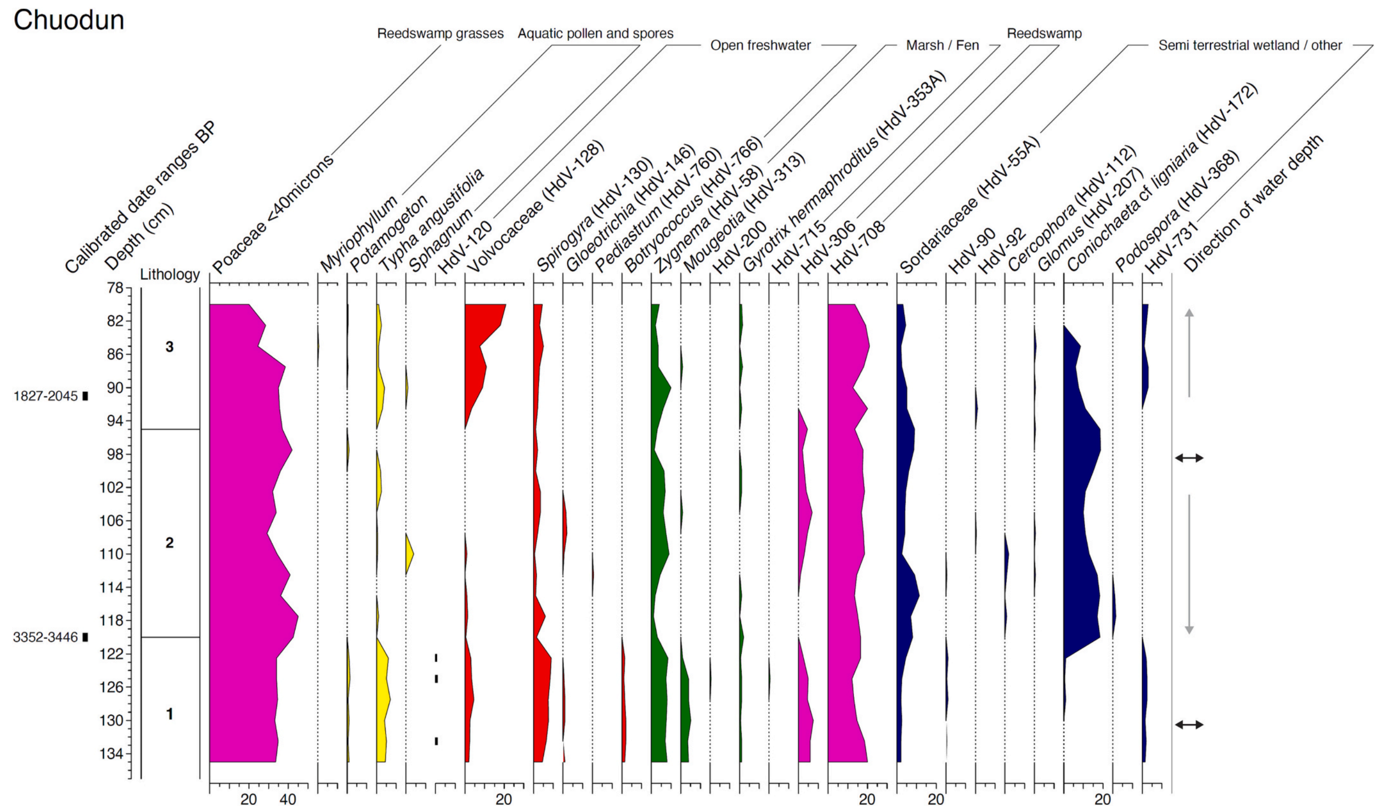

Fig. 5. Aquatic pollen, spore and NPP percentages from Chuodun. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey clay mud 2. Black-grey clay mud 3. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

1, with almost no change in the microfossil curves and so a stable wetland environment. At the end of unit 1 there are some slight indications of a water level fall, as *Zygnema* declines, culminating in the appearance of several semi-terrestrial types in lithology unit 2, a blackish-grey clayey mud, at about 6400 cal. BP. This more organic unit coincides with cultural material recorded nearby to this profile. A slight fall in water levels is indicated, as Volvocaceae and *Spirogyra* are reduced in frequency and *Typha* increases greatly, but the fluctuations in the curves are very small and the more terrestrial aspect of the assemblage fades away by the end of unit 2, when open water taxa increase again. Lithology unit 3 is a greenish-grey clayey mud, and this limnic sediment together with the microfossil changes indicates a renewed rise in the water table, with fully aquatic conditions restored, and these are maintained for the rest of the profile until about 3850 cal. BP, a period of wetland stability, during which microfossil frequencies are virtually unchanged.

3.9. Longnan (LD) 120°35′06″E 30°58′48″N

The Longnan profile (Fig. 10) is located about 10 km to the southeast of Lake Tai, has previously been studied palynologically as part of archaeological investigations (Xiao, 1991), and its ground altitude is 2.0 m YSD. The lower lithology unit at Longnan is a greenish-grey clayey mud typical of limnic and detrital sedimentation. Microfossil counts begin at the start of lithology unit 2, a blackish-grey clayey mud that is organic and suggests deposition nearer to the water surface. The NPPs include types from all the aquatic niches, from reedswamp with HdV-708 and abundant small Poaceae, through marsh/fen with *Zygnema* and *Mougeotia*, to open water with Volvocaceae and *Spirogyra*. A period of stable wetland with high water tables is indicated. Semi-terrestrial NPPs are almost absent, but just before c.730 cal. BP Sordariaceae and *Coniochaeta* cf. *ligniaria* rise sharply, mainly replacing the open water algae in the assemblage. A relative fall in water depth is indicated, with some surface waterlogged organic soils at the site, which continued for some time as algal aquatic types continue to fall, apart from HdV-120, which enters the assemblage late in this period. There is evidence of cultural activity nearby during this phase of lower water tables, taking advantage of the more accessible organic waterlogged soils. This wetland assemblage is stable near the top of lithology unit 2. During lithology unit 3, however, a return to greenish-grey clayey mud, water depth seems to have increased again, with limnic sedimentation returning. The semi-terrestrial NPPs decline, while most of the range of aquatic types increase in frequency, including reedswamp, marsh and open water taxa. *Typha* also increases, suggesting a moderate but significant increase in water depth. Although semi-terrestrial types are still present, there is a clear trend at the top of the profile towards deeper water conditions.

4. Discussion

The evidence presented above, allied to previously published data, allows a more nuanced reconstruction of changing wetland habitats and depositional environments, which will have been extremely complex (Junk et al., 1989; Zong et al., 2011; Jing et al., 2020), in the floodplain of the southern flank of the Yangtze Delta lowlands. The two lines of evidence, lithostratigraphic (sedimentary) and palynomorphic, are complementary and together allow local reconstructions of wetland history. They can also be compared in terms of their relative value as indicators of on-site wetland habitats and depositional systems. While there is an abundance of evidence from previous research regarding the Holocene sedimentary sequences of the area, there are few palaeoecological papers in which detailed NPP data, including algae, have been recorded and interpreted, other than those of the present authors in the central Taihu lowlands (Zong et al., 2012; Innes et al., 2014, 2019),

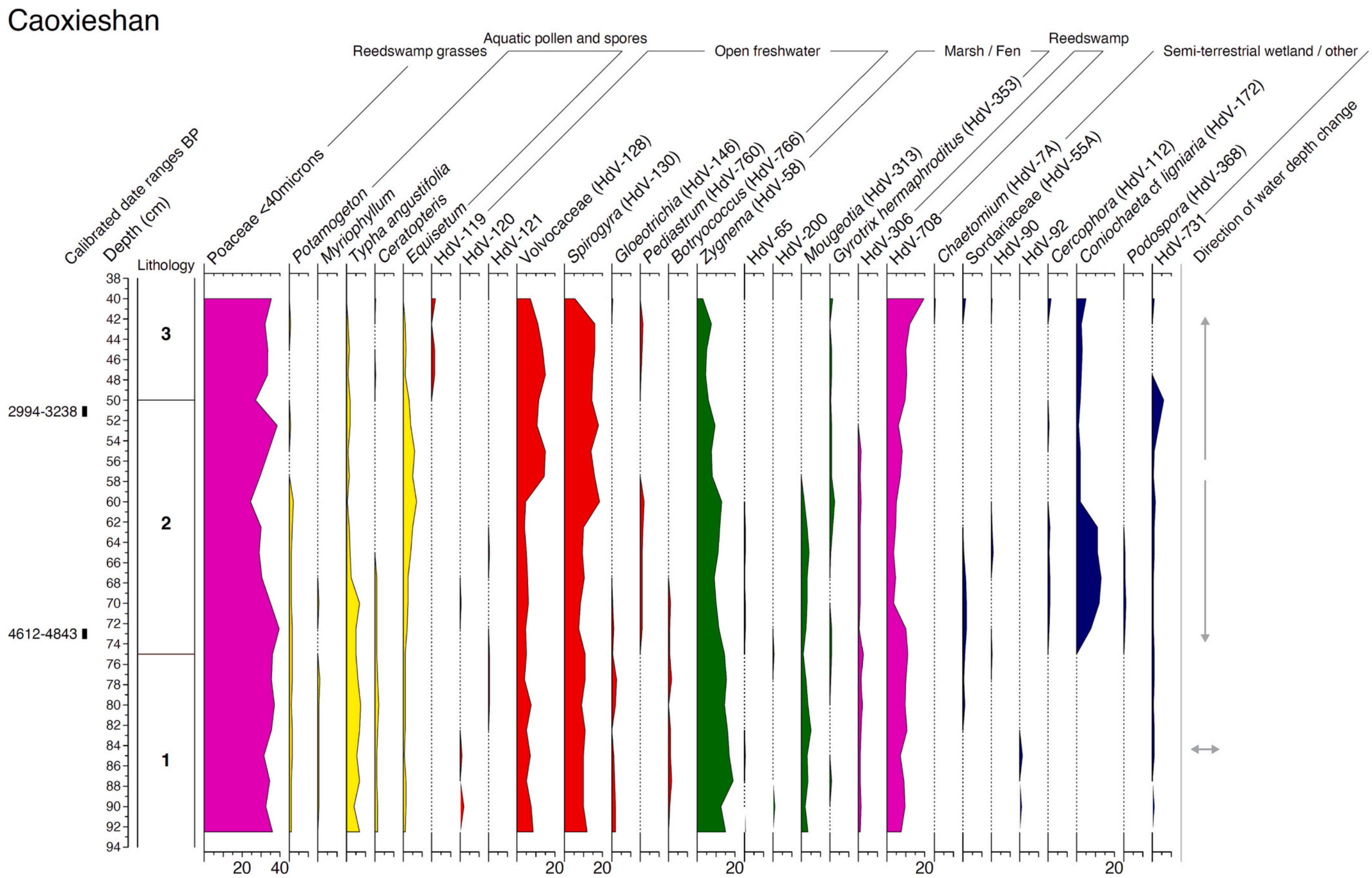

Fig. 6. Aquatic pollen, spore and NPP percentages from Caoxieshan. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey clay mud 2. Black-grey clay mud 3. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

although some grouped 'freshwater algae' curves have been published, as at Chuodun (Long et al., 2014) and YJ1503 near Jingtoushan (Liu et al., 2020b). Most of the other NPP examples are from sites on the fringes of the Taihu lowlands, well to the northeast at cores CM97 and YZ07 (Yi et al., 2006; Ye et al., 2022), to the northwest at core Zk01 (Shu et al., 2007), to the south at Kuahuqiao (Zong et al., 2007), Majiabang (Long et al., 2014) and Wujiabang (Qin et al., 2011), and in the analogous Ningshao Plain lowland south of Hangzhou Bay at Tianluoshan (Ouyang et al., 2019; Zhang et al., 2019), Luojiang (Qin et al., 2011) and Hemudu (Liu et al., 2016), although other papers in the wider region have recorded frequencies of the commoner freshwater algae, such as *Pediastrum* (Ke et al., 2023) and *Zygnema* (Liu et al., 2015). The data in this paper from the central Taihu lowland increases the spatial distribution of evidence for these important (van Geel, 2001) palaeoecological indicators.

4.1. Sedimentary evidence

The sedimentary successions at the nine study sites are shown in detail in Supplementary Table S1, and those sections that correspond to the palynomorph data are explained in the figure captions. They, and almost all of the published lithostratigraphic records from the area, are alike in recording sediments formed in standing water, limnic and detrital, with differing proportions of clastic fluvial components. Many published profiles from this area (e.g. Wang et al., 2006; Chen et al., 2018; Liu et al., 2018b; He et al., 2020; Fu et al., 2023) record similar limnic sediments as their main freshwater deposit, as almost all of the Taihu lowland plain would have been under standing water of various depths, either permanently or at least periodically, depending on factors of climate, sea level and topography (Liu et al., 2021). The limnic and detrital sediments at almost all profiles are either a greenish-grey to grey gyttja laid down in freshwater environments, shown in this paper by the high frequencies of freshwater algae but in some cases also by the presence of an entirely freshwater diatom assemblage (e.g., Chen et al., 2018; He et al., 2021), or a darker organic gyttja associated with nearby or in situ human land use, as at Tinglin and Tangcunmiao in the central lowland area (Zong et al., 2011). All these limnic gyttjas have a small clay component that probably comprises the fine-grained clastic material routinely inwashed during seasonal overbank flooding (Chen et al., 2001; Wang et al., 2006) from the main rivers, primarily the Yangtze, to which all profiles would have been subject, and which is an important factor in floodplain wetland development in many major river valleys (e.g., Muzaffar and Ahmed, 2007). The widespread reedswamp and marsh habitats would have been able to tolerate such periodic, and even prolonged, flooding (Jing et al., 2020). Sometimes, as at Dianshan and Guoyuancun, for example (Zong et al., 2012; Innes et al., 2019), in the lower Pingwang profile (Innes et al., 2014) and in several other places in the Taihu lowlands (Zhu and Zhang, 2006; Chen and Stanley, 1998; Tao et al., 2006; Itzstein-Davey et al., 2007; Qin et al., 2011; Innes and Zong, 2021), terrestrialisation proceeded and water levels fell sufficiently far so that surface peat formed instead of submerged marshland. As well as peat, deposition of much darker, organic clayey gyttjas characterises this wetland type, because of in situ vegetation growth, mostly herbaceous but sometimes swamp carr and fenwood (Innes et al., 2009). Such relative falls in water depth could often have been caused by local high sedimentation rates rather than an actual water level fall, which would have been more likely to have affected the wider area. Changes in water level caused by seasonal changes in precipitation would have been too

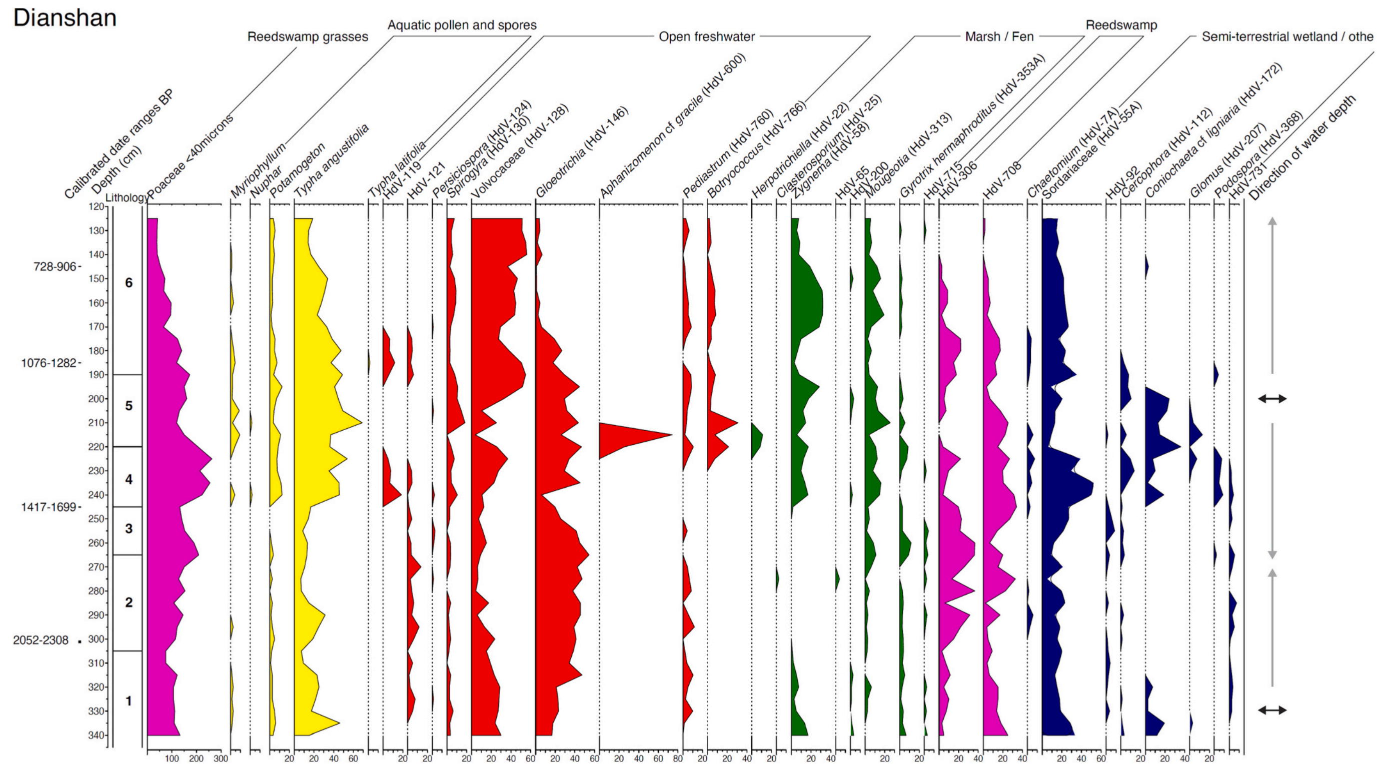

Fig. 7. Aquatic pollen, spore and NPP percentages from Dianshan. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Grey clay mud with calcium carbonate patches 2. Green-grey clay mud 3. Black peat and mud 4. Green-grey highly organic clay mud 5. Dark grey clay mud 6. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

temporary to be reflected in sedimentation, and a change in depositional regime would have required climate change and extreme fluvial flooding, such as the thick clay layers noted above several late-Neolithic sites (Zhang et al., 2004), for example at Maoshan (Zhuang et al., 2014), Caoxieshan (Zhang et al., 2004) and Qingpu (Itzstein-Davey et al., 2007), or elevated water tables and coastal floods (Wang et al., 2012; Wang et al., 2018; Zhang et al., 2022; Fu et al., 2023) initiated by sea-level rise.

4.2. Palynomorph evidence

The aquatic pollen and NPP evidence from the nine profiles is similar in showing a wide range of wetland habitats coexisting at each site and, as the NPPs in particular are not widely dispersed, represents a complex, shifting mosaic of water depths across a very small area. This is particularly the case for the profiles from the central lowland that lies between the 'lake district' near Taihu and the eastern chenier region. It indicates that at any one time the central lowland was not dominated by a particular wetland type, but was a very complex mosaic of surface peats, reedswamps, marshes, fens, swamps and deeper pools, with aquatic microhabitats of all kinds at the site scale, probably regulated by microtopographical variations in surface altitude (Raulings et al., 2010). It must have had very steep hydrological gradients, and most likely resembled a swamp-fen with small pools, shallow marsh, reedswamps and hummocks with occasional semi-terrestrial waterlogged organic soils. These peats that formed at and above the water surface must have been more common than the sedimentary evidence suggests, as the semi-terrestrial NPPs are present throughout all of the profiles, to a varying degree. Natural changes in the spatial arrangement of these wetland habitats occurred as the Holocene progressed because of sedimentation, autochthenous and allochthenous, and because of wetter climate and increased overbank flooding (Cao et al., 2011; Tian et al., 2016) or periods of higher sea level raising ground water tables (Chen et al., 1990; Zong et al., 2011). The wetland would have changed across the landscape as a whole when regional water tables rose and fell, but all wetland niches would have continued to exist although their spatial location might change (Liu et al., 2006). The central lowland area was never a uniform body of a particular wetland type, therefore, but remained a complex wetland mosaic until its drainage and reclamation in recent times (Yoshinobu, 1998; Hou et al., 2020).

Although the overall history of wetland environmental change in the Yangtze coastal floodplain is similar in the central lowlands and the area of shallow lakes nearer to Taihu, there are subtle differences between the two regions that the current research has clarified. The sites nearer to Taihu where lakes have existed since the mid-Holocene, such as Pingwang, Dianshan and Longnan, tend to have higher proportions of open water taxa, perhaps suggesting deeper water pools and even times when the site was incorporated into a lake body. Although there will not be a direct relationship between aquatic algal percentages and water depth, there seems to be a broad correlation that might assist environmental reconstruction (Medeanic et al., 2010). While lithological units can be internally uniform, changes in their contained NPP assemblages can allow inferences regarding more subtle changes in wetland conditions, so while the lithology can be interpreted as merely 'limnic and therefore an aquatic depositional regime' the NPPs can record changes in water depth, clarity and trophic status in a much more high resolution way.

4.3. Human influences on wetland history

Although natural factors have played a major role in wetland development and change in the Taihu floodplain lowlands, it is clear that since Neolithic times (Zong et al., 2012) human activities of drainage, water management, irrigation and agriculture have increasingly had an influence on the wetland systems (Jin et al., 2019; Deng et al., 2023), at least locally, just as hydrological factors such as flooding

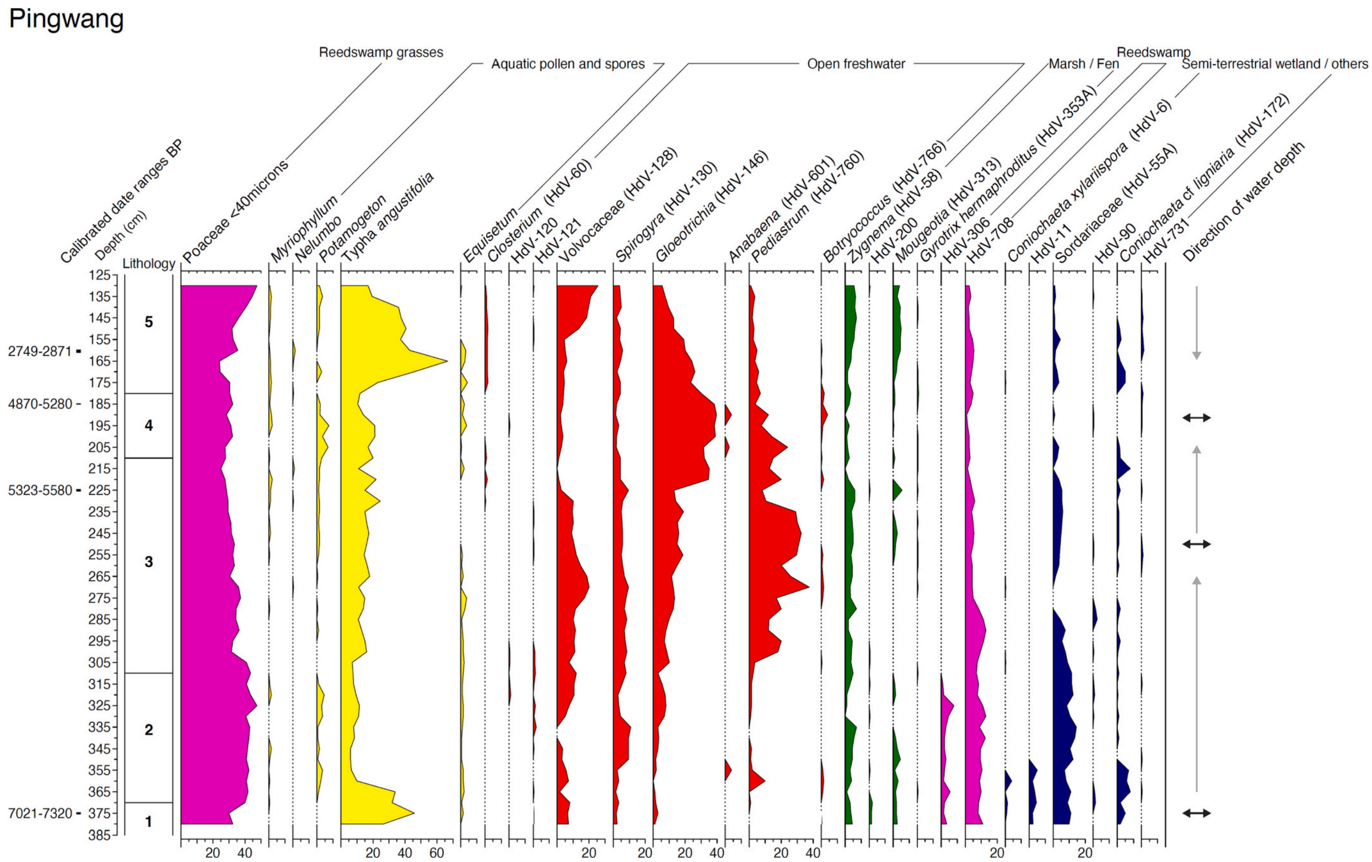

Fig. 8. Aquatic pollen, spore and NPP percentages from Pingwang. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Black-brown peat 2. Green-grey silt and clay mud 3. Dark grey organic clay mud 4. Brown-grey organic clay mud 5. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

have had impacts on human settlement and societies (Yasuda et al., 2004; Qin et al., 2011; Wu et al., 2012, 2014; Innes and Zong, 2021). Areas of deeper water, especially in the Taihu 'lake district' but also more generally, would have discouraged farming and settlement, but would have provided fish and waterfowl and other plant and animal food resources and so would have been exploited economically in other ways (Qin et al., 2010; Zhang et al., 2020b; Hsu et al., 2021), which are not reflected in the microfossil diagrams. Areas of slightly higher ground and shallow or seasonal water, especially amongst the very varied marshland topography of the central lowlands, would have allowed quite intensive land use, particularly in places where peat temporarily formed (Chen and Stanley, 1998; Tao et al., 2006; Liu et al., 2015; Innes and Zong, 2021; Dai et al., 2022), on waterlogged, semi-terrestrial surfaces, for example at Luotuodun (Deng et al., 2023) west of Taihu, DTX4, WZ05, Wujiabang and Maoshan south of Taihu (Chen et al., 2018; Qin et al., 2011; Zhuang et al., 2014; Jin et al., 2019; Fu et al., 2023), at ZX-1 (Tao et al., 2006) and Qingpu in the central lowlands (Atahan et al., 2007; Itzstein-Davey et al., 2007) and south of Hangzhou Bay (Wang et al., 2023), locations where peats are found in mid-profile. Wet rice farming in these areas of shallow water and peat soils supported high-population social and farming systems from the early Neolithic onwards (Innes et al., 2009; Qiu et al., 2020; Shao et al., 2021), at least until environmental, and especially hydrological, conditions changed, when the area became less intensively occupied, or even depopulated (Innes et al., 2014; Long et al., 2014; Yu et al., 2022). Of this paper's sites, Caoxieshan and Chuodun appear to have supported long-term settlement throughout the Neolithic (Zou et al., 2000; Qin et al., 2011), and the others, except for Pingwang, had Neolithic sites close by (Zong et al., 2012).

4.4. Drivers of hydrological change

It remains to consider the forces driving water level movements in the Taihu lowland wetlands. These will have been either local and site specific or else those affecting the wider area because of larger scale environmental forces such as climate and sea-level change. Site-specific changes tend to have been relative falls in water level, apparent at most of the study sites and elsewhere and usually associated with human settlement and cultivation, including water management (Zhuang et al., 2014), which increased vegetation cover in shallow water and waterlogged surfaces, and encouraged sedimentation which varied from site to site.

Changes in water level that affected several sites across the wider area at broadly the same time would have been driven by large scale processes, of which the one most affecting the Taihu 'lake district' and the central lowlands would have been climate change. Li et al. (2018a, 2018b) have reconstructed periods of climate change for the lower Yangtze area, identifying periods around 8.2, 6.2, 4.2, 2.8, 1.8 and 0.8 cal. BP that lasted a few centuries and during which climate sharply deteriorated, becoming colder and wetter (Park et al., 2019; Qiu et al., 2020). These periods coincided with mid- to late Holocene low amplitude transgressive fluctuations in sea level (Zong, 2004; Zong et al., 2011; Zheng et al., 2012; He et al., 2018), which elevated groundwater tables in areas beyond the direct influence of marine inundation in the very low-lying Taihu plain and exacerbated freshwater flooding effects (Zhang et al., 2004; He et al., 2018; Xu et al., 2019). These cold and wet periods, as well as some lower amplitude climatic fluctuations (Song et al., 2017; Yao et al., 2017), would have seen major flooding from the Yangtze and other floodplain rivers across the Taihu lowlands (Innes

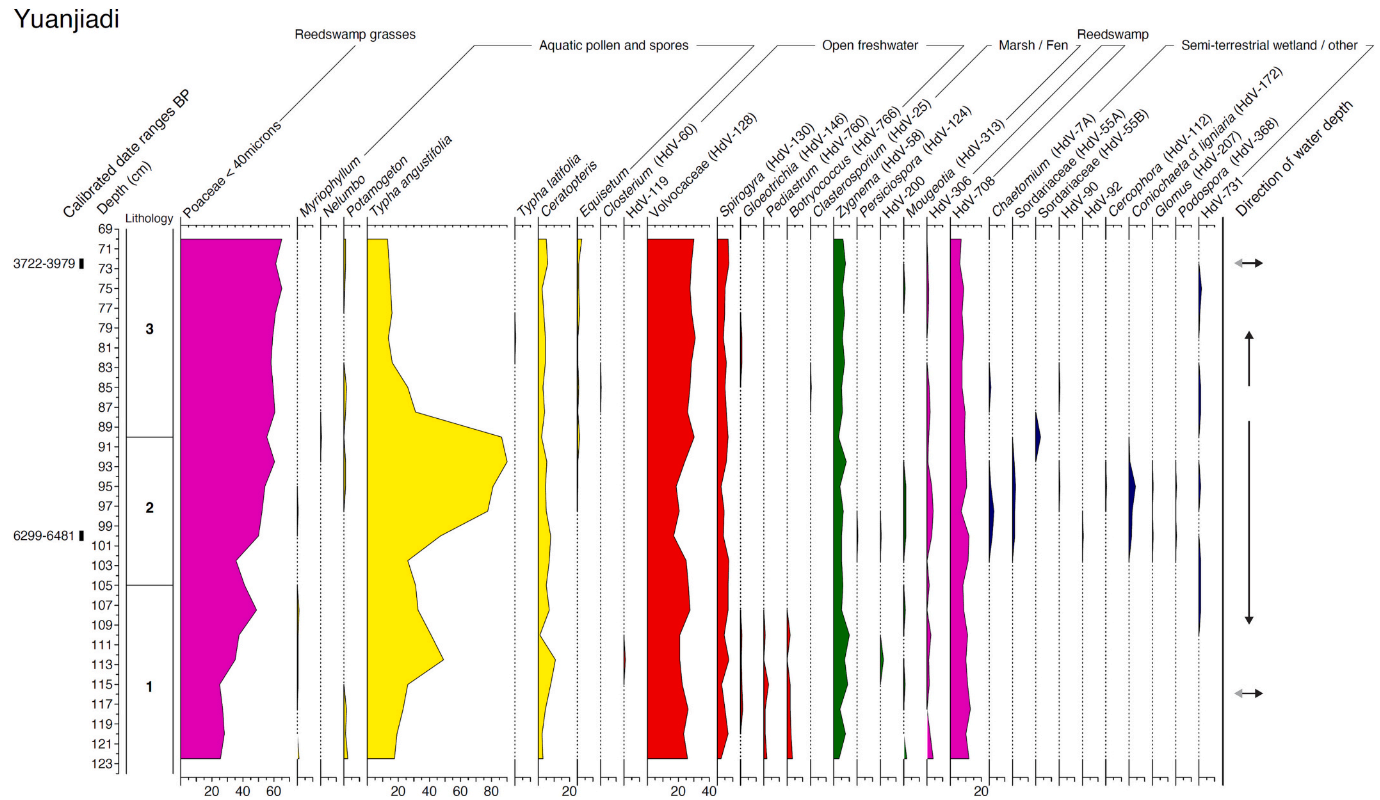

Fig. 9. Aquatic pollen, spore and NPP percentages from Yuanjiadi. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey clay mud 2. Black-grey clay mud 3. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Zong, 2021), leading to greatly increased water depth in the wetlands, the formation and expansion of lakes (Xu et al., 2019) and the widespread transformation of wetland type from reedswamp and marsh to deeper open water. One of the most intense of these climatic deteriorations was that around c.4200 cal. BP (Tao et al., 2006; Li et al., 2018a, 2018b) that caused much greater rainfall intensity and variability (Lu et al., 2019) and which caused extreme overbank flooding and the end of the Neolithic cultures of the area (Wu and Liu, 2004; Yu et al., 2005; Liu and Feng, 2012; Wu et al., 2014; Kajita et al., 2018; Ran and Chen, 2019; Sun et al., 2019). As noted above, the clearest evidence for such extreme freshwater flooding is the presence of thick clastic units at many sites, listed by Innes and Zong (2021), which must represent flood deposits. Sites with major flooding events at this time include Maoshan (Zhuang et al., 2014; Jin et al., 2019), Maqiao (Zhu et al., 1996) and XL (Liu et al., 2018a), but also at many other sites (Stanley and Chen 1996; Zhang et al., 2004). The NPP data from sites of this age in this paper agree with these climate records in showing water depth increases, with rising freshwater algal percentages, at Yuanjiadi, Chuodun and Pingwang, and maintained deep water at Guoyuancun. Several other Taihu lowland sites record flooding events at this time (Innes and Zong, 2021). The earlier 6.2 cold, wet phase (Zhu and Zhang, 2006; Li et al., 2018a, 2018b) and associated high sea level (He et al., 2018) might well have been responsible for rising water levels of that age at Pingwang, while at Yuanjiadi deep water already dominated the site. Zhu and Zhang (2006) recorded flooding of this age at Songze, near Qingpu. Of the later cold and wet climate phases, Caoxieshan and Tianyilu record increased water depth around the 2.8 cal. BP climate change, Chuodun, and Dianshan NPPs show an increase in water depth that corresponds to the 1.8 cal. BP deterioration, while Xiao (1991) noted a flooding event of this age at Longnan, as did Mao et al. (2008) at Shangshan. Dianshan records rising water levels late in the profile that occur at the time of the 0.8 cal. BP cold, wet phase, and Zheng et al. (2006) recorded flooding at other sites at this time. At all of the study sites in periods of warmer or at least more stable climate between these cold and wet climate phases, the NPP data indicate falls in water depth and reedswamp/peat formation, often with increased human settlement and cultivation (Revelles et al., 2016; Gauthier and Jouffroy-Bapicot, 2021) as reflected in the semi-terrestrial fungal NPP assemblage. These periods of reduced water depth match the data for peat formation listed by Innes and Zong (2021) very well.

5. Conclusion

The aim of this paper was to evaluate the potential of aquatic NPPs to reconstruct wetland water depths and quality at a local site scale within the broader mosaic of marshland, in more detail than only recognising flooding events in which open water, limnic NPPs rise suddenly to dominance, useful although that is. This has been successful to a degree, so that at some sites the NPPs of a particular wetland type dominate the assemblage, indicating that type to be more characteristic of that site locality. Differences in water depth over the mid- and late Holocene between the central lowland and the Taihu 'lake district' have become apparent, with generally more limnic sediments and open freshwater algae in the western area where several lakes exist today. Future NPP research in this region should perhaps be directed towards the central lowland area, where more data are needed to inform spatial wetland reconstruction.

While the dating is of variable precision at the study sites, changes in NPP frequencies, particularly rises in open water algal taxa, seem to broadly match the regional climate record in many cases, although not all. Local factors at some sites might have masked the more regional trend. Nevertheless, it seems that NPP data can be used as a low-precision proxy for climate-driven water level changes. It is possible that sites with poor radiocarbon dating control might be assigned a

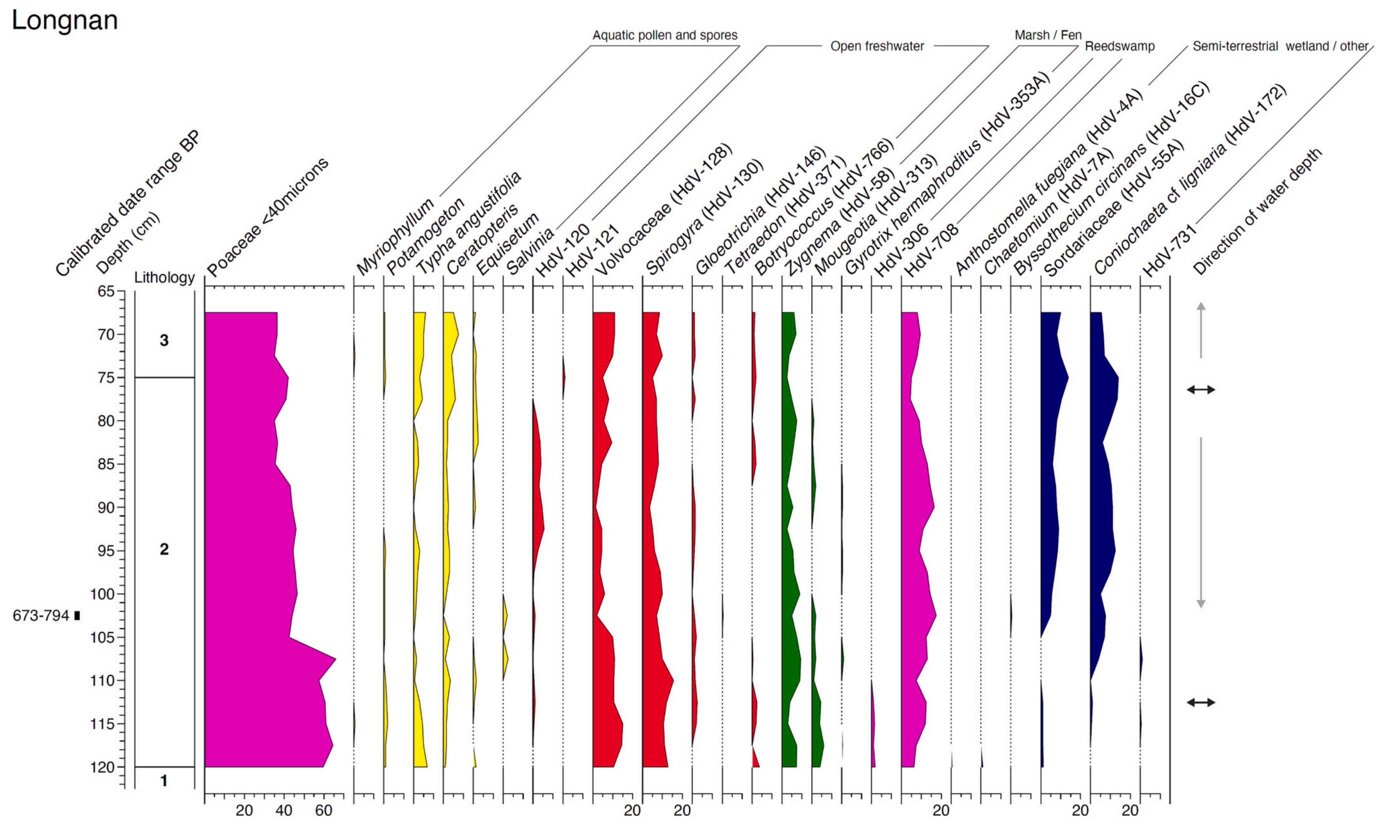

Fig. 10. Aquatic pollen, spore and NPP percentages from Longnan. NPPs are grouped according to their most probable wetland type. Age ranges are calculated using OxCal4.4 and IntCal20 (Reimer et al., 2020). Litho-stratigraphic units are numbered. 1. Green-grey organic clay mud 2. Black-grey clay mud. 3. Green-grey clay mud. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

relative age by comparison with dated records of regional water level changes at other sites across the floodplain.

All of the nine profiles contain the full range of NPP groupings so that although one type might be characteristic, all four wetland types will have been present close to the profile. While the NPP assemblage has in every case proven to be composite, therefore, all the NPPs will have originated not far from the sampling site. This has provided useful insights into the extremely complex character of the wetland, previously known only in general terms.

While knowledge of neoecology and inferences from palaeoenvironmental records allow NPPs to be categorised as broadly indicative of particular wetland types, it is clear that their ecological tolerances are quite wide, so that individual types are not exclusive to those wetland niches but would have been present across a range of trophic and water depth situations. Precise attribution to a distinct aquatic niche is therefore not possible, although factors such as eutrophication can be inferred from the algal record with a degree of confidence. As has been noted in other NPP studies of floodplain and fluvial channel wetlands (e.g., Miola et al., 2006; Innes et al., 2014; Ejarque et al., 2015; Zhao et al., 2022), only niches that are not fully submerged have distinct NPP assemblages, the semi-terrestrial grouping on Table 1, which is usually associated with human activity (Gauthier and Jouffroy-Bapicot, 2021), people taking advantage of the very shallow or surface wetland sediment to settle and cultivate, as seen at many sites in the area (e.g., Zong et al., 2007). Sites that are more submerged, to whatever depth, will have a mixed assemblage of aquatic NPP types. It is acceptable, however, to infer water depth and trophic status by the relative abundance of individual taxa and ecological groupings within the mixed assemblage, although with a low level of precision and data should not be overinterpreted.

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CRediT authorship contribution statement

J.B. Innes: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Y. Zong:** Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that there are no competing financial or other interests regarding this paper.

Data availability

Data are available from the corresponding author upon request.

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