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Dynamic Interaction Between Deforestation and Rice Cultivation During the Holocene in the Lower Yangtze River, China

Keyang He[1], Houyuan Lu[1,2,3]*, Guoping Sun[4], Yonglei Wang[4], Yunfei Zheng[4], Hongbo Zheng[5], Shao Lei[6], Yongning Li[6] and Jianping Zhang[1,2]*

[1]Key Laboratory of Cenozoic Geology and Environment, Institute of Geology and Geophysics, Chinese Academy of Sciences, Beijing, China, [2]Innovation Academy for Earth Science, Chinese Academy of Sciences, Beijing, China, [3]College of Earth and Planetary Sciences, University of Chinese Academy of Sciences, Beijing, China, [4]Zhejiang Provincial Institute of Cultural Relics and Archaeology, Hangzhou, China, [5]Earth System Science Research Center, Yunnan University, Kunming, China, [6]Ningbo Municipal Institute of Cultural Relics and Archaeology, Ningbo, China

Human activity has transformed the Earth's landscapes pervasively for thousands of years, and the most important anthropogenic alteration was the clearing of forests and the establishment of agriculture. As a center of rice domestication and early population growth, the lower Yangtze River has been extensively transformed in the Holocene. However, the timing, extent, and process of deforestation and its relationship with the intensification of rice cultivation remain controversial. Here, four representative archaeological sites ranging from 8,100 to 4,300 cal a BP, that is, Jingtoushan, Hemudu, Yushan, and Xiawangdu sites, were selected for detailed palynological analysis, and evidence of anthropogenic deforestation and subsistence strategy were also synthesized to investigate dynamic human–forest interaction. Although natural vegetation had already been altered at the Jingtoushan site around 8,000 cal a BP, it was more likely to be the management of acorns by limiting burning to open habitats and increasing yield. As the subsistence shifted from acorn exploitation toward rice cultivation after 6,000 cal a BP, real deforestation for agriculture may occur at the Yushan and Xiawangdu sites due to conflict on labor input and land use. However, these deforestations were just confined to the archaeological sites at local scale, and no consistent vegetation change occurred at regional scales induced by human activities until the last 3,000 years.

Keywords: deforestation, rice cultivation, Jingtoushan, palynological analysis, lower Yangtze River

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Edited by:
Ying Guan,
Institute of Vertebrate Paleontology and Paleoanthropology (CAS), China

Reviewed by:
Xinying Zhou,
Institute of Vertebrate Paleontology and Paleoanthropology (CAS), China
Li Wu,
Anhui Normal University, China

Correspondence:
Keyang He
hekeyang1991@163.com
Houyuan Lu
houyuanlu@mail.iggcas.ac.cn

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INTRODUCTION

Human activity has altered the Earth's system pervasively by transforming landscapes, changing vegetational biodiversity, and altering atmospheric composition (Olofsson and Hickler, 2008; Ruddiman et al., 2015; Mottl et al., 2021). Global land-use modeling and ArchaeoGLOBE synthesis revealed that agriculture and pastoralism had become extensive since 6,000 cal a BP, and largely transformed the planet by 3,000 cal a BP (Kaplan et al., 2011; Stephens et al., 2019). In addition, early anthropogenic hypotheses attributed the anomalous increase in atmospheric CO_2 after 7,000 cal a BP and CH_4 after 5,000 cal a BP to prehistoric deforestation and wet-rice farming, respectively (Ruddiman, 2003; Ruddiman et al., 2016). As the most important anthropogenic

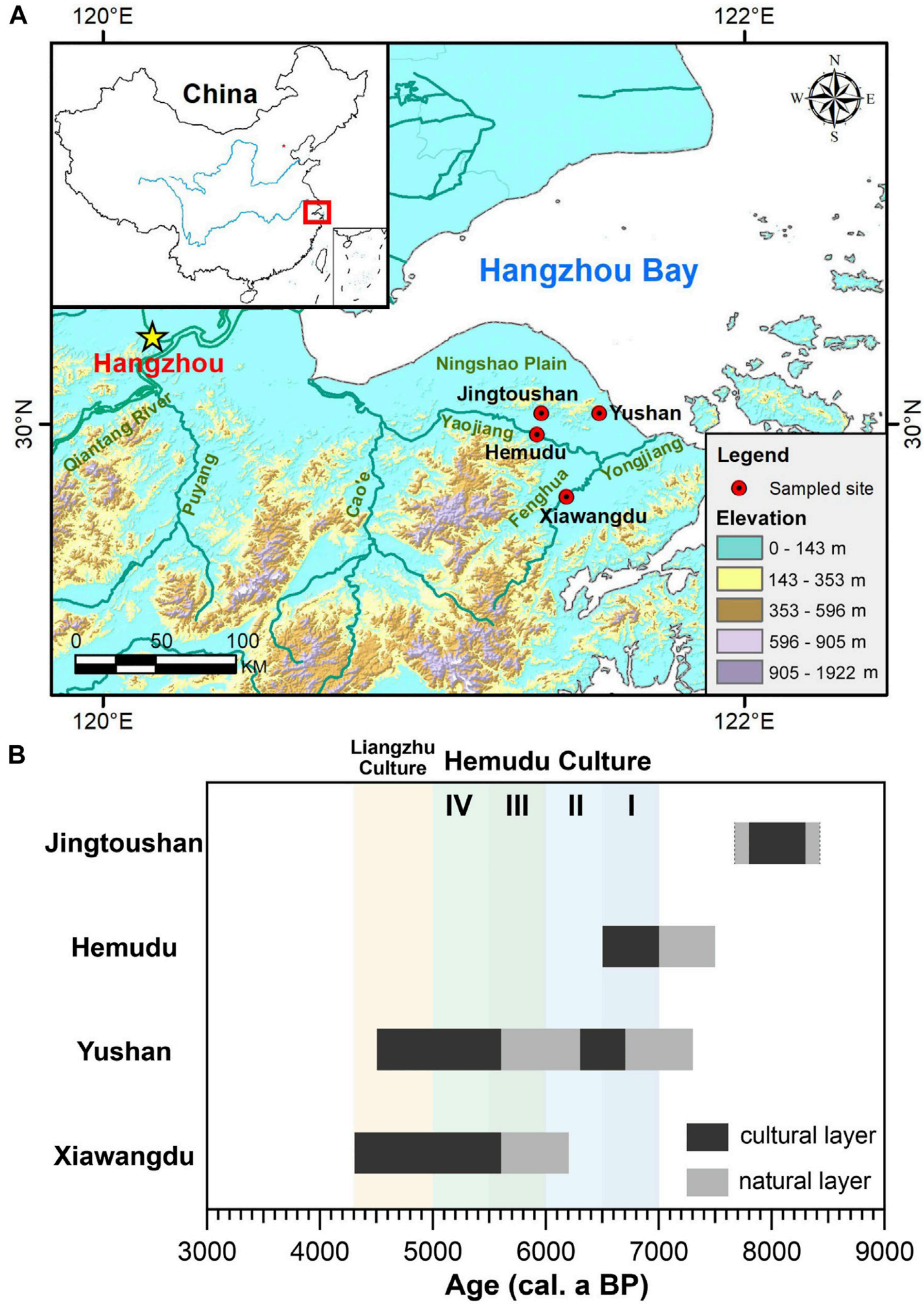

FIGURE 1 | Spatiotemporal distribution of archaeological sites sampled in this study. **(A)** Location of archaeological sites sampled. **(B)** Age range and culture sequence of archaeological sites.

alteration of the natural environment, deforestation and agriculture have been intensively debated by scientists across disciplines (Kaplan et al., 2009; Li et al., 2009).

Although China was widely recognized as a center of rice domestication and early population growth (Lu et al., 2002; Hosner et al., 2016; Zuo et al., 2017), the timing and extent of anthropogenic deforestation were still in dispute. Palynological records indicate human activities have altered the natural vegetated landscapes by deforestation in southern China since 6,000 cal a BP and resulted in a 37% decrease in forest cover in the Yangtze River (Ren, 2006; Cheng et al., 2018). In contrast, synthesis of pollen records in eastern China suggests the effects of human disturbance on vegetation may only occur at some local sites early in the Holocene and have only become an increasingly important factor during the last 2000 years (Liu and Qiu, 1994; Zhao et al., 2009). However, most of these studies have

TABLE 1 | A summary of AMS^{14}C ages from the archaeological sites sampled.

Site	Depth (cm)	Lab code	Material	^{14}C age (a BP, ±1σ)	Calibrated age (a BP, 2σ)	Reference
Jingtoushan	812	Beta412378	Plant[a]	7,150 ± 30	8,019–7,877	This study
Jingtoushan	846	Beta412377	Charcoal	7,180 ± 30	8,025–7,939	This study
Jingtoushan	866	Beta412376	Charcoal	7,210 ± 30	8,165–7,942	This study
Jingtoushan	886	Beta412375	Plant[a]	7,150 ± 30	8,019–7,877	This study
Jingtoushan	906	Beta412374	Charcoal	7,180 ± 30	8,025–7,939	This study
Jingtoushan	857	PLD26540	Fruit	7,130 ± 25	8,011–7,874	This study
Jingtoushan	870	PLD26541	Seed	7,130 ± 25	8,011–7,874	This study
Jingtoushan	887	PLD26542	Wood	7,215 ± 25	8,165–7,958	This study
Jingtoushan	820–870	BA140472	Acorn	6,820 ± 30	7,695–7,584	This study
Jingtoushan	870–920	BA140473	Charcoal	6,995 ± 30	7,932–7,735	This study
Jingtoushan	870–920	BA140474	Acorn	7,060 ± 30	7,961–7,799	This study
Hemudu	172	UGa32508	Charcoal	5,850 ± 35	6,747–6,557	He et al. (2020b)
Hemudu	227	Beta456259	Wood	6,070 ± 30	7,150–6,798	He et al. (2020b)
Hemudu	260	UGa32509	Charcoal	6,190 ± 30	7,235–6,988	He et al. (2020b)
Hemudu	275	Beta456260	Wood	6,010 ± 30	6,943–6,749	He et al. (2020b)
Hemudu	335	UGa32510	Charcoal	6,200 ± 30	7,241–6,995	He et al. (2020b)
Hemudu	484	UGa32511	Charcoal	6,520 ± 30	7,506–7,330	He et al. (2020b)
Yushan	65–70	BA151803	Plant[a]	4,040 ± 30	4,612–4,418	He et al. (2018)
Yushan	100–105	BA151804	Seed	4,365 ± 25	5,030–4,856	He et al. (2018)
Yushan	125–130	BA151805	Seed	4,300 ± 25	4,959–4,830	He et al. (2018)
Yushan	150–155	BA151806	Seed	4,525 ± 25	5,310–5,051	He et al. (2018)
Yushan	180–185	BA151807	Seed	4,785 ± 25	5,585–5,475	He et al. (2018)
Yushan	215–220	BA151808	Seed	5,495 ± 25	6,391–6,211	He et al. (2018)
Yushan	230–235	BA151809	Seed	5,665 ± 25	6,500–6,352	He et al. (2018)
Yushan	245–250	BA151810	Seed	5,860 ± 25	6,745–6,568	He et al. (2018)
Yushan	260–265	BA151811	Seed	6,225 ± 25	7,250–7,010	He et al. (2018)
Xiawangdu	40–35	UGa32514	Charcoal	4,420 ± 30	5,271–4,870	He et al. (2020a)
Xiawangdu	60–55	UGa38688	Rice seed	4,460 ± 20	5,281–4,975	He et al. (2020a)
Xiawangdu	80–75	UGa32515	Rice seed	4,570 ± 30	5,442–5,053	He et al. (2020a)
Xiawangdu	115–110	UGa38687	Rice seed	4,650 ± 20	5,463–5,315	He et al. (2020a)
Xiawangdu	140–135	UGa32516	Rice seed	5,100 ± 30	5,920–5,747	He et al. (2020a)
Xiawangdu	150–145	UGa38686	Rice seed	4,760 ± 20	5,583–5,467	He et al. (2020a)
Xiawangdu	160–155	UGa32517	Rice seed	4,850 ± 30	5,654–5,479	He et al. (2020a)
Xiawangdu	175–165	UGa38685	Rice seed	5,070 ± 20	5,902–5,746	He et al. (2020a)

[a]*Plant indicates fragments of unidentifiable plant that has not been fully charred.*

been conducted on natural sediments and have exhibited indirect signals of human activities, lacking archaeological evidence.

In the lower Yangtze River, pollen and charcoal data from the Kuahuqiao site demonstrated that alder-dominated wetland scrub or oak-pine-dominated forests had been cleared using fire by early rice-cultivators after 7,700 cal a BP (Zong et al., 2007; Innes et al., 2009; Shu et al., 2012). Nevertheless, charcoal analysis from cores near the Kuahuqiao site suggested that human-induced fires were restricted to a small geographic area with no constant large-scale slash-and-burn farming activities (Hu et al., 2020). Pollen data from paddy fields at the Tianluoshan site also suggested no evidence of slash-and-burn agriculture from 7,000 to 4,200 cal a BP (Li et al., 2012). Black carbon analysis of paddy soils from the Chuodun site further demonstrated that the fire was applied to burn crop residue rather than natural vegetation (Hu et al., 2013). Thus, whether the deforestation and slash-and-burn agriculture were adopted in the lower Yangtze River remains controversial.

To investigate the timing, extent, and process of deforestation in the lower Yangtze River and its relationship with the intensification of rice cultivation, four representative archaeological sites (i.e., Jingtoushan, Hemudu, Yushan, and Xiawangdu) (**Figure 1A**) were selected for detailed palynological analysis in this study. Furthermore, evidence of deforestation induced by human activities and the transition of subsistence strategy in this region were also synthesized to offer insight into the dynamic interaction between deforestation and rice cultivation in the Holocene.

MATERIALS AND METHODS

Study Site and Sample Collection

The four archaeological sites are located on the Ningshao Plain on the southern shore of Hangzhou Bay in eastern China (**Figure 1A**). The sequence of Neolithic cultures mainly consisted of the Hemudu Culture (7,000–5,000 cal a BP), which is generally subdivided into four periods at approximately 500-year intervals (Wang, 2000), and the Liangzhu Culture (5,000–4,300 cal a BP) (**Figure 1B**). The mean annual precipitation and temperature in this region are c.1000–1,400 mm and c.15–16°C, respectively. Regional

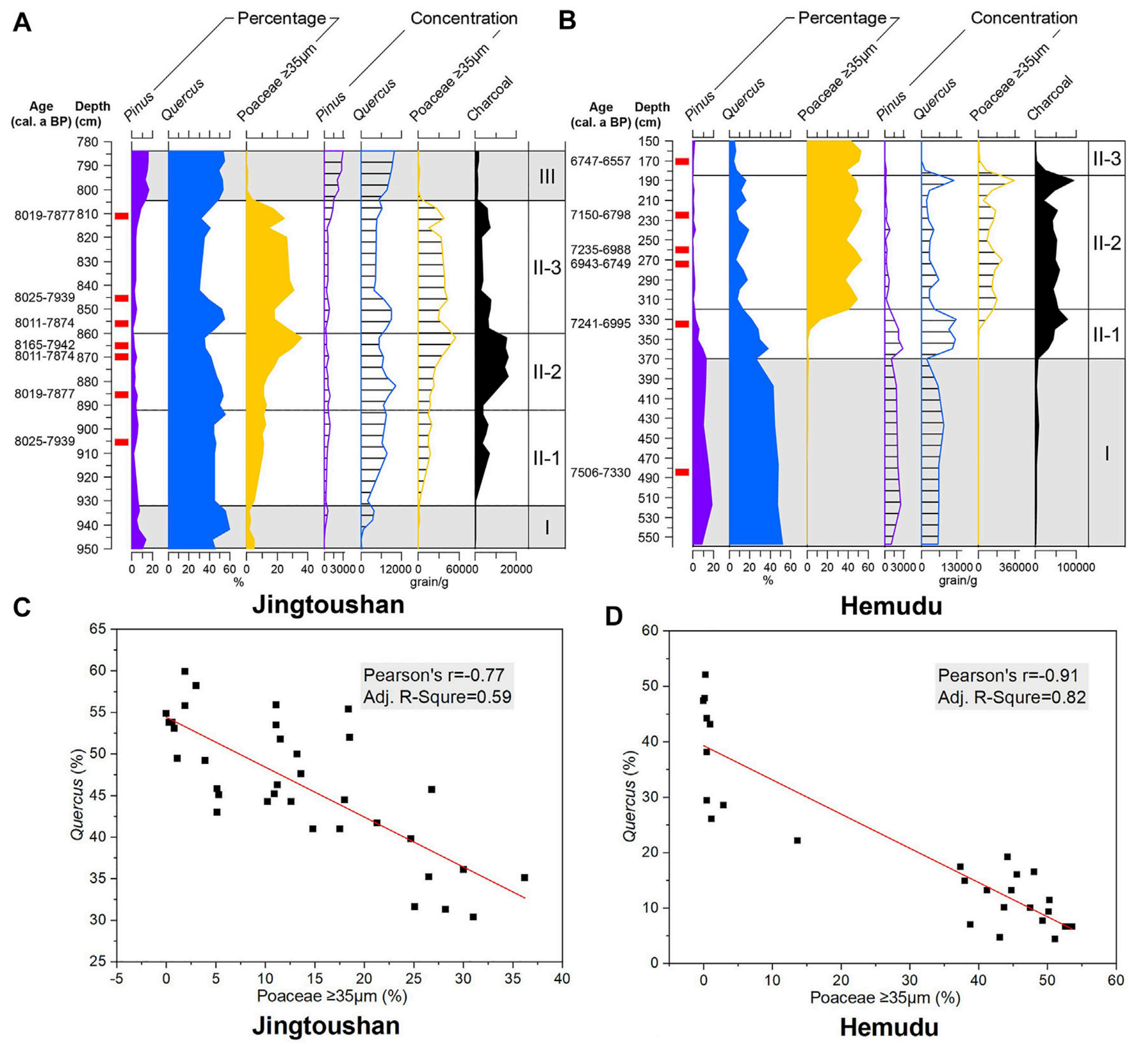

FIGURE 2 | Pollen diagram and relationship between selected taxa at the Jingtoushan and Hemudu sites. **(A,B)** Percentage and concentration pollen diagram with selected taxa. Gray horizontal bars denote the natural layers without human activities. Locations of the dating samples are shown on the right side of the depth scale by red rectangles. **(C,D)** Relationship between percentage of *Quercus* and Poaceae ≥35 μm pollen.

vegetation is under the influence of the East Asian Monsoon and is characterized by subtropical mixed forests of evergreen trees, for example, *Lithocarpus*, *Cyclobalanopsis*, and *Quercus*, and deciduous trees, for example, *Liquidambar*, *Castanea*, and *Celtis*.

Jingtoushan site (30°2′N, 121°22′E) is situated in the Yaojiang Valley, about 2.3 km west of the Tianluoshan site and 7.6 km north of the Hemudu site, with elevation of 2.5 m above local mean sea level (Zhejiang Provicial Institute of Cultural Relics and Archaeology et al., 2021). The Jingtoushan site was first discovered and drilled in 2014, and the cultural layers were about 7–8 m below the ground, which was the deepest archaeological site in the coastal region of China. Three sections of No. 4 core were selected for pollen analysis, that is, 4 h (1,020–920 cm), 4 g (920–820 cm), and 4f (820–720 cm). The cultural layer (930–805 cm) was subdivided into three layers: the silt layer (930–890 cm), the charcoal layer (890–860 cm), and the shell layer (860–805 cm), which was formed upon weathered crust and overlaid by thick marine sediments (**Supplementary Figure S1**). A total of 35 samples were collected at 4 cm intervals, including 25 samples from the cultural layer and five samples from the natural sediment layers below and above, respectively.

The Hemudu site (29°58′N, 121°21′E) is situated beside the Yaojiang River and has been excavated twice in 1973 and 1977, covering approximately 50000 m^2 (Zhejiang Provincial Institute of Relics and Archaeology, 2003). A 715-cm long core HMD1602 was retrieved from the site reservation of pile dwellings southeast of the Hemudu museum in 2016. The upper 140 cm was composed of continental and artificial layers that were not analyzed. The sediment of 370–140 cm was the Hemudu cultural layer and was sampled at 10 cm intervals. The sediment of 558–370 cm containing numerous foraminifera and marine diatoms was interpreted as a neritic layer and sampled at approximately 20 cm intervals (**Supplementary Figure S2**) (He et al., 2020b). A total of 27 samples were

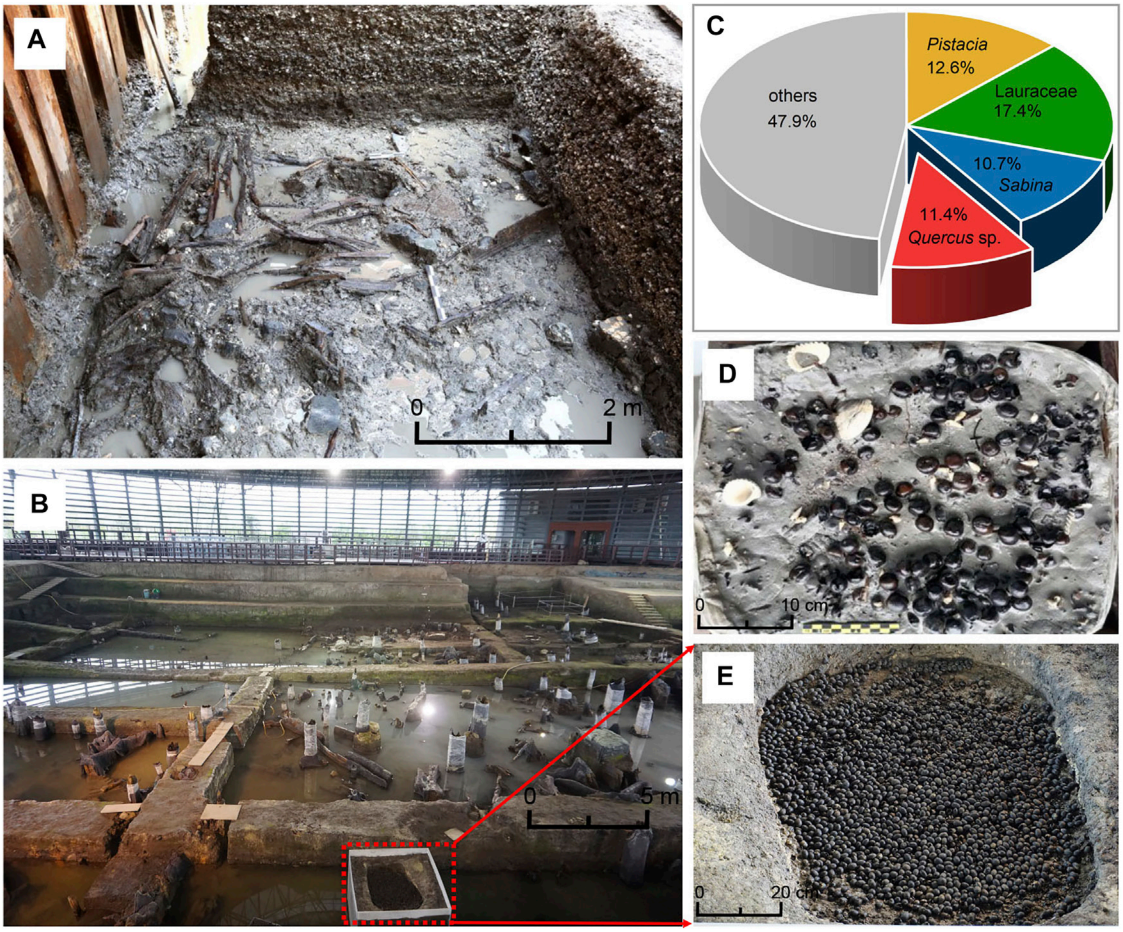

FIGURE 3 | Wooden remains and pits of acorns excavated at the Jingtoushan and Tianluoshan sites. **(A)** Wooden remains excavated below layer 17 in T508 trenches of the Jingtoushan site, including wooden handle and paddle. **(B)** Pile dwellings excavated below layer 6 at the Tianluoshan site. **(C)** Identification of tree species of archaeological woods from the Tianluoshan site (Suzuki et al., 2011). **(D,E)** Pits of acorns from the Jingtoushan (H13) and Tianluoshan sites.

collected for pollen analysis, including 17 samples from the cultural layer and 10 samples from the natural layers below.

The Yushan site (30°02′N, 121°33′E) is situated on the eastern entrance of the Yaojiang Valley, 7.3 km west to the present coastline (Ningbo Municipal Institution of Cultural Relics and Archaeology et al., 2016). The Yushan site was excavated in 2013, and a 275-cm long profile was collected from the south section of trench T0213 (**Supplementary Figure S3**). The upper 60 cm of the profile encompassed historic and modern sediment and was not sampled. The lower 215 cm was subdivided into three natural layers of marine transgression at 275–250 cm, 215–180 cm, and 120–60 cm, and two cultural layers of Hemudu Period II (250–215 cm) and Hemudu Period III-Liangzhu Culture (180–120 cm) (He et al., 2018). A total of 43 samples were collected at 5 cm intervals for pollen analysis.

The Xiawangdu site (29°46′N, 121°26′E) is situated beside the Fenghua River, which merges with Yaojiang River to form Yongjiang River at Ningbo City (Ningbo Municipal Institution of Cultural Relics and Archaeology et al., 2019). This site was excavated in 2017, and a 195-cm long profile sampled was in the west section of trench T0602 (**Supplementary Figure S4**). The upper 10 cm of the profile encompassed historic and modern sediment and was not sampled. The lower 185 cm encompassed three main units, including natural layers of marine transgression at 195–160 cm, cultural layers of Hemudu Period III—IV (160–50 cm), and Liangzhu Culture (50–10 cm) (He et al., 2020a). A total of 40 samples were collected at approximately 5 cm intervals for pollen analysis.

In total, 145 samples were collected from cores/profiles of the four archaeological sites, which were located in the core region of each archaeological site with the most complete cultural sequence and sediments, ranging from the coast to foothills in space and spanning the middle Holocene (8.2–4.2 cal ka BP) in time. Previously, pollen records of profiles from the Yushan and Xiawangdu sites have been reported (He et al., 2018; He et al., 2020a). For this study, palynological analysis of the cores at the Jingtoushan (**Supplementary Figure S5**) and Hemudu (**Supplementary Figure S6**) sites was conducted to get a full view of human–environment interaction during the whole

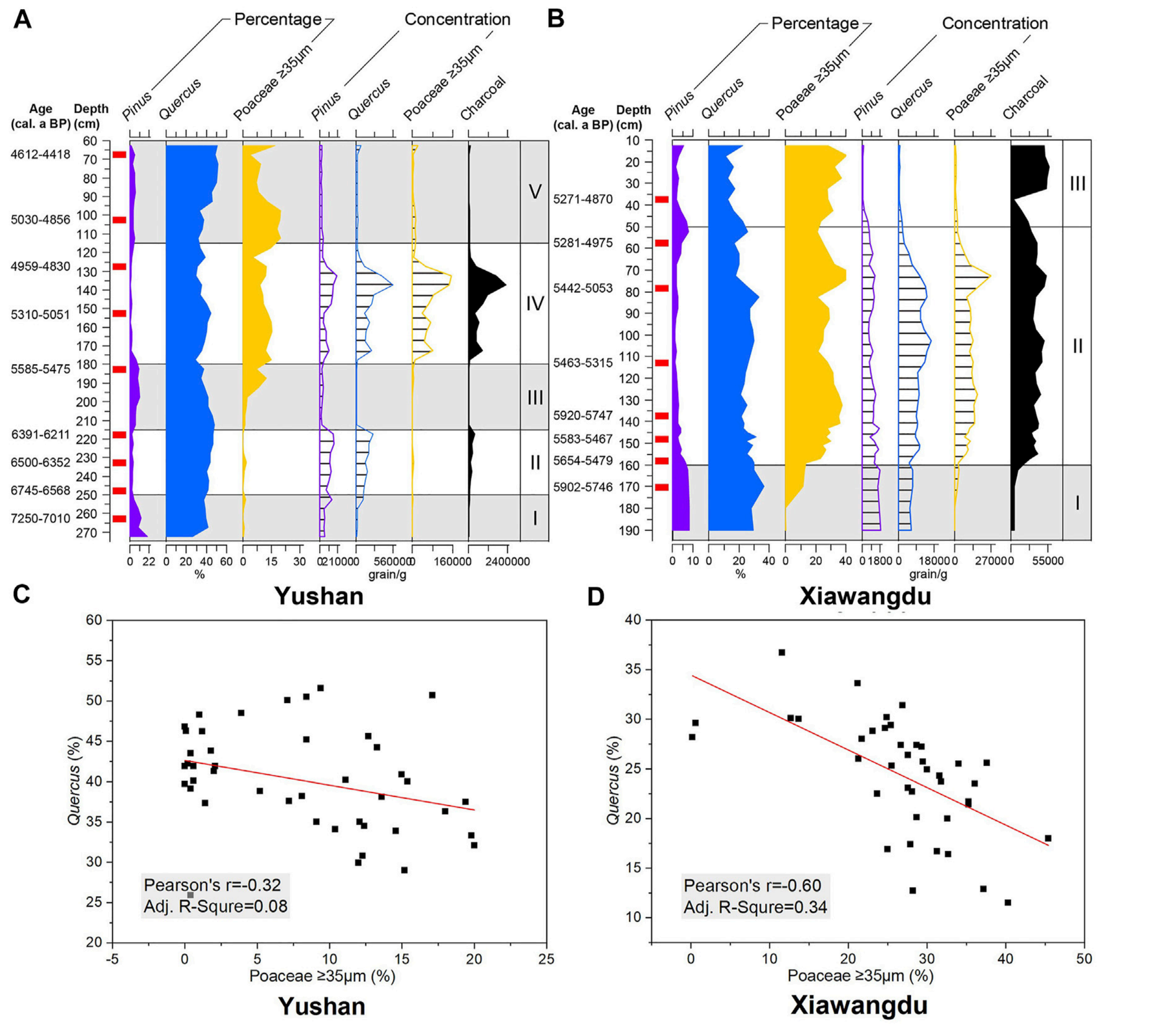

FIGURE 4 | Pollen diagram and relationship between selected taxa at the Yushan and Xiawangdu sites. **(A,B)** Percentage and concentration pollen diagram with selected taxa. Gray horizontal bars denote the natural layers without human activities. Locations of the dating samples are shown on the right side of the depth scale by red rectangles. **(C,D)** Relationship between percentage of Quercus and Poaceae ≥35 μm pollen.

middle Holocene. Each core/profile encompassed both natural (light gray) and cultural layers (dark gray) (**Figure 1B**) for further comparison of environmental change and human activities.

Radiocarbon Dating

Thirty-four samples in total were collected for dating, which have been conducted in four radiocarbon laboratories: Beta Analytic (Beta), Peking University (BA), Paleo Labo Co. (PLD), and the University of Georgia (UGa). With regard to the cores at the Jingtoushan and Hemudu sites, plants and charcoal were collected systematically during sampling; as to the profiles of the Yushan and Xiawangdu sites, samples were collected at the boundaries of each layer and screened to retrieve short-lived seeds and charcoal for dating. The radiocarbon ages were calibrated uniformly using the IntCal20 dataset with the OxCal v4.4 program (Bronk Ramsey, 2009; Reimer et al., 2020). Dates of the Jingtoushan site are first published in this study, and details of all the dates are displayed in **Table 1** and **Figures 2**, **4**.

Pollen Analysis

Two grams of each sample were weighed for pollen analysis. Pollen samples were treated according to the standard procedure developed by Moore et al. (1991), and generally, over 400 grains were counted for each sample using a Leica DM 750 microscope at ×400 magnification. Microscopic charcoal was counted on the pollen slides while identifying pollen. Identification of pollen and spores was made with reference to modern and Quaternary atlases (Institute of Botany and South China Institute of Botany, 1982; Wang et al., 1995; Tang et al., 2016). *Quercus* (oak) pollen included two categories based on the surface, tricolporoidate and size, that is, *Quercus*-deciduous and *Quercus*-evergreen (including *Cyclobalanopsis*) (Tang et al., 2018). Poaceae pollen was divided into three size categories (<35, 35–40, and

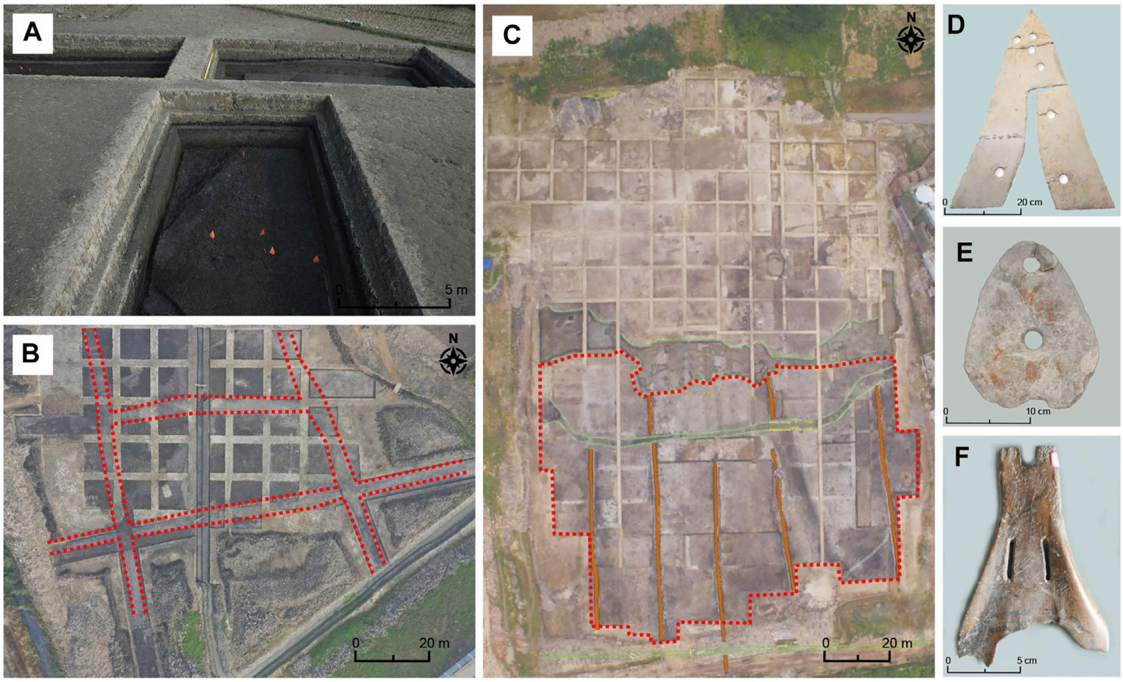

FIGURE 5 | Paddy system and farm tools excavated in the lower Yangtze River. **(A)** Paddy system in T803 and T703 trenches from the Tianluoshan site, dated 5,290 to 5,040 cal a BP (Zheng et al., 2009). **(B)** Paddy system excavated at the Shi'ao site, covering about 4,650 m^2, dated 4,900 to 4,500 cal a BP. **(C)** Paddy system excavated at the Maoshan site, covering about 55000 m^2, dated 4,700 to 4,200 cal a BP (Zhuang et al., 2014). **(D)** Split type stone plow excavated at the Maoshan site. **(E,F)** Integrative type stone plow and bone spade excavated at the Xiawangdu site.

>40 μm), and the large size category (≥35 μm) had been identified as domesticated rice pollen in the sediment of eastern China (Yang et al., 2012). Zones in the pollen diagram were divided according to the sediment and pollen assemblages using C2 software (Juggins, 2007). In addition, a correlation analysis between the percentage of *Quercus* and Poaceae ≥35 μm pollen was conducted by Origin 2021 software.

RESULTS AND DISCUSSION

Deforestation and Rice Cultivation Inside the Archaeological Sites

In this study, the terrestrial pollen assemblages of the four archaeological sites were all predominated by arboreal *Quercus* (average 20.4–46.3%) and herbaceous Poaceae (average 16.9–51.8%), and exhibited diverse patterns with time. In the natural layers of the Jingtoushan (Zones I and III) and Hemudu (Zone I) sites, the pollen diagram was dominated by the primeval vegetation of *Quercus* and *Pinus*. In contrast, the percentage of *Quercus* declined conspicuously and was progressively replaced by that of rice-type Poaceae ≥35 μm in the cultural layers of the Jingtoushan (Zone II, 8,100–7,800 cal a BP) and Hemudu (Zone II, 7,100–6,500 cal a BP) sites (**Figures 2A,B**). However, the percentages were problematic among different sedimentary facies. The decrease of *Quercus* in the cultural layer may not result from deforestation but be caused by the relative rise of Poaceae ≥35 μm instead (Li et al., 2012), which could be corroborated by the strong negative correlation between that of *Quercus* and Poaceae (**Figures 2C,D**).

In addition, the decline in the percentage of *Quercus* and the increase of charcoal in the cultural layer of the Jingtoushan (Zone II-2) and Hemudu (Zone II-1) sites may imply the management of thinning the stands of acorn using fire to harvest efficiently (Pan et al., 2017). Although large quantities of wooden remains, such as pile dwellings, had been excavated at the Jingtoushan and Tianluoshan sites (**Figures 3A, B**), only a few were identified as *Quercus* (11.4%) (**Figure 3C**) (Suzuki et al., 2011), which implied that *Quercus* may have been consciously protected for the collection and storage of acorns (**Figures 3D, E**) rather than deforestation.

In the profiles of the Yushan and Xiawangdu sites, the concentration of *Pinus*, *Quercus*, and Poaceae almost changed synchronously, implying that the relative abundance may not be affected by different sedimentary facies (**Figures 4A, B**). Moreover, the negative correlation between the percentage of *Quercus* and Poaceae was weak (**Figures 4C, D**), indicating these two pollen types change independently and the percentage could reflect the real evolution of local vegetation. In the later stages of the cultural layers of the Yushan (Zone IV, 5,600–5,000 cal a BP) and Xiawangdu (Zone II and III, 5,600–4,300 cal a BP) sites, the decline of the percentage of *Quercus* and *Pinus* coincided with the increase of that of Poaceae ≥35 μm and charcoal, suggesting deforestation of *Quercus* forest induced by the intensification of rice cultivation. Archaeobotanical research suggested that extensive paddy systems, such as Tianluoshan, Shi'ao (ca 4,650 m^2), and Maoshan sites (ca 55000 m^2) (**Figures 5A–C**) (Zheng et al., 2009; Zhuang et al., 2014), and new farm tools, such as stone plow and bone spade (**Figures 5D–F**) (Fuller et al., 2008), had been applied

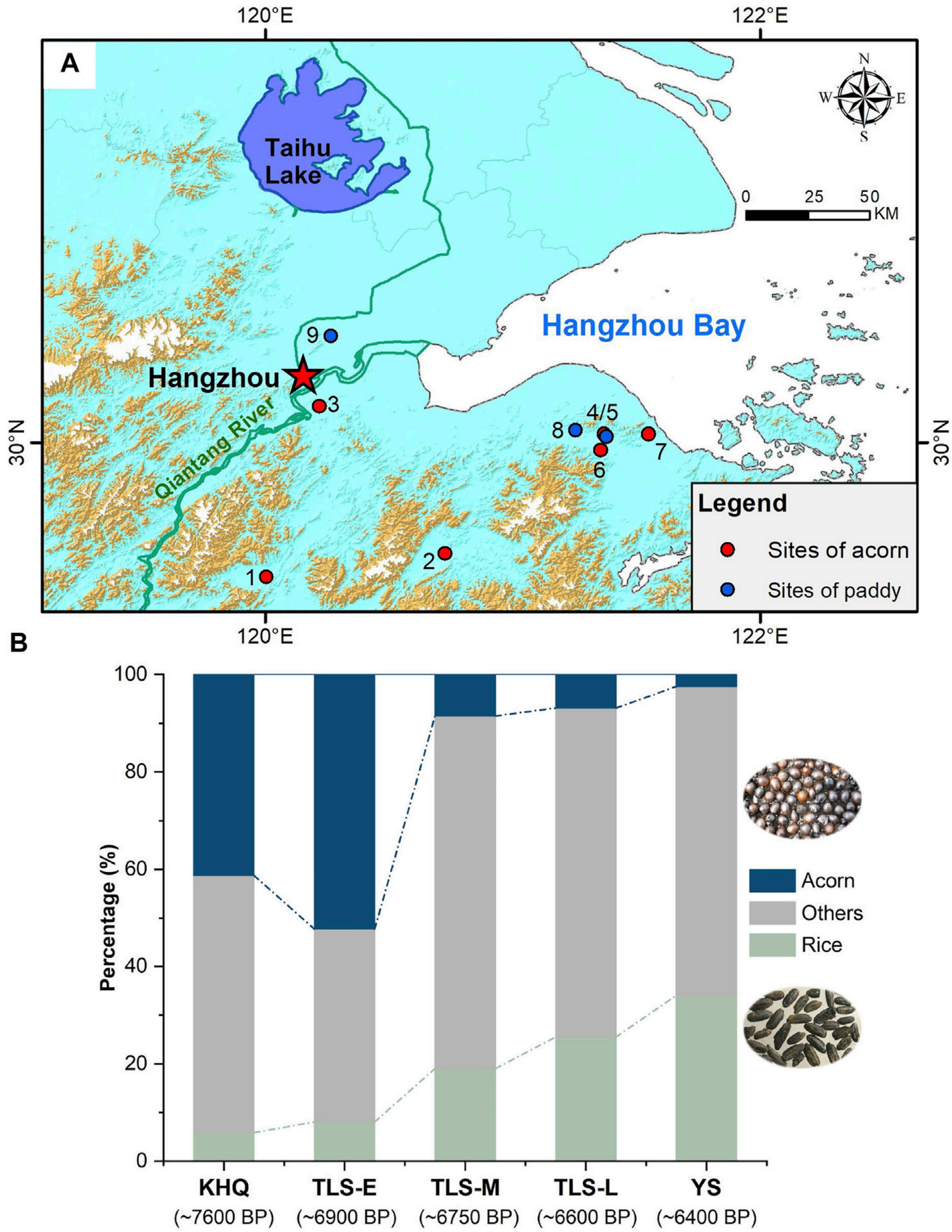

FIGURE 6 | Shift in subsistence from acorn exploitation to rice cultivation. **(A)** Location of sites with acorns (1–7) and paddy (8–9) excavated in the lower Yangtze River. 1. Shangshan, 2. Xiaohuangshan (Liu et al., 2010b), 3. Kuahuqiao, 4. Jingtoushan, 5. Tianluoshan, 6. Hemudu, 7. Yushan, 8. Shi'ao, 9. Maoshan (Zhuang et al., 2014). **(B)** Proportion of plant remains from three sites, Kuahuqiao (KHQ) (Pan, 2011), Tianluoshan (TLS) (Fuller et al., 2009), and Yushan (YS) (Zheng et al., 2019), indicating percentages of rice, acorns, and others.

since late Hemudu-Songze and Liangzhu culture, which further support the hypothesis of slash-and-burn practices due to the possible shortage of cultivated land.

Evolution of Subsistence Strategy: Acorn Exploitation vs. Rice Cultivation

Acorns are the nuts of *Quercus* sp., which are the constructive species of the subtropical mixed forests of evergreen and deciduous trees in southern China, and constitute the main arboreal component in the palynological records since the late Quaternary (Tang et al., 2018). Ethnographic and archaeological evidence suggest that acorn is a significant resource commonly consumed by Native Americans (Anderson, 2005) and recovered from prehistoric sites in Levant Upper-Palaeolithic (Barlow and Heck, 2002), Japanese Jomon (Takahashi and Hosoya, 2002), and Chinese Early-Middle Neolithic (Yang et al., 2009; Liu et al., 2010a). The earliest evidence for the exploitation of acorn in the lower Yangtze River was starch grains extracted from grinding stones of the Shangshan culture (10,000–8,500 cal a BP) (Liu

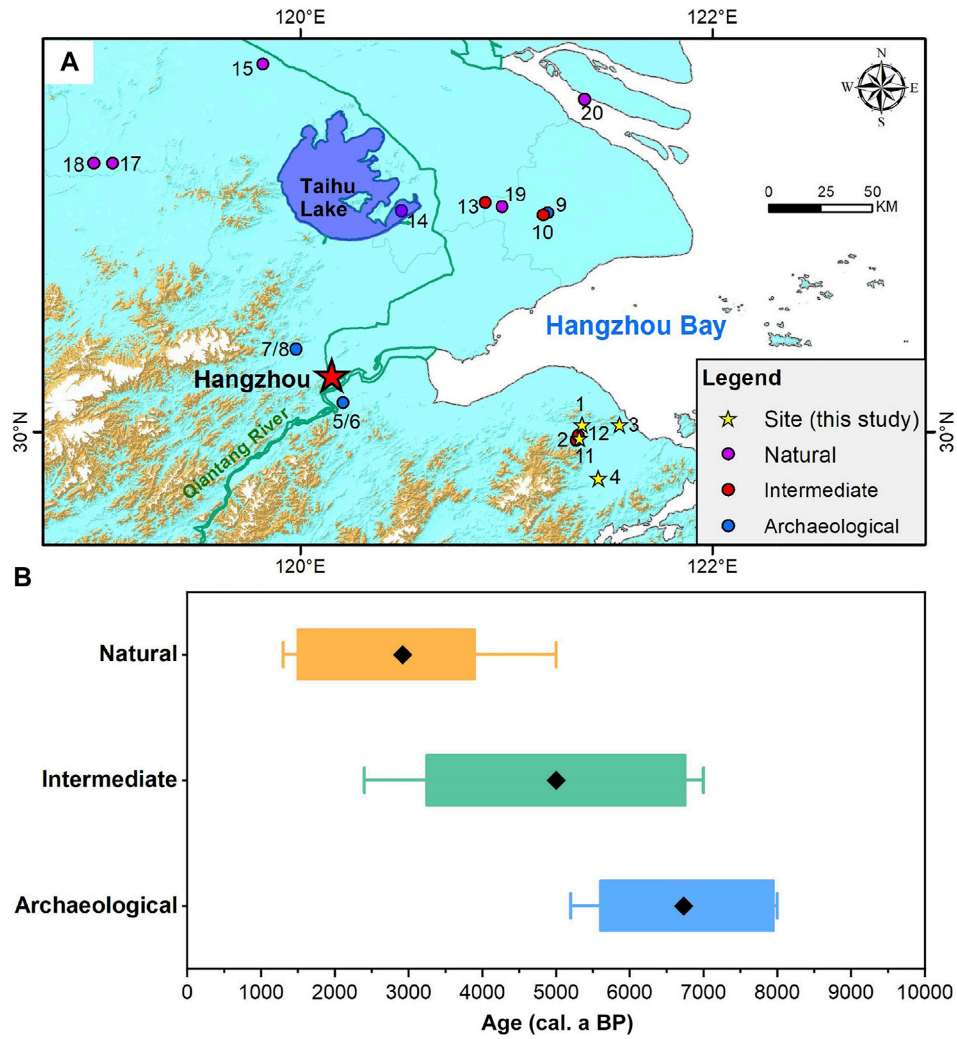

FIGURE 7 | Records of deforestation induced by human activities in the lower Yangtze River. **(A)** Location of sites with records of deforestation. **(B)** Boxplot of deforestation timing recorded in natural, intermediate, and archaeological sites. Detailed information of the sites numbered is shown in **Table 2**.

et al., 2010b; Wang and Jiang, 2021). In addition, large quantities of acorns have been excavated from the storage pits at the Kuahuqiao, Hemudu, and Tianluoshan sites (**Figure 6A**) (Zhejiang Provincial Institute of Relics and Archaeology, 2003; Fuller et al., 2011; Jiang, 2014).

Acorn is a starch-rich resource that was likely to be exploited as a staple food, predating the establishment of rice agriculture. In the early stages of rice cultivation, acorns accounted for approximately 41.2 and 52.2% of the whole plant remains at the Kuahuqiao and Tianluoshan sites (**Figure 6B**), respectively (Fuller et al., 2009; Pan, 2011). In addition, more than twenty storage pits of acorns had been recovered at the Tianluoshan site, and pieces of acorn shells had also been sieved out (Sun, 2013). Thus, in the subsistence strategy, acorn can be used as a staple food for both reserve resources and daily consumption. As a result, the *Quercus* may have been managed consciously by limiting burning to open habitats and increasing per-tree yield (Pan et al., 2017), and the decline of the concentration of *Quercus* in the cultural layer of Jingtoushan (Zone II-2, ca 8,000 cal a BP) and Hemudu (Zone II-1, ca 7,000 cal a BP) sites may have just reflected this human activity. Considering the low-level production of rice cultivation prior to 6,000 cal a BP, ancient humans may not sacrifice the resource of acorns to give way to undependable rice cultivation.

However, several factors may restrict the acorn exploitation. First, acorns are a seasonal resource, concentrated from August to October, and their annual yields vary dramatically (Pan et al., 2017). Second, acorns need special processing methods to remove tannins and an appropriate temperature and humidity during storage (Takahashi and Hosoya, 2002). Finally, a cooling trend through the middle to late Holocene may cause regional declines in oaks (Fuller and Qin, 2010). Therefore, the proportion of acorns in plant remains declined significantly to approximately 6.8 and 2.4% during the later stages of the Tianluoshan and Yushan sites, while that of rice increased progressively to 25.5 and 34.0% (**Figure 6B**), respectively (Fuller et al., 2009; Zheng et al.,

TABLE 2 | Detailed information on the start time of deforestation induced by human activities in the lower Yangtze River (see **Figure 7** for locations).

No.	Site	Start time (cal. a BP)	Category	Location Lat. (N); Long. (E)	Reference
1	Jingtoushan	8,000	Archaeological	30.03°, 121.36°	This study
2	Hemudu	7,000	Archaeological	29.96°, 121.35°	This study
3	Yushan	5,600	Archaeological	30.03°, 121.55°	This study
4	Xiawangdu	5,600	Archaeological	29.77°, 121.44°	This study
5	Kuahuqiao	7,950	Archaeological	30.14°, 120.21°	Shu et al. (2010)
6	Kuahuqiao	7,750	Archaeological	30.14°, 120.21°	Zong et al. (2007)
7	Liangzhu	5,200	Archaeological	30.4°, 119.98°	Li et al. (2010)
8	Liangzhu	4,800	Archaeological	30.4°, 119.98°	Liu et al. (2015)
9	Guangfulin	4,635	Archaeological	31.06°, 121.20°	Tang et al. (2019)
10	Guangfulin	7,000	Intermediate	31.05°, 121.18°	Itzstein-Davey et al. (2007b)
11	Hemudu	6,500	Intermediate	29.96°, 121.34°	Liu et al. (2016)
12	Luojiang	4,100	Intermediate	29.98°, 121.35°	Atahan et al. (2008)
13	Qingpu	2,400	Intermediate	31.11°, 120.9°	Itzstein-Davey et al. (2007a)
14	E2A	5,000	Natural	31.07°, 120.49°	Xu et al. (1996)
15	ZK01	3,900	Natural	31.78°, 119.82°	Shu et al. (2007)
16	ACN	3,750	Natural	31.53°, 117.37°	Chen et al. (2009)
17	Gaochun	3,000	Natural	31.30°, 119.09°	Yao et al. (2017)
18	Caoduntou	2000	Natural	31.30°, 119.00°	Okuda et al. (2003)
19	Dianshan	1,500	Natural	31.09°, 120.98°	Innes et al. (2019)
20	CM97	1,300	Natural	31.61°, 121.38°	Yi et al. (2003)

2019). As the subsistence economy shifts toward an increasing focus on rice, acorns may degenerate from a staple to a famine food reserve (Hosoya, 2011). The labor input and land use of rice cultivation conflicted with that of acorn exploitation, resulting in the local deforestation that is recorded at the Yushan and Xiawangdu sites.

Timing and Extent of Deforestation Induced by Human Activities

Deforestation for farming was the main type of impact on land use made by prehistoric humans on vegetation that has been detected in Europe and China since the middle Holocene (Ren, 2000; Fyfe et al., 2015; Roberts et al., 2018). The entire ecological process of human-induced deforestation could be modeled into five stages, that is, primeval vegetation, deforestation, cultivation, abandonment, and restoration, which can be reflected in the palynological records (Li et al., 2008). The pollen assemblage of anthropogenic deforestation was generally characterized by a decrease of zonal broadleaf wood (e.g., *Quercus*) and a rise of secondary pioneer trees (e.g., *Pinus*), ferns, and herbs (e.g., Poaceae), accompanied by an increase in charcoal (Zheng et al., 2004; Li et al., 2008; Xu et al., 2010). The lower Yangtze River was densely distributed with over 4,000 archaeological sites during the Neolithic and Bronze Age (Hosner et al., 2016) and was substantially transformed by humans. Based on the relative distance to the archaeological sites, palynological research works on the timing of deforestation induced by human activities can be divided into three categories: natural (>3 km), intermediate (50 m-3 km), and archaeological sites (**Figure 7A**), respectively.

The earliest signals of anthropogenic deforestation in the lower Yangtze River could be traced back to ca 8,000 and 7,700 cal a BP from the Jingtoushan and Kuahuqiao sites (**Table 2**) (Zong et al., 2007; Shu et al., 2012); however, the average and median dates of deforestation among archaeological sites were ca 7,000 cal a BP. As to the intermediate site that is situated 50–3,000 m outside the adjacent archaeological site, the timing of deforestation ranged from ca 7,000 to 3,000 cal a BP, with an average and median date of ca 5,000 cal a BP. Finally, the timing of deforestation from the natural sediments ranged from ca 4,000 to 1,500 cal a BP, which was generally later than ca 3,000 cal a BP. Significantly, the timing of deforestation decreased progressively from ca 7,000 cal a BP of the archaeological to ca 5,000 cal a BP of the intermediate site and ca 3,000 cal a BP of the natural sites at the end (**Figure 7B**).

Therefore, the synthesized pattern of pollen records in the lower Yangtze River suggested that possible anthropogenic deforestation in the middle Holocene was confined to local scales (Zhao et al., 2009), and no consistent vegetation change occurred at regional scales induced by human activities as reported previously (Ren, 2006). Instead, the main driver of regional vegetation change at the mid-late Holocene transition in eastern China may be attributed to climatic deterioration (Innes et al., 2014). In general, the effects of human disturbance on vegetation at local scales intensified gradually from archaeological to intermediate sites since the middle Holocene, and became an increasingly important factor in the vegetation of natural sites at regional scales until the last 3,000 years (Liu and Qiu, 1994; Zheng et al., 2021), which coincided with a noticeable increase in the number of archaeological sites after 3,500 cal a BP in southern China (Hosner et al., 2016).

CONCLUSION

In this study, synthesized palynological analysis was applied to the Jingtoushan, Hemudu, Yushan, and Xiawangdu sites, and shed light on the timing, extent, and process of deforestation accompanied by the intensification of rice cultivation in the lower Yangtze River. Although natural vegetation had already been altered at the Jingtoushan site around 8,000 cal a BP, it was more likely to be management of acorns by limiting burning to open habitats and increasing per-tree yield. As the subsistence economy shifted toward rice cultivation after 6,000 cal a BP, real deforestation for agriculture may happen due to conflict of acorn exploitation on labor input and land use, which was just confined to local scale inside the archaeological site. Possible synchronous deforestation that occurred in archaeological, intermediate, and natural sites at regional scales may be postponed until the last 3,000 years.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**; further inquiries can be directed to the corresponding authors.

AUTHOR CONTRIBUTIONS

HL and KH designed the research plan. GS, YZ, HZ, SL, and YL provided the archaeological samples. YW and JZ assisted in the collection and extraction of samples. KH analyzed the data and created the figures. KH and HL wrote and revised the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/feart.2022.849501/full#supplementary-material

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