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Enhanced human activity altered the late Holocene vegetation composition in subtropical East Asia

Yunping Song [a], Hai Xu [a,*], Jianghu Lan [b], Jin Zhang [a], Kang'en Zhou [a], Siwei Shi [a], Jing Wang [a], Chukun Hu [a], Jun Cheng [c], Bing Hong [d], Xinying Zhou [e]

[a] Institute of Surface-Earth System Science, School of Earth System Science, Tianjin University, Tianjin 300072, China
[b] Institute of Earth Environment, Chinese Academy of Sciences, Xi'an 710061, China
[c] Nanjing University of Information Science and Technology, Nanjing, China
[d] Institute of Geochemistry, Chinese Academy of Sciences, Guiyang 550081, China
[e] Laboratory of Human Evolution and Archeological Science, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China

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ABSTRACT

Understanding past climate and vegetation changes is essential to assessing the role of climate and human activity in dominating regional vegetation compositions. Here we show a wetting trend from mid- to late-Holocene over subtropical East Asia based on peat cellulose $\delta^{18}O$ and a compilation of other robust hydroclimatic records. Under such a wetter condition, subtropical East Asia is expected to be covered by denser forests. However, our peat pollen records, together with those of other studies, show that the vegetation composition did not follow as envisaged but changed from evergreen broad-leaved forests to more open landscapes since the late Holocene over the extended subtropical East Asia. We ascribe this dramatic vegetation shift to the contemporaneous enhanced human activities, which is further confirmed by the sharp increases in peat charcoal concentrations and the number of regional archaeological sites. Proper policies are therefore necessary to protect the regional ecology and sustainability.

1. Introduction

Human activities and climatic changes influence regional vegetation composition, but which one plays a dominant role in a certain area is still controversial. Mottl et al. (2021) pointed out that climate change was the main driving force of vegetation changes from the late Pleistocene to early Holocene, while over the past several thousand years, increases in global vegetation change rates were mainly ascribed to the impact of anthropogenic activities. In the late Holocene, the rates of vegetation change accelerated dramatically, even higher than that at the end of the Last Glacial Period (Mottl et al., 2021). Hence, it is crucial to assess the contributions of climate change and human activity to regional vegetation composition.

In subtropical East Asia, the hydroclimatic condition is favorable for vegetation growth, human activities increased largely during the late Holocene, and anthropogenic impacts play an increasingly important role in regulating regional vegetation coverages (Chen et al., 2019; Cheng et al., 2018; Li et al., 2013; Liew et al., 2006; Ma et al., 2016, 2018; Yue et al., 2015; Zhao et al., 2017; Zheng et al., 2021). The pollen and charcoal records from the Daiyun Mountain (Zhao et al., 2016, 2017), Shuizhuyang peat bog (Ma et al., 2018), Lantianyan peat bog (Ma et al., 2016), Fuzhou Basin (Yue et al., 2015), Taiwan Toushe peat bog (Chen et al., 2019; Li et al., 2013; Liew et al., 2006) all show signs of early human activities in the late Holocene. The pollen records from the northern South China Sea also suggest that human activities could have altered the natural vegetation development trends since ~6000 years ago (Cheng et al., 2018). These suggest that human activities could have overtaken the natural climate in regulating regional vegetation coverage in the late Holocene. Recently, Zheng et al. (2021) compiled 14 pollen records from lowland to mountain sites in southern China and Southeast Asia, and found that forest landscape began to fragment in some lowlands since 4000 a BP, and such fragmentations were widely spread at around 2000 a BP, with considerable areas transformed from forests into semi-open forest landscapes. Alternatively, such transformations could be caused by either stronger human activity, like intensified agriculture and deforestation (Zheng et al., 2021), or drier hydroclimatic conditions. However, at present, the subtropical East Asia hydroclimates are still not fully understood, especially during the late Holocene.

* Corresponding author.
E-mail address: xuhai@tju.edu.cn (H. Xu).

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Hydroclimatic trends in subtropical East Asia are generally recognized to be dominated by the East Asian Summer Monsoon (EASM), of which the long-term trend is shaped by northern hemisphere (NH) solar insolation. However, recent decades have witnessed a growing number of geological records indicating wetting late Holocene hydroclimatic trends over subtropical East Asia, which is obviously in contrast to the contemporary precipitation trends in typical EASM regions and NH insolation trend. For example, Xie et al. (2013) presented the record of accumulation rates of aerobic hopanoid and proposed a dry mid-Holocene and a wet late Holocene in Dajiuhu Peatland. Based on beach evidence at Lake Chenghai, Xu et al. (2020) reconstructed a long-term lake level history and found that lake level was higher in the late-Holocene than the mid-Holocene (Fig. 2g). Therefore, additional evidence is needed to confirm the natural hydroclimatic trends in subtropical East Asia and to further evaluate whether vegetation change is controlled by climate change or human activity.

In this study, we studied $\delta^{18}O_{cell}$ extracted from samples in a peat profile collected in Jiangshan Peatland (JSP) (25°46′22″N, 118°6′47″E) (see location in Fig. 1; Supp. 1 & 2). The profile was well-dated by radiocarbon dating and the results show that the peatland was developed ~5500 years ago (Fig. S4; Table S1). We also examined pollen assemblages in this profile and reconstructed the vegetation history of the past ~5500 years (see details in Supp. 3&4). Charcoal concentrations in the JSP profile were further analyzed to assess the potential impacts of human activities. Our results suggest that the regional climate became gradually wetting after ~5500 a BP (Fig. 2), but the vegetation composition did not follow the traditionally recognized "vegetation-climate" response pattern, a clear shift occurred at ~2800 a BP (Fig. 3), and the subsequently enhanced human activities largely altered regional vegetation composition (Fig. 4).

2. Late Holocene hydroclimatic change in subtropical East Asia

Plant cellulose isotopes have been widely used in paleo-hydroclimate studies (Hong et al., 2003; Roland et al., 2015; Xu et al., 2019). The peat $\delta^{18}O_{cell}$ signals derive from those in rainfall $\delta^{18}O$, which are in combination affected by rainfall amount, temperature, humidity, etc. The Jiangshan Peatland is a blanket ombrotrophic peatland, fed only by atmospheric precipitation, therefore peat $\delta^{18}O_{cell}$ is expected to capture the rainfall $\delta^{18}O$ signal. Because variations in rainfall $\delta^{18}O$ around the study areas are mainly ascribed to changes in precipitation (see details in Supp. 2), the variations in JSP $\delta^{18}O_{cell}$ are used to indicate changes in precipitation in this study. The JSP $\delta^{18}O_{cell}$ shows a decreasing long-term trend (Fig. 2b), indicating a gradually wetting trend since ~5500 a BP, which is obviously in contrast to the generally recognized EASM trends, but broadly synchronous with a large number of paleoclimate records over subtropical East Asia. For example, except for the lake-level record in Lake Chenghai (Xu et al., 2020) (Fig. 2g) and the aerobic microbial biomarker record in Dajiuhu Peatland (Xie et al., 2013) (as mentioned above), the stalagmite $IRM_{soft\text{-}flux}$ record in Heshang Cave (Fig. 2f) also indicates increased rainfall and storm frequency/strength after 3400 a BP (Zhu et al., 2017). The TOC percentages in the Daping swamp increased gradually in the late Holocene (Fig. 2e), suggesting a wetting trend (Zhong et al., 2017). In Lake Nanyi of southern China, the higher sedimentary Rb/Sr ratios imply increased late Holocene precipitation (Fig. 2c) (Liu et al., 2021). In subtropical northeastern Taiwan, the K/Rb ratios in Lake Dahu sediment, which have been documented to be closely linked to rainfall intensity, increased markedly over the past 2000 years, indicating again an increasing precipitation trend over the late Holocene (Fig. 2d) (Chen et al., 2012). These multi-proxy records of hydroclimatic changes are also similar in trends with the simulated precipitation over subtropical East Asia, as extracted from the TraCE-21 ka simulation (Fig. 2a) (Liu et al., 2014); they are also broadly consistent with the simulated spatial distribution where late Holocene is wetter than mid-Holocene (see Fig. 1b) (Liu et al., 2014).

3. Regional vegetation reconstruction

The pollen assemblages changed dramatically in the JSP area during the late Holocene (Fig. S8), reflecting an obvious shift in regional vegetation composition (see details in Supp. 3). From ~5455–3500 a BP, the arboreal pollen (AP) percentages were high (~80%) in the JSP, with a dominance of *Lithocarpus/Castanopsis* and *Quercus*-evergreen/*Cyclobalanopsis*, indicating that the study area was mainly covered with dense forest (Fig. 3; Supp. 3). The pollen records also show high AP percentages in the Daiyun Mountain (Zhao et al., 2017) (~80%), Lantianyan peat bog (~80%) (Ma et al., 2016) and Shuizhuyang peat bog (~60%) (Ma et al., 2018) (Fig. 3) at this stage. The AP/NAP (non-arboreal

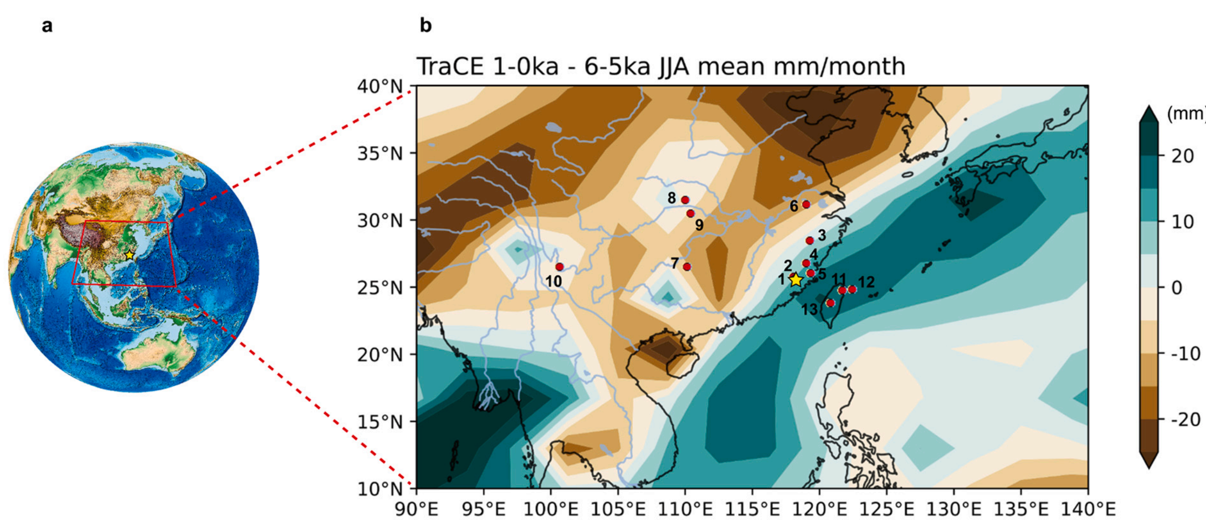

Fig. 1. **a**, Location of Jiangshan peatland (yellow asterisk), the red square sketchily shows the extent investigated in this study. **b**, difference in precipitation of June–July–August between 1–0 ka and 6–5 ka extracted from TraCE-21 ka simulations (Liu et al., 2014). The blue shades show the areas where the late Holocene is generally wetter than the mid-Holocene. Also shown are the sites mentioned in the text: (1) Jiangshan Peatland (yellow asterisk); (2) Daiyun Mountain (Zhao et al., 2017); (3) Lantianyan peat bog (Ma et al., 2016); (4) Shuizhuyang peat bog (Ma et al., 2018); (5) Fuzhou Basin (Yue et al., 2015); (6) Lake Nanyi (Liu et al., 2021); (7) Daping swamp (Zhong et al., 2017); (8) Dajiuhu peatland (Xie et al., 2013); (9) Heshang Cave (Zhu et al., 2017); (10) Lake Chenghai (Xu et al., 2020); (11) Taiwan Lake Dahu (Chen et al., 2012); (12) the South Okinawa Trough off northeastern Taiwan (Chen et al., 2019); (13) Toushe peat bog (Li et al., 2013). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

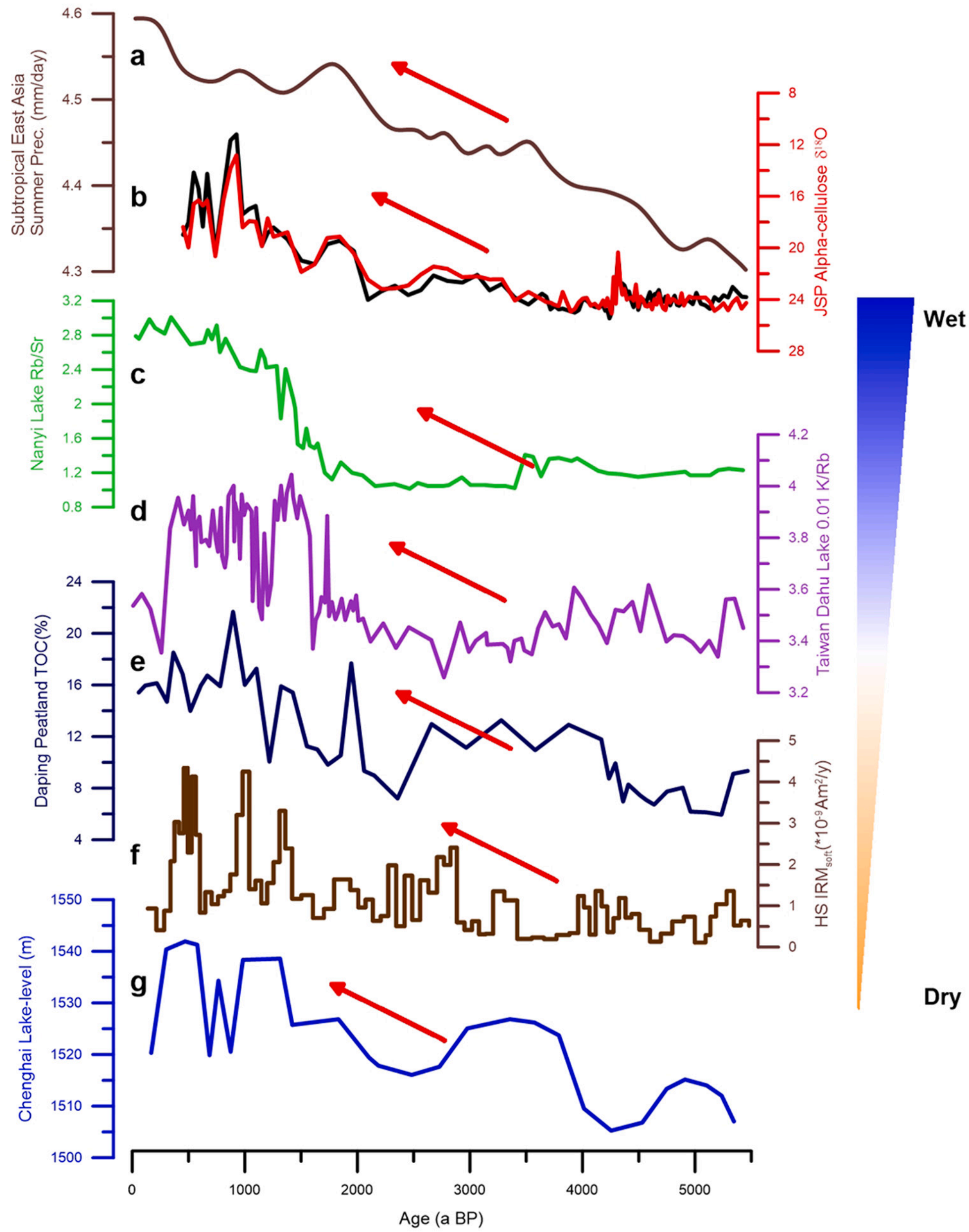

Fig. 2. Comparison between JSP alpha-cellulose $\delta^{18}O$ and other proxy indices in subtropical East Asia. a, Simulated subtropical East Asia summer (June–July-August) precipitation extracted from TraCE-21 ka simulation (Xu et al., 2020) (Liu et al., 2014). **b**, JSP alpha-cellulose $\delta^{18}O$ record (this study; red and black curves represent two independent measurements, see details in Supp.2). **c**, Lake Nanyi Rb/Sr ratio in Anhui province of southern China (Liu et al., 2021). **d**, Lake Dahu K/Rb ratio in northeastern Taiwan (Chen et al., 2012). **e**, Daping swamp total organic carbon content (TOC%) (Zhong et al., 2017). **f**, Heshang cave $ISM_{soft\text{-}flux}$ record (Zhu et al., 2017). **g**, Lake Chenghai lake-level reconstruction (Xu et al., 2020). The red arrows indicate the late Holocene wetting trends over the subtropical East Asia areas. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pollen) percentages were relatively high in the Fuzhou Basin at that time (Yue et al., 2015) (Fig. 3e). In contrast, the NAP and fern spores had relatively lower percentages (Fig. 3f, h; Supp. 3). Then, the JSP AP percentages showed a modest decrease from ~3500–2800 a BP, simultaneously the NAP and fern spore percentages began to increase (Fig. 3; Supp. 3). These changes were not obvious in the Daiyun Mountain and Shuizhuyang peat bog, but clearer in the Lantianyan peat bog and Toushe peat bog at this stage (Fig. 3). After ~2800 a BP, most of the subtropical East Asia regions experienced striking shifts in vegetation composition. The JSP pollen assemblages show a dramatical increase in NAP and fern spore percentages, especially Composite (including *Artemisia* and *Aster*), Poaceae and Trilete spores (Fig. S8). Simultaneously the AP percentages decreased further (to less than 50%), suggesting a gradually opening forest landscape in the study area (Fig. 3; Supp. 3). In the adjacent Daiyun Mountain, the Poaceae and Asteraceae pollen and fern spore percentages relatively increased, with a high proportion of *Pinus*, reflecting a more open landscape and a spread of secondary pine forests after 2450 a BP (Zhao et al., 2017). In subtropical Taiwan, the fern spore percentages also showed a similar trend in the Toushe peat bog and South Okinawa Trough off northeast Taiwan during the late Holocene (Fig. 3k, l) (Chen et al., 2019; Li et al., 2013; Liew et al., 2006). The pollen records from river deltas and coastal plains in southern China and Southeast Asia showed that AP percentages decreased to below 50% around 2000 a BP (Zheng et al., 2021). However, the timing and amplitudes of changes in pollen assemblages are slightly different between different studies, which is likely due to the variable regional topography, elevations, sampling and dating methods.

4. Human activity altered vegetation composition

As discussed above, the climate became gradually wetting in subtropical East Asia during the late Holocene. Temperature dropped slightly during the late Holocene due to decreased NH solar insolation (Marcott Shaun et al., 2013), which may lead to reduced subtropical evergreen broad-leaved taxa, such as *Lithocarpus/Castanopsis* and *Quercus*-evergreen/*Cyclobalanopsis*, but increases in the deciduous and

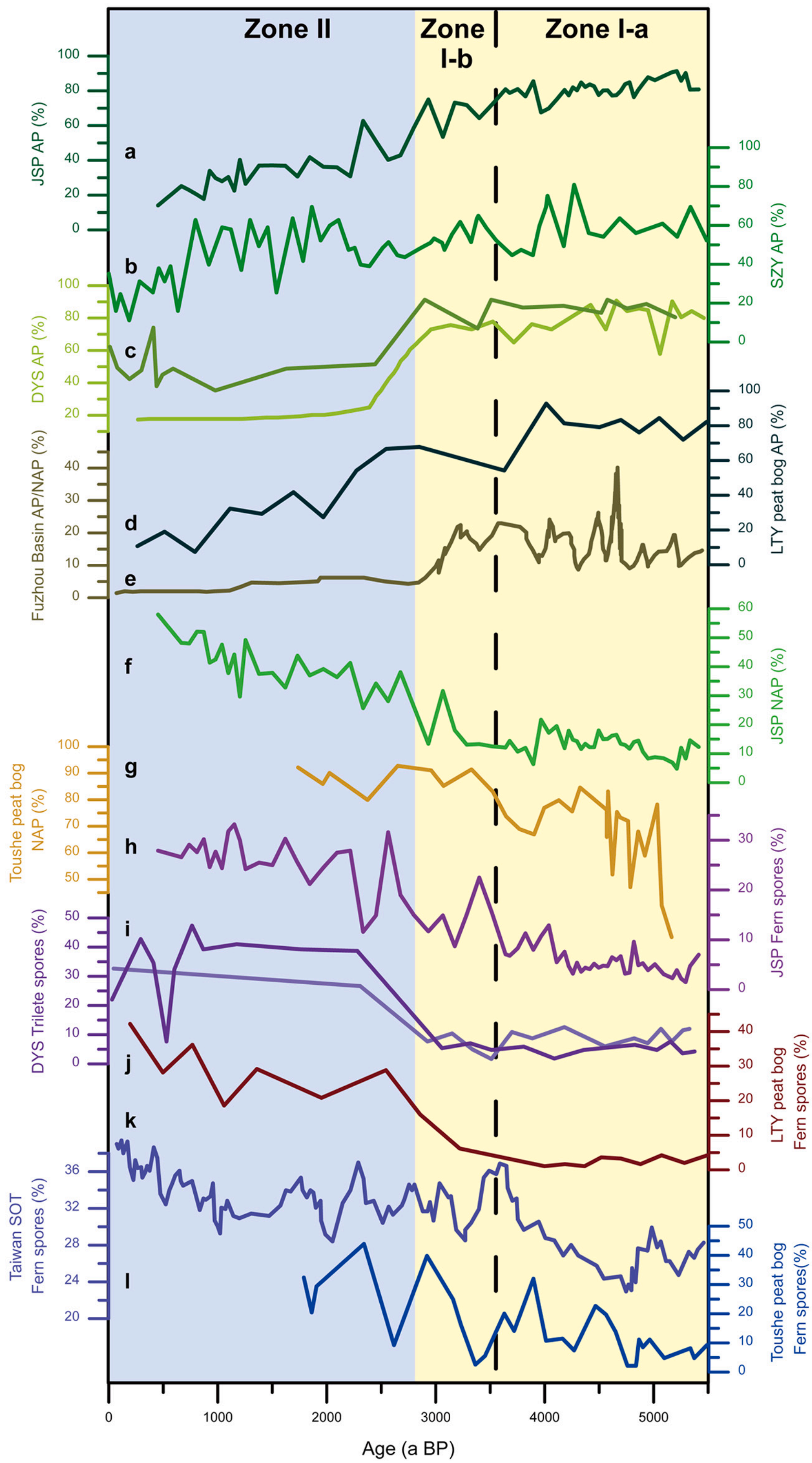

Fig. 3. Comparison between JSP pollen record and other pollen records in subtropical East Asia. **a**, the arboreal pollen (AP) percentages in the JSP (this study). **b**, the AP percentages in the Shuizhuyang peat bog (Ma et al., 2018). **c**, the AP percentages in the Daiyun Mountain (different colored lines denote different profiles) (Zhao et al., 2017). **d**, the AP percentages in the Lantianyan peat bog (Ma et al., 2016). **e**, the AP/NAP percentages in the Fuzhou Basin (Yue et al., 2015). **f**, the non-arboreal pollen (NAP) percentages in the JSP (this study). **g**, the NAP percentages in the Toushe peat bog (Li et al., 2013). **h**, the fern spore percentages in the JSP (this study). **i**, the Trilete spore percentages in the Daiyun Mountain (different sediment profiles) (Zhao et al., 2017). **j**, the fern spore percentages in the Lantianyan peat bog (Ma et al., 2016). **k**, the fen spore percentages from the South Okinawa Trough off northeastern Taiwan (Chen et al., 2019). **l**, the fern spore percentages in the Toushe peat bog (Liew et al., 2006). The vertical yellow and blue shaded columns indicate pollen Zone I and Zone II, respectively. The dashed line shows the two subzones of pollen Zone I (I-a and I-b). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

coniferous taxa (Li et al., 2018). However, under such a wetting and slightly cooling situation (but relatively warm background), changes in temperature are more likely to slightly change the regional vegetation composition, while the AP proportions are expected to remain high and/or even increase in subtropical East Asia. For example, in the adjacent middle subtropical vegetation zone, Yue et al. (2012) reconstructed vegetation changes based on pollen records over the last 50,000 a BP in the Shuizhuyang subalpine peat bog, and they found that vegetation composition varied between subtropical evergreen broad-leaved forest and warm temperate deciduous broad-leaved forest during the last glacial-interglacial cycle; even in the Last Glacial Maximum (LGM), the NAP did not exceed 10% (Yue et al., 2012). In the Dahu swamp, the area was mainly covered with broad-leaved forest during ~18,330–6000 a BP (Xiao et al., 2007). In the southeast coastal area, the pollen records from the tidal flat of Sanduao Bay show that AP remained at a high proportion since late MIS5, and a distinct decrease occurred after ~7000–3000 a BP (Dai et al., 2021). In the JSP area, pollen records showed a dramatic decrease in AP (down to less than 50%) and spread of

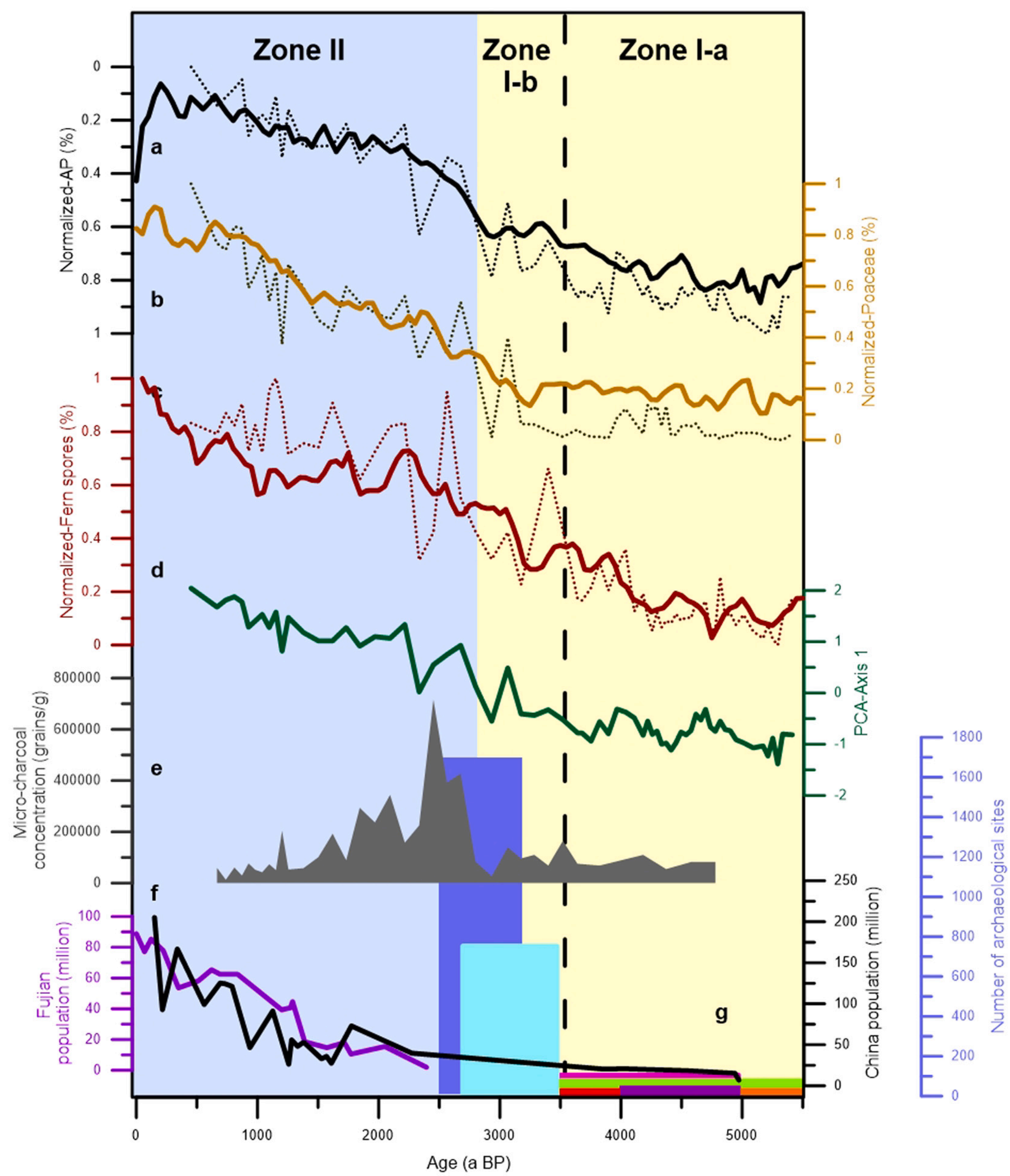

Fig. 4. Comparison between JSP pollen and charcoal records and other proxy indices in subtropical East Asia. a, Normalized stacked AP percentage index (solid line) and JSP AP percentages curve (dashed line) (note that the ordinate is inversely plotted); **b**, Normalized stacked Poaceae percentage index (solid line) and JSP Poaceae percentages curve (dashed line); **c**, Normalized stacked fern spore percentage index (solid line) and JSP fern spore percentages curve (dashed line); See details of the curves **a, b** and **c** in Supp.3 and Fig.S9. **d**, PCA-Axis 1 of the pollen data in the JSP (this study). **e**, the micro-charcoal concentrations in the JSP (this study). **f**, Fujian population (purple line) (Zhao et al., 2017) and China population (black line) (Li et al., 2009). **g**, the number of archaeological sites in Fujian province (blue: Baizhuduan culture and undistinguished Bronze Age cultures between 3200 and 2500 a BP; cyan: Fubin culture and Huangtulun culture between 3500 and 2700 a BP; red shade: Huangguashan culture and Hulushan culture between 4000 and 3500 a BP; orange shade: Keqiuto culture between 6000 and 5000 a BP; purple shade: Niubishan culture and Tanshishan culture between 5000 and 4000 a BP; green shade: undistinguished Neolithic cultures between 6000 and 3500 a BP; pink shade: undistinguished Neolithic cultures between 5000 and 3500 a BP) (Hosner et al., 2016). The vertical blue-shaded and yellow-shaded columns and the dashed line are the same as those in Fig. 3. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

herbaceous (mainly Poaceae) and ferns (mainly Trilete spores) after ~2800 a BP, which did not follow the expected natural response pattern under a wetter condition (as mentioned above). The deciduous and coniferous taxa, such as *Pinus*, *Tsuga*, *Betula*, Juglandaceae, and wetland and aquatic taxa, such as Cyperaceae, Ranunculaceae, Potamogetonaceae, didn't show marked changes and remained at extremely low levels during the late Holocene (Fig. S8; The percentages of *Tsuga*, Cyperaceae and Potamogetonaceae were very low and were not shown in the figure). We therefore contend that such a big change in vegetation composition is most likely caused by anthropogenic impacts, which could have surpassed the natural climate in regulating regional vegetation coverage since 2800 a BP in the JSP area. Of course, the global cooling event caused by reduced solar activity at 2800 a BP (Chambers et al., 2007; Van Geel et al., 1996) could also lead to environmental deterioration and reduce AP content to a certain extent.

During the early Neolithic, the subsistence strategies were mainly fishing and hunting in the Fujian region, different from the development of intensive agriculture in the middle and lower reaches of the Yangtze River (Zhang and Hung, 2009). Carbonized seeds of rice and millet were found at the Nanshan archaeological site, and the ^{14}C ages confirm that agricultural activities had already appeared as early as 5000 a BP in southeastern China (Yang et al., 2018). It is generally recognized that the complex society in Fujian Province appears later than 3500 years ago (Allard, 2014; Zhao et al., 2017), which is supported by the spatiotemporal distribution of archaeological sites during the Neolithic and Bronze Age (Fig. 4g) (Hosner et al., 2016). There were 96 archaeological sites before 3500 a BP, sparse site distribution indirectly indicates that human activities may not have had a profound impact on the regional landscape at this period (Hosner et al., 2016). After ~3500 a BP, the number of sites increased largely and extensively, rising to 2428, implying great changes in human lifestyles, agricultural production, social complexity, and populations, etc. (Hosner et al., 2016). Pollen and charcoal records also suggest enhanced human activity and landscape clearance in the Lantianyan peat bog at about 3600 a BP (Ma et al., 2016).

The deposition rates of the JSP during ~5500–3500 a BP were relatively high (0.073 cm/a), indicating a natural deposition process under a generally wetter condition from the mid-Holocene. After ~3500 a BP, the deposition rates systematically slowed down (to ~0.022 cm/a), and pollen concentrations and percentages began to change (Supp. 3), but the charcoal concentrations remained relatively low (Fig. 4e), suggesting that large-scale human activities might have disturbed the original depositional environment at this stage. Since ~2800 a BP, a sharp increase in charcoal concentration was observed in the JSP area, accompanied by the significant increase in Poaceae, *Aster*, *Artemisia* pollens and Trilete spores (including *Dicranopteris*) and contemporarily decrease in AP percentages (as mentioned above), suggesting further enhanced human activities, like forest clearance and biomass burning (Fig. 4). The pollen assemblages, like Poaceae, *Dicranopteris*, *Artemisia*, *Pinus*, etc., are closely associated with agriculture and forest clearance (Yang et al., 2012). For example, Yang et al. (2012) found that pollen percentages of Poaceae, *Dicranopteris*, Asteraceae, *Artemisia* and *Pinus* were abruptly increased at ~2200 a BP in the deltaic plain of the Pearl River, which is analogous to those of the modern disturbed landscapes around rice paddies, suggesting that human activity was largely enhanced at 2200 years ago around their study site. We further carried out Principal Component Analysis (PCA) of the JSP pollen assemblages (Fig. S10; Supp. 4) and found that the first principal component (Axis 1) can be used to reflect human activity. The scores of the Axis 1 samples show a gradually increasing trend (Fig. 4d), indicating that regional vegetations were strongly affected by human activities. In other regions of subtropical East Asia, the 34–40 μm Poaceae pollen increased and peaked at about 2100 a BP in the Jiufeng Mountain (Zheng et al., 2021) and Lantianyan peat bog (Fig. S9) (Ma et al., 2016). In the Shuizhuyang subalpine peat bog, Poaceae and *Dicranopteris* increased abruptly, and NAP percentages increased to 52% after 2000 a BP (Yue et al., 2012), also suggesting that human activities had altered the original forest landscape during this period. We standardized and stacked pollen records in subtropical East Asia (see detail in Supp. 3 and Fig. S9), and found that the stacked Poaceae pollen percentages increased distinctly after ~3200 a BP, and the stacked fern spore percentages also increased simultaneously (Fig. 4b, c). The stacked AP percentages decreased abruptly at ~2800 a BP (Fig. 4a), suggesting an extended transformation of the original dense forest to a more open landscape over subtropical East Asia areas. All these lines of evidence suggest that human activities were significantly enhanced during the late Holocene in the subtropical East Asia areas, consistent with the contemporaneous increase in population (Fig. 4f) and intensified agriculture activities.

Lines of archaeological evidence further support our view. Around ~2800 a BP was the transition period from the late Western Zhou Dynasty (877–771 BCE) to the Spring and Autumn Period (770–476 BCE) in Chinese history. The plenty of ancient cultural sites of Fubin culture, Huangtulun culture and Baizhuduan culture (Fig. 4g) reflect flourished societies and rapidly developed productivity. The excavations of grey pottery, stamped hard pottery and proto-porcelain show the pottery industry's prosperity, corresponding to intensified fires and reduced trees, and consistent with the peak of charcoal concentrations as recorded in Jianshan peatland during this period.

With the development of society and the growth of population (Fig. 4f), the agricultural economy gradually occupied a dominant role, replacing the fishing and hunting culture. Yang et al. (2018) suggested that rice farming spread southward to western Fujian and northern Guangdong during ~5000 a BP and reached coastal areas at ~4500–4000 a BP. Ma et al. (2020) contend that intensive agricultural production developed until ~2000–3000 a BP around the studied area due to the limitation of mountainous terrain. Improved agricultural techniques may also promote the rice spread into the mountains, further destroying native forests by "slash-and-burn" and other agricultural methods.

Subtropical East Asia is the home of rare late Neogene/Quaternary plant taxa. These relict species require humid habitats, and most of them are found in mountains of the humid subtropical and warm-temperate areas (Tang et al., 2018). During the late Holocene, the gradually wetting climate of the study area is favorable, and these species are expected to be more abundant. However, due to the forest destruction by human activities, many rare species have declined sharply or even disappeared. For example, Zheng et al. (2021) suggested that intensified anthropogenic pressures may be responsible for the endangered *Glyptostrobus*. At present, some pre-Quaternary plants are still thriving in the Daiyun Mountain Nature Reserve (~12 km to our study site), such as the *Cibotium barometz*, *Glyptostrobus pensilis*, *Taxus chinensis* var. *mairei*, *Podocarpus neriifolia*, *Tsuga longibracteata*, *Chimonanthus nitens*, among others (Lin, 2003). It is urgent to make proper strategies to protect these rare species.

5. Conclusion

We show a gradually wetting trend based on peat $\delta^{18}O_{cell}$ records in JSP (this study) and confirmed this trend by other robust hydroclimatic records over the extended subtropical East Asia areas. Under such a wetter background, the subtropical East Asia areas are expected to be covered with denser forests; yet the vegetation coverage inferred from pollen records at the JSP and those at surrounding areas are not as expected. Vegetation coverages changed from dense forests to more open landscapes from the mid- to late-Holocene. A dramatic vegetation shift inferred from pollen assemblages was observed around 2800 a BP, which was synchronous with the high occurrences of archaeological sites and the abrupt changes in fire events (inferred from charcoal concentrations), suggesting that enhanced human activities, like forest clearance, biomass burning, etc., have altered the regional vegetation response patterns. The results of this study suggest that human activities could have surpassed the natural climates in regulating regional vegetation compositions over subtropical East Asia, and therefore appropriate policies are needed to protect regional rare species and to regulate the regional environment, ecology, and sustainability.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gloplacha.2022.103850.

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