










RESEARCH ARTICLE

Human activities have reduced plant diversity in eastern China over the last two millennia

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Abstract

Understanding the history and regional singularities of human impact on vegetation is key to developing strategies for sustainable ecosystem management. In this study, fossil and modern pollen datasets from China are employed to investigate temporal changes in pollen composition, analogue quality, and pollen diversity during the Holocene. Anthropogenic disturbance and vegetation's responses are also assessed. Results reveal that pollen assemblages from non-forest communities fail to provide evidence of human impact for the western part of China (annual precipitation less than 400mm and/or elevation more than 3000m.a.s.l.), as inferred from the stable quality of modern analogues, principal components, and diversity of species and communities throughout the Holocene. For the eastern part of China, the proportion of fossil pollen spectra with good modern analogues increases from ca. 50% to ca. 80% during the last 2 millennia, indicating an enhanced intensity of anthropogenic disturbance on vegetation. This disturbance has caused the pollen spectra to become taxonomically less diverse over space (reduced abundances of arboreal taxa and increased abundances of herbaceous taxa), highlighting a reduced south–north differentiation and divergence from past vegetation between regions in the eastern part of China. We recommend that care is taken in eastern China when basing the development of ecosystem management strategies on vegetation changes in the region during the last 2000 years, since humans have significantly disturbed the vegetation during this period.

KEYWORDS

analogue quality, human–vegetation interaction, land use, latitudinal zonation, plant diversity, pollen

1 | INTRODUCTION

Knowledge of spatiotemporal patterns and drivers of vegetation change is essential for predicting vegetation trends in the future and for developing strategies to sustainably manage ecosystems (Abel et al., 2021; Liu, Jiao, et al., 2020; Martin et al., 2021; Piao et al., 2015). Recently, based on remote-sensing data, many studies have been completed on the spatiotemporal patterns and drivers of vegetation change during the last decades for China, and have concluded that human activities are the most important drivers of recent vegetation changes (e.g., Jiang et al., 2020; Qu et al., 2020; Shi et al., 2020; Yin et al., 2020; Zhao et al., 2021). However, the degree to which human activities and climate drive these vegetation changes shows remarkable regional individuality (Hao et al., 2020; Kou et al., 2021; Ma et al., 2020; Shi et al., 2020). Remote-sensing data have only been available for the past few decades so the vegetation data being gathered could already be in a disturbed state (i.e., is not natural vegetation). Hence, it is necessary to identify signals of human disturbance to natural vegetation at a long-term scale.

Past pollen assemblages archived in lake sediments and peat deposits contain information about plant communities (relative abundances of pollen can be calibrated to plant relative abundances), and have been successfully employed in long-term climate and vegetation reconstructions (e.g., Cao et al., 2015; Chen, Xu, et al., 2015; Herzschuh et al., 2019; Liu et al., 2015; Tian et al., 2016, 2018). They can also indicate past human impacts on vegetation via anthropogenic pollen indicators (e.g., Huang, Ren, et al., 2021; Huang, Zhang, et al., 2021). However, interpretations of Holocene pollen data in terms of the relationship between vegetation change and human activity in China are contradictory. For instance, pollen data mapping (Cao et al., 2015; Ren, 2007), a pollen-based tree-cover reconstruction (Tian et al., 2016), and a land-cover reconstruction using the REVEALS model (based on the modern pollen productivity data; Li et al., 2020) at subcontinental scale suggest that the decrease in tree cover during the late Holocene (ca. 4–0 cal. ka BP) in eastern China is due to human impacts to some extent, but other studies suggest that anthropogenic deforestation may have been restricted to within the last 2 millennia at smaller spatial scale (e.g., Yao et al., 2017; Zheng et al., 2021). The contradiction implies that pollen data together with pollen-based reconstructions fail to provide robust evidence for human impacts on vegetation (e.g., Li et al., 2020), and previous studies may also have neglected that the occurrence of anthropogenic pollen indicators does not represent human had already disturbed and heavily modified natural vegetation (e.g., Li et al., 2009; Miehe et al., 2009; Zong et al., 2007). Contradiction and uncertainty also occur in the non-forest communities. For instance, Miehe et al. (2019) found that grazing pollen indicators occur at ca. 8.7 cal. ka BP on the southern Tibetan Plateau, while widespread human occupation of the Tibetan Plateau might not have occurred until after 3.6 cal. ka BP (Chen, Dong, et al., 2015). These contradictions could be caused by regional differences in the history of human-vegetation interactions; hence, the synthesis of multiple Holocene pollen records is necessary to investigate past human impacts on

vegetation at broad spatial scales using novel numerical analysis, to answer when and where the past vegetation had been disturbed or modified by human activities in China, and to decide whether and when the land use changes from sustainable and unsustainable.

China can be divided into three major geographic units, including the Tibetan Plateau, the low plateaus and basins (including the Mongolia Plateau, the Loess Plateau, the Yunnan-Guizhou Plateau, the Sichuan Basin, etc.), and the eastern plains and lowlands. The plains and lowlands (with high human population currently) have long histories of agriculture dating back to about 10 cal. ka BP (e.g., Li et al., 2009; Lu et al., 2009; Wang et al., 2014; Yang, Wan, et al., 2012). The eastern part of China (including the eastern plains and lowlands, part of the low plateaus and basins) is covered by different forest types with strong latitudinal zonation, from south to north, consisting of tropical rainforest and seasonal rainforest, subtropical evergreen broadleaved forest, warm-temperate deciduous forest, temperate mixed conifer-deciduous broadleaved forest, and boreal conifer forest. The western part of China (including the Tibetan Plateau, the Mongolian Plateau, and north-west China) is mainly covered by steppe, meadow, and desert, and human impact is largely limited to grazing in restricted areas (Hou, 1983). The various geographic units and vegetation types, together with its long history of human activities (different land-use types), make China an ideal laboratory for investigating past human impacts on vegetation as recorded by changes in pollen data.

The fossil and modern pollen datasets for China and east Asia (Cao et al., 2013, 2014) were recently updated and have been used to assess the similarity between modern and fossil pollen assemblages and to investigate the temporal changes of their composition and diversity. Here, we use these datasets to determine (1) when vegetation began to closely resemble modern vegetation (represented by pollen assemblages) and what factors governed this change: climate and/or human land use; and (2) Holocene changes in pollen diversity and what factors triggered those changes.

2 | DATA AND METHODS

2.1 | Modern and fossil pollen datasets

The modern pollen dataset from China and Mongolia (comprising 2626 sampling sites; Cao et al., 2014) has been extended by pollen data from central Asia ($n = 973$, Bordon et al., 2009), central Inner Mongolia ($n = 396$, Liu, Wang, et al., 2020), Japan and south-eastern Russia (including arboreal taxa only; $n = 798$, Tarasov et al., 2011), the Tibetan Plateau ($n = 70$, Zhang, 2013; $n = 117$, Cao et al., 2021; $n = 168$, Wang et al., 2022), the anthropogenic vegetation communities in eastern China (croplands, economic gardens, etc.; $n = 472$, Wang et al., 2010; Pang et al., 2011; Yang, Zheng, et al., 2012; Li et al., 2015; Ding et al., 2017), and other regions. The extended modern pollen dataset covers eastern and northern Asia including 9165 sampling sites with 245 harmonized pollen taxa (harmonization follows Cao et al., 2013). The available sites are generally evenly

distributed and cover all the main vegetation types within eastern and northern Asia, but geographic gaps do still exist (e.g., the central Siberian Plateau; Figure 1).

The taxonomically harmonized and temporally standardized fossil pollen dataset from eastern and northern Asia ($n = 444$, Cao et al., 2013, 2020) was supplemented by 48 recently published pollen spectra. An age-depth model has been re-established for each pollen record using Bayesian age–depth modeling with the “Bacon” software (Blaauw & Christen, 2011) in R (R Core Team, 2019) and the IntCal09 radiocarbon calibration curve (Reimer et al., 2009; detailed information about the standardized chronology is presented in Cao et al., 2013). Since the data quality has already been evaluated during the dataset establishment (Cao et al., 2013), all available pollen records ($n = 254$) from China covering the Holocene (11.5–0 cal. ka BP) entirely or partly were employed in this study without further selection, to be representative of past spatiotemporal patterns of vegetation communities (Figure 1).

2.2 | Numerical methods

To determine the difference in human impacts on vegetation from different land-use types (crop cultivation and grazing), the 254 fossil pollen records were separated into two groups based on the elevation and modern annual precipitation of the sites, which was obtained from the Chinese Meteorological Forcing Dataset (CMFD; gridded near-surface meteorological dataset with a spatial resolution of 0.1°; He et al., 2020). Pollen records with more than 400 mm modern annual precipitation and less than 3000 m a.s.l. elevation were clustered into the “east China” group, where forest is the dominant natural vegetation community with a long history of land cultivation and high-density human disturbance (Li et al., 2009; Wang et al., 2014); while the remaining pollen records were clustered into

the “west China” group, where non-forest plant communities (e.g., steppe, meadow, desert) are dominant across the landscape with pastoralism as the major land-use type (crop cultivation is restricted spatially) and relatively weak human disturbance (Appendix S1). Since temporal patterns of climate change during the Holocene have strong regional peculiarities in eastern China (Liu et al., 2015), fossil pollen records within the “east China” group were separated into two subgroups north and south of 31.5° N, called “north China” and “south China.” Because of the small number of available sites in the two subgroups (Appendix S2), their pollen records were only used in diversity estimations and results are presented in Supplementary Materials.

Pollen percentages were interpolated for 116 time slices at 100-year intervals between 11.5 and 0 cal. ka BP using the *interp.data-set* function (method = linear) in the *rioja* package (version 0.9-15.1; Juggins, 2018) for R (version 3.6.0; R Core Team, 2019). To identify the temporal patterns of major pollen taxa and their relationships, ordination techniques were employed on datasets for all time slices from the “east China” and “west China” groups separately, based on square-root transformed pollen data of selected taxa (those present in at least 10 samples and with a maximum $\geq 10\%$ in at least one sample) to stabilize variances and optimize the signal-to-noise ratio (Prentice, 1980). A series of detrended correspondence analyses (DCA; Hill & Gauch, 1980) for all time slices showed that the lengths of the first axes for all pollen datasets were below 4 SD (most of them below 3 SD), suggesting that principal component analysis (PCA) is appropriate for these pollen datasets (ter Braak & Verdonschot, 1995). DCA and PCA were performed for each time slice using the *decorana* and *rda* functions in the *vegan* package (version 2.5-4; Oksanen et al., 2019). To further explore the similarity among key time slices (10, 9, 8, 7, 6, 5, 4, 3, 2, 1, and 0.5 cal. ka BP), Procrustes rotation and the associated PROTEST permutation test were applied to the pollen scores of PCA (Gower, 1971; Peres-Neto &

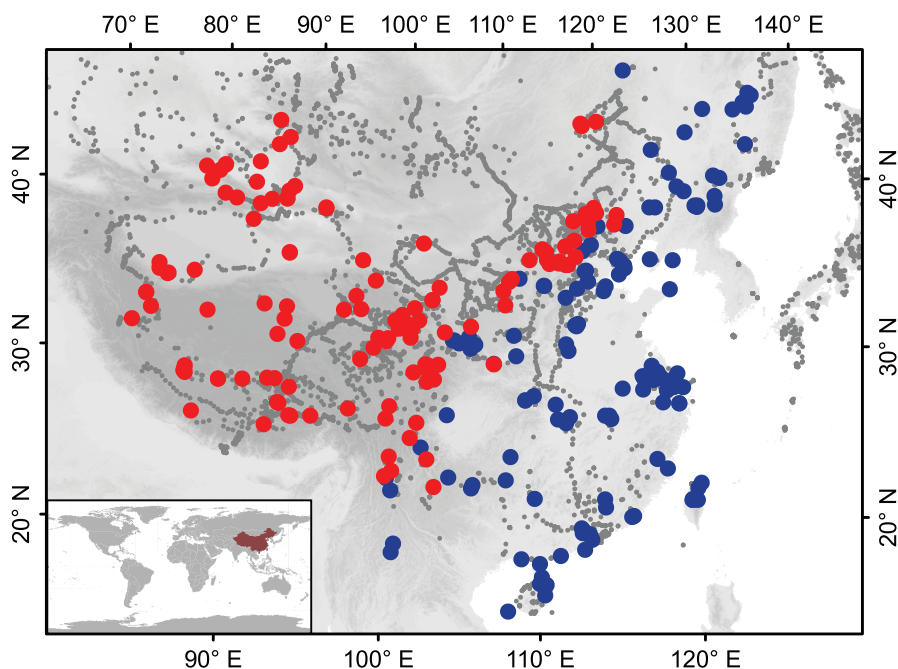


FIGURE 1 Location of modern pollen sites for east Asia (small grey dots) and Holocene fossil pollen records from China; these fossil pollen records are separated into an “east China” group (blue dots) and a “west China” group (red dots) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/terms-and-conditions)]

Jackson, 2001). PROTEST performs a random permutation test and assesses the degree of concordance between two datasets, producing significance of the Procrustes fit as an r -value with an associated p -value to indicate the likelihood of the relationship occurring by chance; a high r -value and low residual value indicate a good agreement between datasets, while high residual values for pollen taxa indicate significant variations between datasets (Jackson, 1995). Procrustes analyses and PROTEST were carried out in R using the *Procrustes* and *protest* functions of the *vegan* package (version 2.5-4; Oksanen et al., 2019).

Beta diversity was employed to assess the spatial variation of fossil pollen spectra for each time slice. The temporal change of beta diversity is a valuable index to represent biotic homogenization (decrease) or differentiation (increase) (Anderson et al., 2011; Rolls et al., 2021). Beta diversity is defined as the ratio between gamma and alpha diversities in this study. We used the inverse Simpson index to quantify diversity (Simpson, 1949; see also Wang & Loreau, 2016). Alpha diversity is the average value of the local diversity of all sites weighted by the total abundance of the sites; gamma diversity is calculated using the species distribution in the metacommunity (further details are described in Wang & Loreau, 2016).

Geographic distance (great circle distance; km) between each modern sample site and each fossil site was calculated using the *rdist.earth* function in the *fields* package (version 6.8; Furrer et al., 2013) based on their longitude/latitude. The taxonomic distance from fossil pollen assemblage to modern pollen assemblage (based on percentages of all pollen taxa) is a common diagnostic for evaluating analogue quality. A distance shorter than the fifth percentile of all distances between the modern assemblages is commonly used as a threshold for good analogues, while a distance above the 10th percentile is assumed to signify a no-analogue assemblage (bad analogue), and a moderate distance between the 10th and 5th percentiles represents poor analogues (Birks et al., 1990). In this study, the squared chord distance between each fossil pollen assemblage and each modern pollen assemblage within a 1000 km distance around the fossil site (Cao et al., 2017) was calculated with the *MAT* function in the *rioja* package (version 0.9-15.1; Juggins, 2018). The squared chord distances between all modern assemblages within each 1000 km subset were calculated using the *paldis* function in *rioja* (version 0.9-15.1; Juggins, 2018).

3 | RESULTS

3.1 | Temporal pattern of pollen diversity

For the “east China” group, the number of common pollen taxa reaches a maximum between ca. 7 and 2 cal. ka BP (around 30 taxa), then decreases strongly to 11 taxa at 0 cal. ka BP, which is even lower than the values between 11.5 and 7 cal. ka BP (generally more than 20 taxa). The number of total recorded taxa has an increasing trend from 11.5 to 9 cal. ka BP and maintains high values until ca. 2 cal. ka BP, when a decreasing trend follows that is consistent with the

number of common pollen taxa (Figure 2a). For the “north China” and “south China” subgroups, numbers of both total taxa and common taxa show a decreasing trend after ca. 2 cal. ka BP (Appendix S3a,b). Relative to the “east China” group, both the number of common pollen taxa and total taxa show less dynamic temporal patterns for the “west China” group throughout the Holocene (Figure 2b). The trend in the number of total taxa increases from 11.5 to ca. 8 cal. ka BP, before decreasing from 7 to 5.5 cal. ka BP, and then fluctuating prior to reaching a low point at 0.5 cal. ka BP. There is no significant temporal pattern for the number of common taxa during the Holocene until 0.5 cal. ka BP, but there is a slight reduction afterwards (Figure 2b).

Beta diversities for the “east China” group are higher than those for the “west China” group throughout the Holocene. For the “east China” group, the highest beta diversities occur in the early Holocene (range: 2.5–2.9; between 11.5 and 8.7 cal. ka BP), then the values fluctuate around 2.4 (range: 2.3–2.6) until 2 cal. ka BP, after which they reduce sharply and stay low in the last millennium (this pattern is also found for the two subgroups; Appendix S3c). Beta diversities for the “west China” group show minor fluctuations throughout the

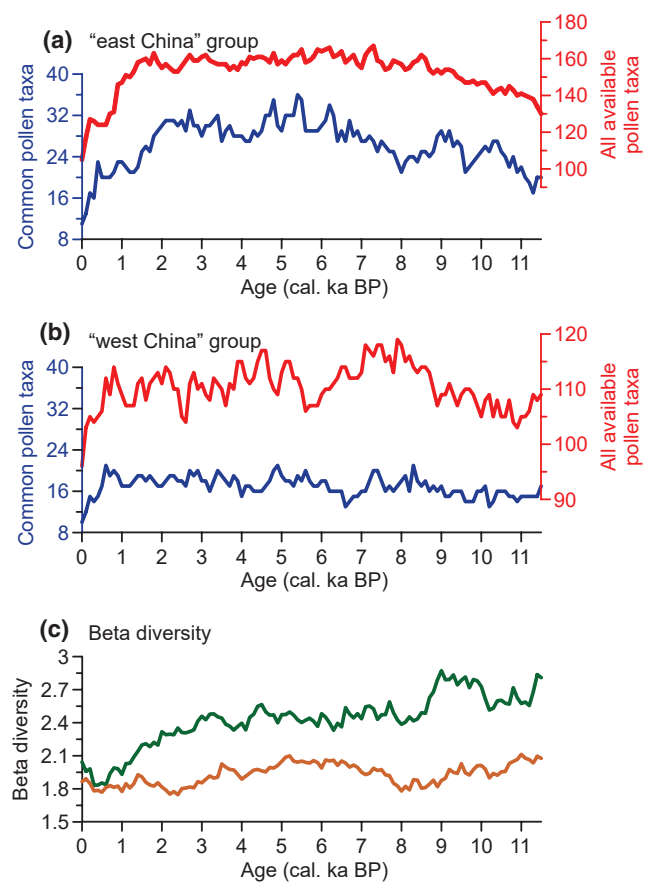


FIGURE 2 Temporal changes in the number of all recorded pollen taxa (red curves) and common pollen taxa (those present in at least 10 samples and with a maximum $\geq 10\%$ in at least one sample; blue curves) within the Holocene. (a) “East China” group, (b) “west China” group. (c) temporal changes of beta diversities for “east China” group (green curve) and “west China” group (brown curve) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16274)]

Holocene with values ranging between 1.8 and 2.1, with relatively high values between 7 and 5 cal. ka BP (Figure 2c).

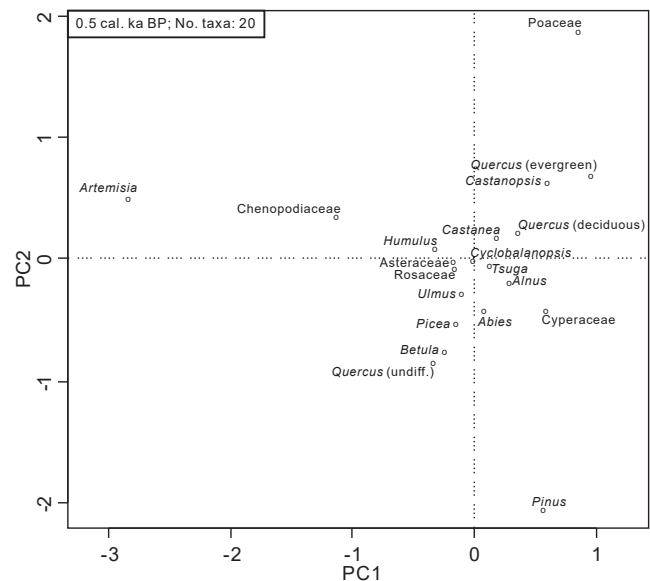
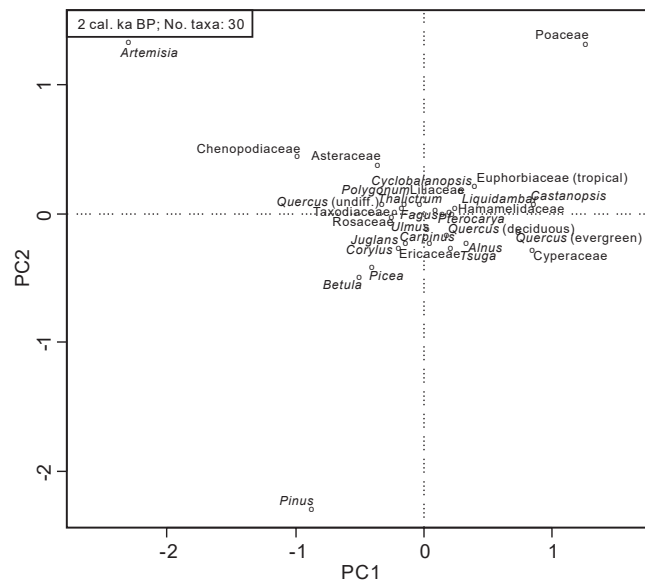
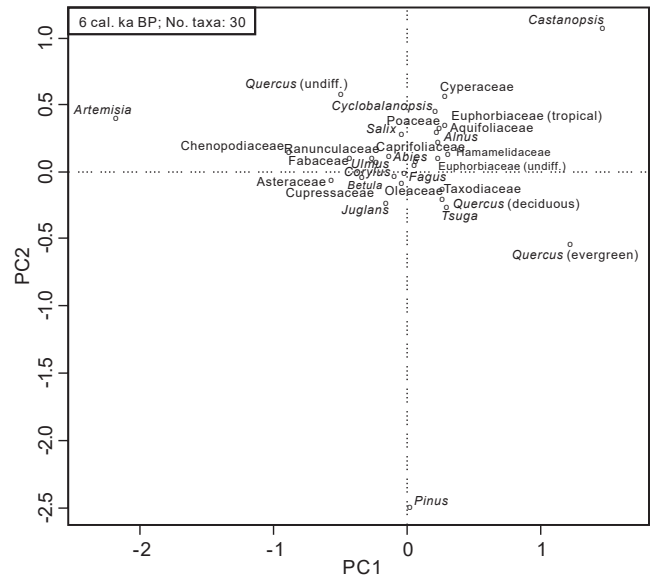
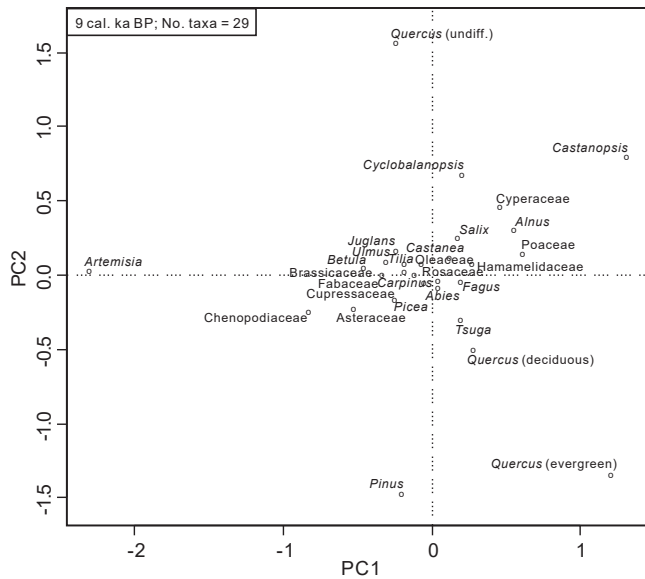
3.2 | Temporal changes in major taxa of pollen assemblages

In pollen spectra from the “east China” group, the scores of *Artemisia* (negative direction of the first PCA axis) and *Pinus* (negative direction of the second PCA axis) are relatively stable throughout the Holocene. However, some other dominant or common taxa have clear temporal changes in their PCA scores during the late Holocene, such as thermophilous broadleaved trees (including *Quercus* [undiff.], *Quercus* [evergreen], *Castanopsis*, and *Cyclobalanopsis*) and Poaceae. For instance, scores of *Quercus* (undiff.) shift from a positive direction in the early and mid-Holocene to a negative position on the first PCA axis in the late Holocene (Figure 3a; Appendix S4).

In contrast to the temporal patterns in the “east China” group, pollen spectra from “west China” are dominated by herbaceous pollen taxa, such as *Artemisia*, Poaceae, Chenopodiaceae, and Cyperaceae, with *Pinus* as the dominant arboreal taxon. The scores of dominant pollen taxa on PCA plots have no obvious temporal changes throughout the Holocene, indicating their stable distribution and relationship (Figure 3b; Appendix S5).

Generally, the Procrustes fit between each pair of neighbor time slices (from 10 to 0.5 cal. ka BP) for the “west China” group produce higher r -values and lower residuals for major pollen taxa than that for the “east China” group (Figure 4), indicating the relatively weak temporal changes of pollen distribution in the western part of China. For the Procrustes fits of “east China,” the temporal comparison of 2–1 cal. ka BP is relatively poor with the lowest r -value (.68) and highest residuals for dominant and major taxa, including Poaceae (0.50), *Pinus* (0.33), *Quercus* (evergreen) (0.19), *Castanopsis* (0.13), *Betula* (0.12), *Quercus* (undiff.) (0.11), Cyperaceae (0.10), and *Artemisia* (0.10) (Figure 4a),

(a)



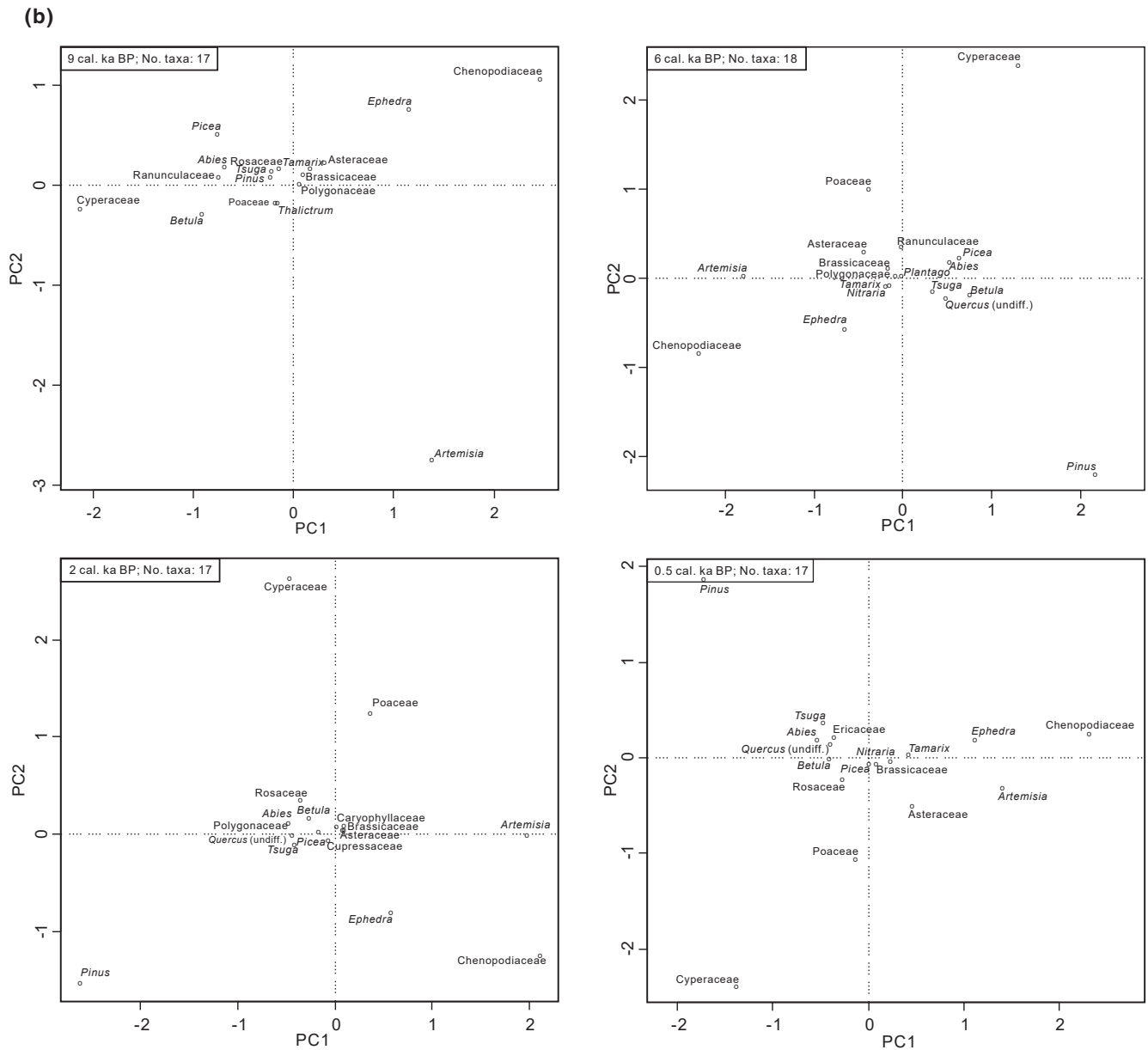


FIGURE 3 Plots of the principal component analysis (PCA) based on common pollen taxa (those present in at least 10 samples and with a maximum $\geq 10\%$ in at least one sample) for four key time slices (9, 6, 2, and 0.5 cal. ka BP). (a) “East China” group and (b) “west China” group

suggesting that the most remarkable change occurred between 2 and 1 cal. ka BP; while the Procrustes fits for other pairs of time slices perform well with high r -values (from 0.97 to 0.99) and low residuals. For the “west China” group, the most remarkable change occurs between 5 and 4 cal. ka BP, and the low r -value (0.88) could be caused by changes in the abundances of *Pinus* (residual 0.35), *Cyperaceae* (residual 0.22), and *Poaceae* (residual 0.17) (Figure 4b).

3.3 | Temporal evolution of analogue quality during the Holocene

Modern pollen data within a 1000 km radius from the fossil site can support good or poor analogues for most Holocene pollen spectra in

the “east China” group generally (Figure 5; Appendix S6). However, a detailed assessment finds spatiotemporal patterns of analogue quality for these pollen spectra. Pollen spectra without good analogues are mainly located in north-east and south China. Analogue quality for pollen spectra from north-east China does not improve throughout the Holocene, while for pollen spectra from south China it clearly improves after ca. 2 cal. ka BP (particularly after 1 cal. ka BP; Figure 5; Appendix S6). The statistical results show that about 50% of available pollen spectra can find good analogues within their 1000 km radius boundary before 3 cal. ka BP, and about 30% of them can be matched by poor analogues. After ca. 3 cal. ka BP (particularly after 2 cal. ka BP), more and more pollen spectra can be matched by good analogues, and the percentage increases to ca. 80% at 0 cal. ka BP, indicating the increasing similarity between fossil and modern

pollen data (Figure 6a). The statistical results of analogue quality for the two subgroups from the eastern part of China also show the increasing similarity between fossil and modern pollen data in the late Holocene; however, it begins ca. 1000 years earlier for the “north China” subgroup (ca. 3 cal. ka BP) than the “south China” subgroup (ca. 2 cal. ka BP; Appendix S7).

For the pollen spectra from the “west China” group, modern pollen data within 1000 km around the fossil site include good analogues for most pollen spectra (ca. 80%), and the percentage has no significant temporal pattern throughout the Holocene (Figures 5 and 6b; Appendix S6).

4 | DISCUSSION

4.1 | Pollen assemblages from non-forest communities might be insensitive to human impacts

The impact of human activities on vegetation (represented by pollen assemblages) is highly debated, particularly for the arid and sub-arid parts of China (e.g., Herzschuh et al., 2010; Miehe et al., 2019). Taking the eastern Tibetan Plateau as an example (currently alpine meadow), modern vegetation surveys suggest that in the plant communities there are grazing resilient and that overgrazing is limited (Miehe et al., 2011; Mipam et al., 2019; Wang et al., 2017). However, the degree of human impact on vegetation over a long temporal scale is still debated due to ambiguities in the pollen data. Based on a series of Holocene pollen spectra, Herzschuh et al. (2010, 2011) conclude that the increase in Cyperaceae percentage since ca. 7 cal. ka BP might be caused by changes in climate and atmospheric CO₂ concentration; but this phenomenon could also be explained as the consequence of pastoralism (Liu et al., 2021; Miehe et al., 2009, 2014, 2019; Schlütz & Lehmkuhl, 2009). In addition, the regional plant-cover changes (based on pollen data) during the late Holocene in arid and subarid parts of China are ascribed to enhanced land use, although there is no convincing archeological evidence (Li et al., 2020). It is thus necessary to address the contradiction and uncertainty with more evidence.

In this study, we assume that modern pollen assemblages should be indicative of greater human impact than past pollen assemblages, because human populations are currently at their highest level. The similarity between modern and fossil pollen assemblages (analogue quality) could thus be a potential and feasible index to assess the intensity of human impacts.

In the western part of China with less than 400 mm precipitation and/or higher than 3000 m a.s.l. elevation, steppe, meadow, and desert dominate the landscape with simple community components at family or genus level. It is quite difficult to distinguish whether the modern plant community is disturbed by humans or not during sample collection. PCA reveals that the fossil pollen spectra are dominated by herbaceous pollen taxa such as *Artemisia*, Poaceae, Chenopodiaceae, and Cyperaceae with *Pinus* as the dominant arboreal taxon. Their prominence in pollen spectra shows little temporal variation

throughout the Holocene (Figure 3b; Appendix S5), implying that the major compositions and their abundance in the vegetation have been relatively stable at the regional spatial scale during the Holocene. From the analogue quality testing, 80% of fossil pollen spectra can be matched with good modern analogues within a 1000 km distance, and this proportion shows insignificant temporal changes (Figure 6b). This phenomenon can be explained in two potential ways: (1) the pollen assemblages from “west China” indicate that this region has not been disturbed by human activities during the Holocene (including at present); or (2) the simple pollen assemblages dominated by only a few herbaceous taxa might be insensitive to human impacts (mostly pastoralism) because of the low taxonomic resolution of pollen identification (family level for herbaceous taxa generally).

Procrustes rotation reveals slight temporal changes for pollen spectra from the “west China” group, with the most notable change occurring between 5 and 4 cal. ka BP (Figure 4b). Past climate records based on non-pollen proxies and model estimation reveal reducing precipitation in the monsoon fringe areas (e.g., Chen et al., 2021; Chen, Xu, et al., 2015; Cheng et al., 2016; Liu et al., 2014) and increasing precipitation in arid central Asia (e.g. Chen et al., 2016) during the transition from mid-Holocene to late Holocene. We argue that the notable changes in the pollen spectra between 5 and 4 cal. ka BP could be caused mainly by precipitation changes with strong regional peculiarities (increasing or decreasing). The slightly enhanced biotic homogenization between 5 and 3 cal. ka BP, indicated by decreasing beta diversity (Figure 2c), might also be caused by the convergent moisture conditions in the western part of China (increasing precipitation in arid areas and decreasing precipitation in subarid areas). In addition, there is a slight change in the pollen spectra after 2 cal. ka BP (revealed by Procrustes rotation) when human populations increase sharply (Figure 7). Hence, we conclude that the modern and Holocene pollen assemblages from “west China” provide inconclusive evidence of human impact at a regional spatial scale. Investigating past human impacts on vegetation based on pollen data should be done with caution for non-forest regions, and comparisons with an independent regional climate record and archeological data are essential (Li et al., 2020).

4.2 | Pollen assemblages after 2 cal. ka BP from the “east China” group record vegetation disturbance due to human impacts

The extended modern pollen dataset employed in this study includes abundant pollen samples collected from vegetation communities which are obviously affected by human disturbance (or even modification) from the north-east, north-central, east, and south China, including cropland, abandoned cropland, economic gardens, etc. (Ding et al., 2017; Li et al., 2015; Pang et al., 2011; Wang et al., 2010; Yang, Zheng, et al., 2012). We argue that the better quality of modern analogues over time for pollen spectra can be used as an index of land-use intensity as they become more and more similar to the present.

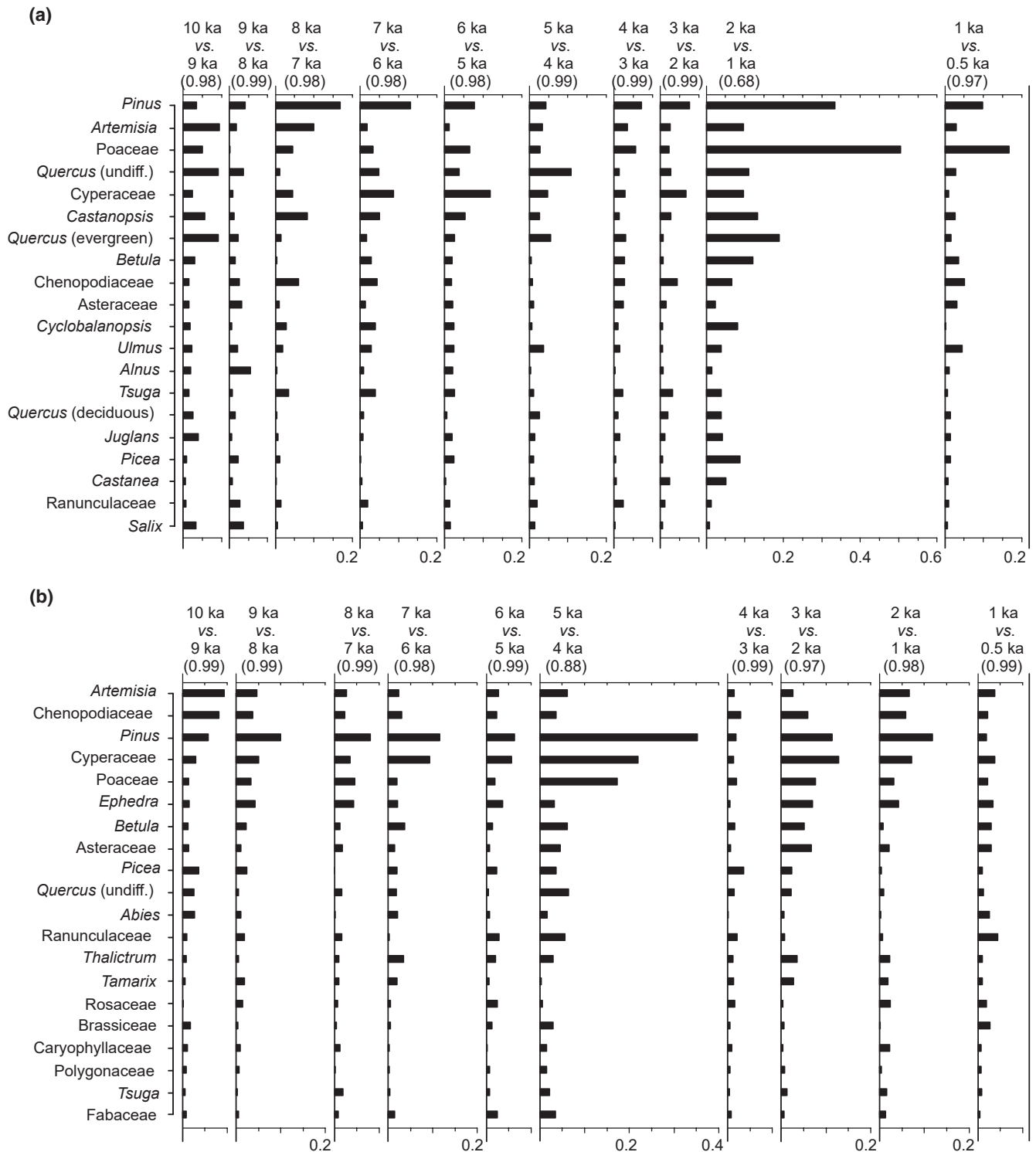


FIGURE 4 Procrustes analysis results comparing the pollen abundances among the temporal datasets at 10 key time scales (at 1 ka interval, plus 0.5 cal. ka BP; all p -values are .001). The residuals of Procrustes fit for the 20 major taxa are presented as bar lengths. (a) “East China” group and (b) “west China” group. Pollen taxa for each group are arranged by their abundance in the datasets. The values in brackets are the r -values of the Procrustes fits

For those pollen spectra from north-east China, the poor and bad analogue quality throughout the Holocene can be explained by the sparsity of available modern pollen data (e.g., no data from the Korean Peninsula; Figure 1) and incomplete modern pollen assemblages from Russia and Japan (Tarasov et al., 2011). Statistical results

of analogue quality for the “east China” group show that analogue quality rises notably from ca. 2 cal. ka BP and the proportion of good analogues increases from around 50% before 3 cal. ka BP to ca. 80% at 0 cal. ka BP (Figures 5 and 6a), with the rising analogue quality occurring in both the “north China” and “south China” subgroups

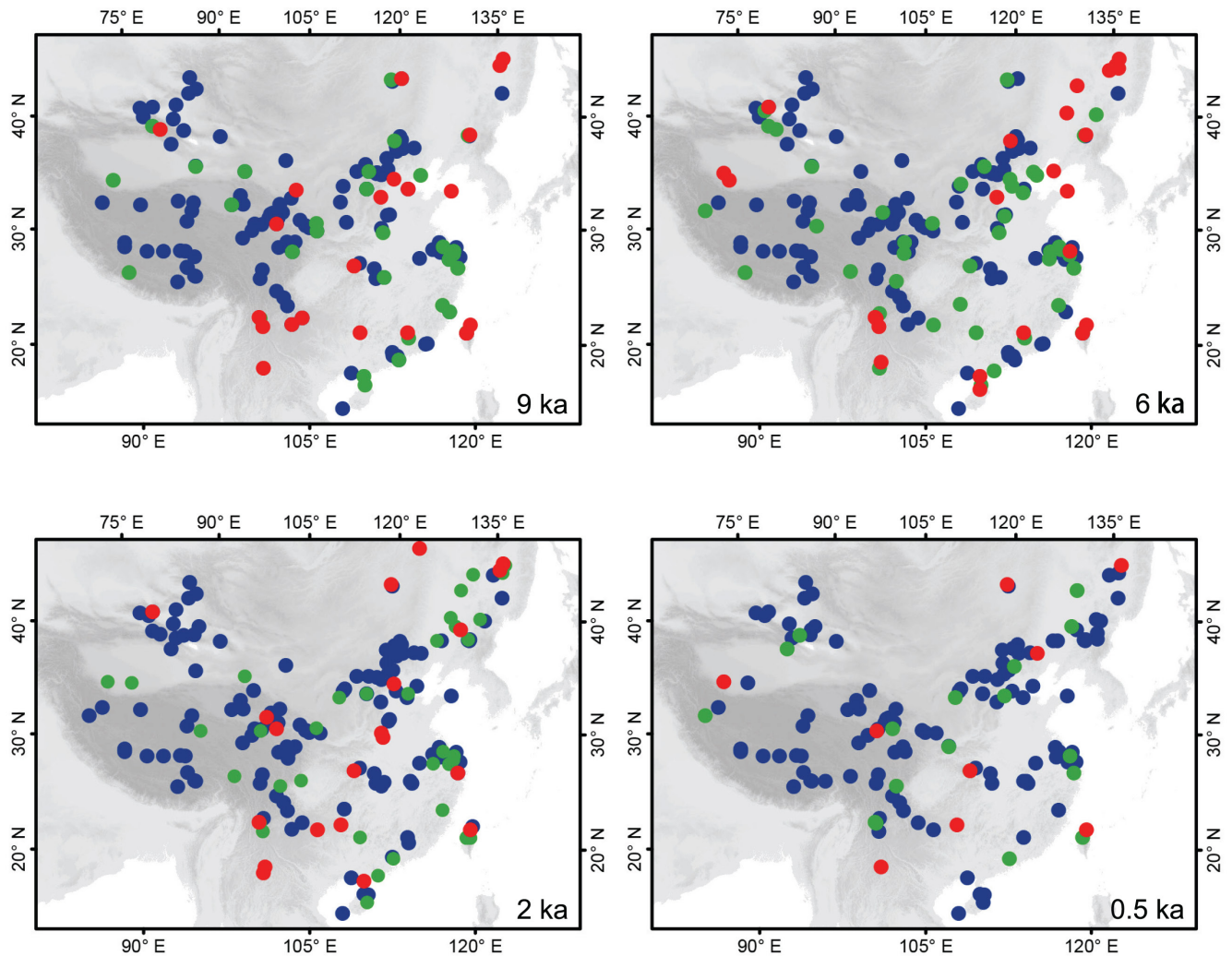


FIGURE 5 Spatial distribution of analogue quality for four key time slices (9, 6, 2, and 0.5 cal. ka BP). Blue dots indicate fossil pollen spectra with a good analogue, green dots indicate a poor analogue, while red dots indicate a bad analogue [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16274)]

(Appendix S7). The clear improvement of analogue quality after ca. 2 cal. ka BP indicates that the fossil pollen spectra become more and more similar to the modern pollen assemblages over time, and we argue that the pollen spectra from the “east China” group are recording disturbance by human activities since ca. 2 cal. ka BP at a regional spatial scale and the degree of this impact increases strongly, particularly after ca. 1 cal. ka BP.

Numbers of both the total pollen taxa and the common taxa (representing plant diversity) in the “east China” group decrease markedly after ca. 2 cal. ka BP, with abundances of thermophilous broadleaved trees (including *Quercus* [undiff.], *Quercus* [evergreen], *Castanopsis*, and *Cyclobalanopsis*) decreasing, while those of herbaceous taxa (*Artemisia*, Poaceae, Chenopodiaceae, etc.) and *Pinus* increase (Figure 3a; Appendix S4). The changes between 2 and 1 cal. ka BP in the pollen spectra are confirmed to be the most significant temporal changes during the Holocene by Procrustes rotation (Figure 4). The low pollen diversities (Figure 2a; Appendix S3) and enhanced openness of the landscape after ca. 2 cal. ka BP might reflect high population levels and enhanced land cultivation (Figure 7).

The clear reduction in the pollen beta diversities also indicates homogenization of the vegetation since 2 cal. ka BP in the eastern part of China (Figure 2c). Proxy-reconstructed and model-estimated climate records indicate a drying trend since ca. 5 cal. ka BP for north-central China, while a wetting trend is seen since ca. 4 cal. ka BP for south China (Chen, Xu, et al., 2015; Cheng et al., 2016; Herzschuh et al., 2019; Liu et al., 2014, 2015; Liu, Shen, et al., 2020). These different spatial patterns of climate change fail to explain the same processes in diversity loss in north and south China (Appendix S3). Improvement of analogue quality and the reduction in pollen diversity since ca. 3 cal. ka BP for the “north China” subgroup might be caused (at least partly) by the drying climate; however, as the analogue quality improves sharply after ca. 2 cal. ka BP, it is likely that human impact is responsible, since there have been no notable climatic fluctuations at either the global or regional scales during the last 2 ka (relative to the entire Holocene; global scale, e.g., Andersen et al., 2004; Pailler & Bard, 2002; regional scale, e.g. Chen, Xu, et al., 2015; Cheng et al., 2016; Liu et al., 2014). Our analyses of the “south China” subgroup provide

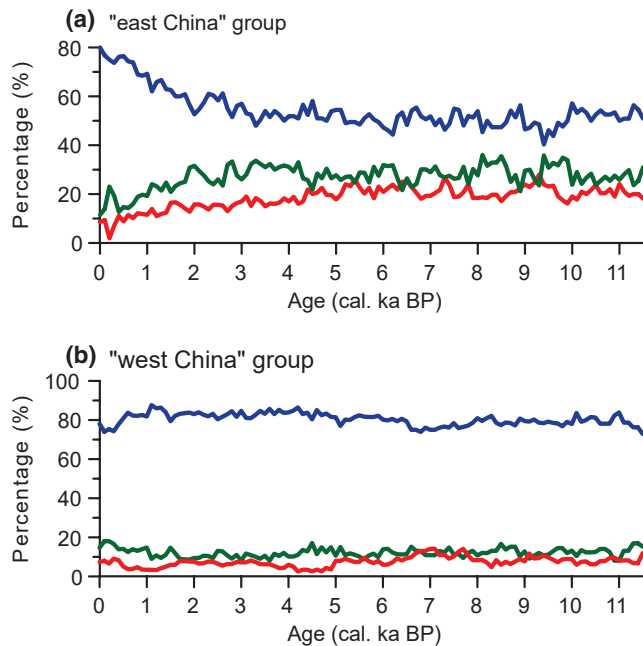


FIGURE 6 Temporal changes of percentages for three analogue types (blue, good analogue; green, poor analogue; and red, bad analogue) at 100-year intervals. (a) "East China" group and (b) "west China" group [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16274)]

further evidence to support the idea that the improvement of analogue quality and reduction in pollen diversity is caused by human impacts because precipitation levels here in the late Holocene have been high and stable (e.g., Herzs Schuh et al., 2019; Liu et al., 2014; Liu, Shen, et al., 2020). In summary, we argue these simple and homogeneous pollen spectra may well reflect anthropogenic deforestation and land cultivation, with rice and wheat as the major crops (both of which are in the Poaceae family).

A series of studies about human-impacted pollen assemblages has been completed for north-east China (Li et al., 2015), the north China Plain (Pang et al., 2011; Wang et al., 2010), and south China (Yang, Zheng, et al., 2012). These previous studies reveal that modern pollen assemblages of cropland and other artificial plant communities are dominated by herbaceous pollen taxa (including Poaceae, *Artemisia*, and Chenopodiaceae) with *Pinus* as the dominant arboreal taxon generally. Other studies about human impacts based on fossil pollen spectra also conclude that the anthropogenic deforestation and land cultivation in eastern China are mostly restricted to the last 2 or 1 ka. Human activities are reflected by decreasing arboreal taxa abundances and increasing herbaceous taxa abundances (including planted Poaceae). Such fossil pollen evidence for human impact has been found for north-central China (e.g., Cao et al., 2010; Huang, Ren, et al., 2021; Xu et al., 2017; Zhang et al., 2010), east China (Wu et al., 2008), and south China (Xiao et al., 2020; Yang, Zheng, et al., 2012; Yue et al., 2015; Zhao et al., 2017; Zheng et al., 2021). In addition, stable climatic conditions (relative to the entire Holocene), at both global and regional scales during the last 2 ka, support our argument that enhanced human impact (Li et al., 2009) is the main reason for the pollen data deviation since ca. 2 cal. ka BP (and

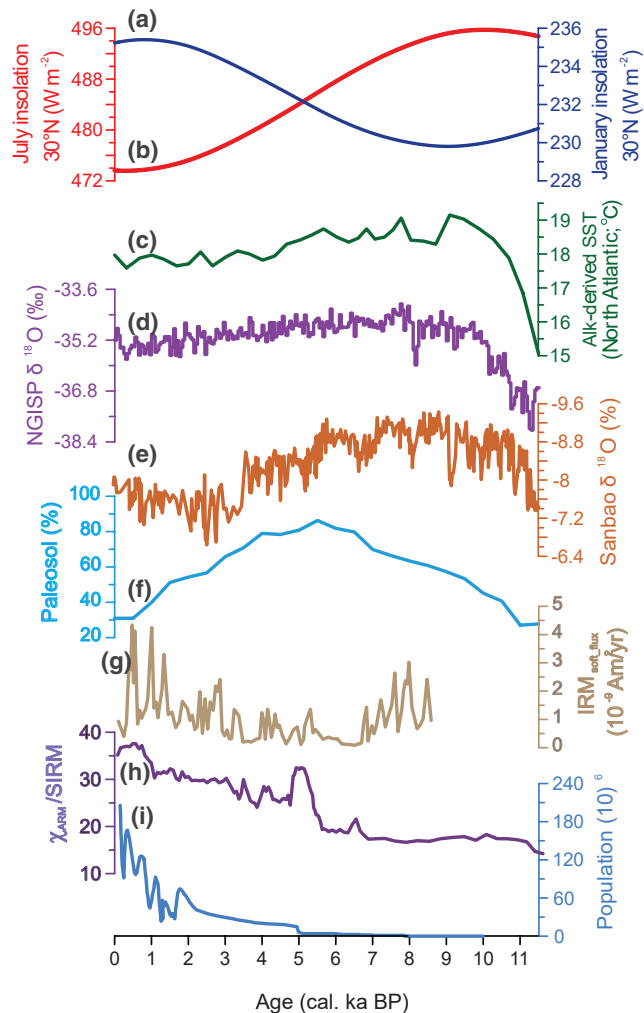


FIGURE 7 Solar insolation in January (a) and July (b) at 30°N (Laskar et al., 2004). (c) Alkenone-derived sea-surface temperature (SST) from deep-sea cores SU8118 and MD952042 (Pailler & Bard, 2002). (d) NGISP: the North Greenland Ice-Core Project (Andersen et al., 2004). (e) Sanbao cave (Cheng et al., 2016). (f) Palaeosol occurrence based on 335 dates from 75 sites in the dune fields of north China (Li et al., 2014). (g) Environmental magnetic record (moisture) of speleothems from Heshang Cave (Zhu et al., 2017). (h) Holocene moisture changes represented by $\chi_{\text{ARM}}/\text{SIRM}$ in the LJW10 section of the Xinjiang Loess (Chen et al., 2016). (i) Estimated and recorded population growth since 8 cal. ka BP for China (Li et al., 2009) [Colour figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/gcb.16274)]

particularly after 1 cal. ka BP) with reduced pollen diversity and simpler and more homogeneous pollen assemblages (Figure 7).

4.3 | Uncertainty of our pollen evidence in investigating past human impacts on vegetation and significance of this research

Our results are based on the synthesis of multiple pollen spectra across a broad spatial scale, where only pollen taxa (including anthropogenic indicators) above a certain abundance are included in

algorithms and analyses; hence, our results about human disturbance on vegetation at a broad spatial scale do not deny the occurrence of pollen signals of human activities for particular areas at particular times. Our analyses cannot therefore provide evidence that the early and mid-Holocene vegetation of the eastern part of China are devoid of ancient human impact. There are, for example, palynological signals of early rice cultivation since ca. 7.7 cal. ka BP in eastern China (Zong et al., 2007) and early crop cultivation and grazing on the north-east Tibetan Plateau (Huang et al., 2017; Wei et al., 2021), which our broader-scale synthesis overlooks.

Our evidence is obtained from a series of numerical analyses based on regional or even subcontinental pollen datasets and comparisons with global and regional independent climate records and archeological data. However, our argument would benefit from more evidence at local scales, for instance, by investigating human impacts for single pollen records alongside local independent climate records and archeological data, which could provide more detailed evidence of human impacts on vegetation (e.g., the tropical south-east China; Zheng et al., 2021). In addition, the available pollen records included in our analyses reduce notably after ca. 0.5 cal. ka BP for both the "east China" and "west China" groups (Appendix S2) such that the decrease in pollen diversities during the last 0.5 cal. ka BP could be an artefact (Figure 2), but this should not influence our conclusion since heavy human disturbance occurs from ca. 2 cal. ka BP in the eastern part of China.

For the western part of China, our evidence confirms that pollen assemblages dominated by herbaceous pollen taxa are mainly unrelated to human impacts, meaning that the pollen-based investigations for past human impacts in non-forest communities could be overestimated to some extent. For example, the transition from alpine steppe to alpine meadow in the mid-Holocene has been attributed to anthropogenic grazing (Miehe et al., 2009, 2014, 2019; Schlütz & Lehmkuhl, 2009), but may have other causes. Pollen analysis fails to provide strong evidence for anthropogenic vegetation change in arid and subarid regions, because the fossil pollen spectra can be matched well to nearby modern pollen assemblages throughout the Holocene. In the eastern part of China, the temporal variation of pollen diversity is relatively stable until the sharp decrease in pollen diversity (including beta diversity) after ca. 2 cal. ka BP, which could indicate that land use was sustainable for long-term maintenance of regional plant diversity until 2 millennia ago (Li et al., 2009; Zong et al., 2007). Land use became less sustainable from ca. 2 cal. ka BP, likely causing a significant decrease in species and community diversities in eastern China as a strongly human-impacted landscape began to form with widespread farmland and patchy forest restricted to mountainous areas (Li et al., 2009). This knowledge suggests people and government should pay more attention in protecting the diversity of species and communities of the patchy forest, because this is where the main plant refugia will be found.

Finally, as both modern pollen assemblages and fossil pollen spectra after ca. 2 cal. ka BP are already impacted by human activities, past vegetation and climate reconstructions based on modern pollen-vegetation and pollen-climate relationships should be

completed with caution for the eastern part of China, because the relationship linking vegetation and climate may be distorted.

5 | CONCLUSIONS

By assessing the quality of modern analogues, and estimating the pollen diversity for Holocene fossil pollen spectra from China, we conclude that human impact on vegetation comparable to modern human disturbance starts after 2 cal. ka BP in the eastern part of China (north-central, east, and south China) where there is a long history and high intensity of human activities. Human disturbance to vegetation is represented by reduced pollen diversity together with simpler and more homogeneous pollen assemblages. For the non-forest plant communities in western China (Tibetan Plateau and north-west China), pollen data with low taxonomical levels of identification and using only the presence/absence of taxa rather than their relative composition (in percentage) are unable to provide robust evidence of non-natural disturbance of vegetation at a regional spatial scale. As our results imply that the modern and late Holocene pollen assemblages from eastern China may have been disturbed by human activities, pollen-based reconstructions of changes in climate and potential vegetation over the last 2 ka should be interpreted with caution.

AUTHOR CONTRIBUTIONS

Research conception and design by Xianyong Cao, Fang Tian, and Fahu Chen; data analyses by Xianyong Cao, Fang Tian, Wenjia Li, and Mingyu Luo; figures and appendixes preparation by Wenjia Li and Yanrong Zhang; pollen data collection by Ulrike Herzschuh, Jian Ni, Qinghai Xu, and Fahu Chen; and initial manuscript draft by Xianyong Cao. Manuscript revisions were contributed by all co-authors.

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CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

DATA AVAILABILITY STATEMENT

Both of the modern and Holocene pollen datasets that support the findings of this study are openly available at the National Tibetan Plateau Data Center (DOI: [10.11888/Paleoenv.tpdc.272378](https://doi.org/10.11888/Paleoenv.tpdc.272378) and [10.11888/Paleoenv.tpdc.272379](https://doi.org/10.11888/Paleoenv.tpdc.272379), respectively). Similar datasets can be found in publication Herzschuh et al. (2019) at <http://doi.org/10.1038/s41467-019-09866-8>.

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REFERENCES

- Abel, C., Horion, S., Tagesson, T., Keersmaecker, W. D., Seddon, A. W. R., Abdi, A. M., & Fensholt, R. (2021). The human-environment nexus and vegetation-rainfall sensitivity in tropical drylands. *Nature Sustainability*, 4, 25–32. <https://doi.org/10.1038/s41893-020-00597-z>
- Andersen, K. K., Azuma, N., Barnola, J. M., Bigler, M., Biscaye, P., Caillon, N., Chappellaz, J., Clausen, H. B., Dahl-Jensen, D., Fischer, H., Flückiger, J., Fritzsche, D., Fujii, Y., Goto-Azuma, K., Grønbold, K., Gundestrup, N. S., Hansson, M., Huber, C., Hvidberg, C. S., ... White, J. W. C. (2004). High resolution record of Northern Hemisphere climate extending into the last interglacial period. *Nature*, 431, 147–151. <https://doi.org/10.1038/nature02805>
- Anderson, M. J., Crist, T. O., Chase, J. M., Vellend, M., Inouye, B. D., Freestone, A. L., Sanders, N. J., Cornell, H. V., Comita, L. S., Davies, K. F., Harrison, S. P., Kraft, N. J. B., Stegen, J. C., & Swenson, N. G. (2011). Navigating the multiple meanings of β diversity: a roadmap for the practicing ecologist. *Ecology Letters*, 14, 19–28. <https://doi.org/10.1111/j.1461-0248.2010.01552.x>
- Birks, H. J. B., Line, J. M., Juggins, S., Stevenson, A. C., & ter Braak, C. J. F. (1990). Diatoms and pH reconstruction. *Philosophical Transactions of the Royal Society of London B*, 327, 263–278. <https://doi.org/10.1098/rstb.1990.0062>
- Blaauw, M., & Christen, J. A. (2011). Flexible paleoclimate age-depth models using an autoregressive gamma process. *Bayesian Analysis*, 6, 457–474. <https://doi.org/10.1214/11-BA618>
- Bordon, A., Peyron, O., Lezine, A. M., Lezine, A. M., Brewer, S., & Fouache, E. (2009). Pollen-inferred late-glacial and holocene climate in the southern Balkans (Lake Maliq). *Quaternary International*, 200, 19–30. <https://doi.org/10.1016/j.quaint.2008.05.014>
- Cao, X., Herzschuh, U., Ni, J., Zhao, Y., & Böhmer, T. (2015). Spatial and temporal distributions of major tree taxa in eastern continental Asia during the last 22,000 yr. *The Holocene*, 25, 79–91. <https://doi.org/10.1177/0959683614556385>
- Cao, X., Ni, J., Herzschuh, U., & Wang, Y. (2013). A late Quaternary pollen dataset from eastern continental Asia for vegetation and climate reconstructions: Set up and evaluation. *Review of Palaeobotany and Palynology*, 194, 21–37. <https://doi.org/10.1016/j.revpa.2013.02.003>
- Cao, X., Tian, F., Andreev, A., Anderson, P. M., Lozhkin, A. V., Bezrukova, E., Ni, J., Rudaya, N., Stobbe, A., Wieczorek, M., & Herzschuh, U. (2020). A taxonomically harmonized and temporally standardized fossil pollen dataset from Siberia covering the last 40 kyr. *Earth System Science Data*, 12, 119–135. <https://doi.org/10.5194/essd-12-119-2020>
- Cao, X., Tian, F., Li, K., Ni, J., Yu, X., Liu, L., & Wang, N. (2021). Lake surface-sediment pollen dataset from the alpine meadow vegetation type from the eastern Tibetan Plateau and its potential in past climate reconstructions. *Earth System Science Data*, 13, 3525–3537. <https://doi.org/10.5194/essd-13-3525-2021>
- Cao, X., Tian, F., Telford, R. J., Ni, J., Xu, Q., Chen, F., Liu, X., Stebich, M., Zhao, Y., & Herzschuh, U. (2017). Impacts of the spatial extent of pollen-climate calibration-set on the absolute values, range and trends of reconstructed Holocene precipitation. *Quaternary Science Reviews*, 178, 37–53. <https://doi.org/10.1016/j.quascirev.2017.10.030>
- Cao, X., Xu, Q., Jing, Z., Tang, J., Li, Y., & Tian, F. (2010). Holocene climate change and human impacts implied from the pollen records in Anyang, central China. *Quaternary International*, 227, 3–9. <https://doi.org/10.1016/j.quaint.2010.03.019>
- Cao, X. Y., Herzschuh, U., Telford, R. J., & Ni, J. (2014). A modern pollen-climate dataset from China and Mongolia: assessing its potential for climate reconstruction. *Review of Palaeobotany and Palynology*, 211, 87–96. <https://doi.org/10.1016/j.revpa.2014.08.007>
- Chen, F., Jia, J., Chen, J., Li, G., Zhang, X., Xie, H., Xia, D., Huang, W., & An, C. (2016). A persistent Holocene wetting trend in arid central Asia, with wettest conditions in the late Holocene, revealed by multi-proxy analyses of loess-paleosol sequences in Xinjiang, China. *Quaternary Science Reviews*, 146, 134–146. <https://doi.org/10.1016/j.quascirev.2016.06.002>
- Chen, F. H., Dong, G. H., Zhang, D. J., Liu, X. Y., Jia, X., An, C. B., Ma, M. M., Xie, Y. W., Barton, L., Ren, L. L., Zhao, Z. J., Wu, X. H., & Jones, M. K. (2015). Agriculture facilitated permanent human occupation of the Tibetan Plateau after 3600 BP. *Science*, 347(6219), 248–250. <https://doi.org/10.1126/science.1259172>
- Chen, F. H., Xu, Q. H., Chen, J. H., Birks, H. J. B., Liu, J. B., Zhang, S. R., Jin, L. Y., An, C. B., Telford, R. J., Cao, X. Y., Wang, Z. L., Zhang, X. J., Selvaraj, K., Lu, H. Y., Li, Y. C., Zheng, Z., Wang, H. P., Zhou, A. F., Dong, G. H., ... Rao, Z. G. (2015). East Asian summer monsoon precipitation variability since the last deglaciation. *Scientific Reports*, 5, 11186. <https://doi.org/10.1038/srep11186>
- Chen, S., Liu, J., Wang, X., Zhao, S., Chen, J., Qiang, M., Liu, B., Xu, Q., Xia, D., & Chen, F. (2021). Holocene dust storm variations over northern China: transition from a natural forcing to an anthropogenic forcing. *Science Bulletin*, 66(24), 2516–2527. <https://doi.org/10.1016/j.scib.2021.08.008>
- Cheng, H., Edwards, R. L., Sinha, A., Spötl, C., Yi, L., Chen, S., Kelly, N., Kathayat, G., Wang, X., Li, X., Kong, X., Wang, Y., Ning, Y., & Zhang, H. (2016). The Asian monsoon over the past 640,000 years and ice age terminations. *Nature*, 534, 640–646. <https://doi.org/10.1038/nature18591>
- Ding, W., Xu, Q., & Tarasov, P. E. (2017). Examining bias in pollen-based quantitative climate reconstructions induced by human impact on vegetation in China. *Climate of the Past*, 13, 1285–1300. <https://doi.org/10.5194/cp-13-1285-2017>
- Furrer, R., Nychka, D., & Sain, S. (2013). *fields: Tools for spatial data, version 6.8*. <http://cran.r-project.org/web/packages/fields/index.html>
- Gower, J. C. (1971). Statistical methods of comparing different multivariate analyses of the same data. In F. R. Hodson, D. G. Kendall, & P. Tautou (Eds.), *Mathematics in the archaeological and historical sciences* (pp. 138–149). Edinburgh University Press.
- Hao, J., Xu, G., Luo, L., Zhang, Z., Yang, H., & Li, H. (2020). Quantifying the relative contribution of natural and human factors to vegetation coverage variation in coastal wetlands in China. *Catena*, 188, 104429. <https://doi.org/10.1016/j.catena.2019.104429>
- He, J., Yang, K., Tang, W., Lu, H., Qin, J., Chen, Y., & Li, X. (2020). The first high-resolution meteorological forcing dataset for land process studies over China. *Scientific Data*, 7, 25. <https://doi.org/10.1038/s41597-020-0369-y>
- Herzschuh, U., Birks, H. J. B., Ni, J., Zhao, Y., Liu, H., Liu, X., & Grosse, G. (2010). Holocene land-cover changes on the Tibetan Plateau. *The Holocene*, 20(1), 91–104. <https://doi.org/10.1177/0959683609348882>
- Herzschuh, U., Cao, X., Laepple, T., Dallmeyer, A., Telford, R. J., Ni, J., Chen, F., Kong, Z., Liu, G., Liu, K.-B., Liu, X., Stebich, M., Tang, L., Tian, F., Wang, Y., Wischniewski, J., Xu, Q., Yan, S., Yang, Z., ... Zheng, Z. (2019). Position and orientation of the westerly jet determined Holocene rainfall patterns in China. *Nature Communications*, 10, 2376. <https://doi.org/10.1038/s41467-019-09866-8>

- Herzschuh, U., Ni, J., Birks, H. J. B., & Böhner, J. (2011). Driving forces of mid-Holocene vegetation shifts on the upper Tibetan Plateau, with emphasis on changes in atmospheric CO₂ concentrations. *Quaternary Science Reviews*, 30, 1907–1917. <https://doi.org/10.1016/j.quascirev.2011.03.007>
- Hill, M. O., & Gauch, H. G. (1980). Detrended correspondence analysis: An improved ordination technique. *Vegetation*, 42, 47–58. https://doi.org/10.1007/978-94-009-9197-2_7
- Hou, H. Y. (1983). Vegetation of China with reference to its geographical distribution. *Annals of the Missouri Botanical Garden*, 70, 509–549. <https://doi.org/10.2307/2992085>
- Huang, X., Liu, S., Dong, G., Qiang, M., Bai, Z., Zhao, Y., & Chen, F. (2017). Early human impacts on vegetation on the northeastern Qinghai-Tibetan Plateau during the middle to late Holocene. *Progress in Physical Geography*, 41(3), 286–301. <https://doi.org/10.1177/0309133317703035>
- Huang, X., Ren, X., Chen, X., Zhang, J., Zhang, X., Shen, Z., Hu, Y., & Chen, F. (2021). Anthropogenic mountain forest degradation and soil erosion recorded in the sediments of Mayinghai Lake in northern China. *Catena*, 207, 105597. <https://doi.org/10.1016/j.catena.2021.105597>
- Huang, X., Zhang, J., Ren, L., Zhang, S., & Chen, F. (2021). Intensification and driving forces of pastoralism in Northern China 5.7 ka ago. *Geophysical Research Letters*, 48(7), e2020GL092288. <https://doi.org/10.1029/2020GL092288>
- Jackson, D. (1995). PROTEST: a PROcrustean randomization TEST of community environment concordance. *Écoscience*, 2, 297–303. <https://doi.org/10.1080/11956860.1995.11682297>
- Jiang, H., Xu, X., Guan, M., Wang, L., Huang, Y., & Jiang, Y. (2020). Determining the contributions of climate change and human activities to vegetation dynamics in agro-pastoral transitional zone of northern China from 2000 to 2015. *Science of the Total Environment*, 718, 134871. <https://doi.org/10.1016/j.scitotenv.2019.134871>
- Juggins, S. (2018). *rioja: Analysis of quaternary science data, version 0.9-15.1*. <http://cran.r-project.org/web/packages/rioja/index.html>
- Kou, P., Xu, Q., Jin, Z., Yunus, A. P., Luo, X., & Liu, M. (2021). Complex anthropogenic interaction on vegetation greening in the Chinese Loess Plateau. *Science of the Total Environment*, 778, 146065. <https://doi.org/10.1016/j.scitotenv.2021.146065>
- Laskar, J., Robutel, P., Joutel, F., Gastineau, M., Correia, A. C. M., & Levrard, B. (2004). A long-term numerical solution for the insolation quantities of the Earth. *Astronomy and Astrophysics*, 428, 261–285. <https://doi.org/10.1051/0004-6361:20041335>
- Li, F., Gaillard, M.-J., Cao, X., Herzschuh, U., Sugita, S., Tarasov, P. E., Wagner, M., Xu, Q., Ni, J., Wang, W., Zhao, Y., An, C., Beusen, A. H. W., Chen, F., Feng, Z., Goldewijk, C. G. M. K., Huang, X., Li, Y., Li, Y., ... Jia, X. (2020). Towards quantification of Holocene anthropogenic land-cover change in temperate China: A review in the light of pollen-based REVEALS reconstructions of regional plant cover. *Earth-Science Reviews*, 203, 103119. <https://doi.org/10.1016/j.earscirev.2020.103119>
- Li, M., Xu, Q., Zhang, S., Li, Y., Ding, W., & Li, J. (2015). Indicator pollen taxa of human-induced and natural vegetation in Northern China. *The Holocene*, 25, 686–701. <https://doi.org/10.1177/0959683614566219>
- Li, Q., Wu, H., Yu, Y., Sun, A., Marković, S. B., & Guo, Z. (2014). Reconstructed moisture evolution of the deserts in northern China since the last glacial maximum and its implications for the East Asian summer monsoon. *Global and Planetary Change*, 121, 101–112. <https://doi.org/10.1016/j.gloplacha.2014.07.009>
- Li, X., Dodson, J., Zhou, J., & Zhou, X. (2009). Increasing of population and expansion of rice agriculture in Asia, and anthropogenic methane emissions since 5000 BP. *Quaternary International*, 202, 41–50. <https://doi.org/10.1016/j.quaint.2008.02.009>
- Liu, H., Jiao, F., Yin, J., Li, T., Gong, H., Wang, Z., & Lin, Z. (2020). Nonlinear relationship of vegetation greening with nature and human factors and its forecast – A case study of Southwest China. *Ecological Indicators*, 111, 106009. <https://doi.org/10.1016/j.ecolind.2019.106009>
- Liu, J., Shen, Z., Chen, W., Chen, J., Zhang, X., Chen, J., & Chen, F. (2020). Dipolar mode of precipitation changes between north China and the Yangtze River Valley existed over the entire Holocene: Evidence from the sediment record of Nanyi Lake. *International Journal of Climatology*, 41, 1667–1681. <https://doi.org/10.1002/joc.6906>
- Liu, J. B., Chen, J. H., Zhang, X. J., Li, Y., Rao, Z. G., & Chen, F. H. (2015). Holocene East Asian summer monsoon records in northern China and their inconsistency with Chinese stalagmite δ¹⁸O records. *Earth-Science Reviews*, 148, 194–208. <https://doi.org/10.1016/j.earscirev.2015.06.004>
- Liu, L., Wang, W., Chen, D., Niu, Z., Wang, Y., Cao, X., & Ma, Y. (2020). Soil-surface pollen assemblages and quantitative relationships with vegetation and climate from the Inner Mongolian Plateau and adjacent mountain areas of northern China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 543, 109600. <https://doi.org/10.1016/j.palaeo.2020.109600>
- Liu, S., Kruse, S., Scherler, D., Ree, R. H., Zimmermann, H. H., Stoof-Leichsenring, K. R., Epp, L. S., Mischke, S., & Herzschuh, U. (2021). Sedimentary ancient DNA reveals a threat of warming-induced alpine habitat loss to Tibetan Plateau plant diversity. *Nature Communications*, 12, 2995. <https://doi.org/10.1038/s41467-021-22986-4>
- Liu, Z., Wen, X., Brady, E. C., Otto-Bliesner, B., Yu, G., Lu, H., Cheng, H., Wang, Y., Zheng, W., Ding, Y., Edwards, R. L., Cheng, J., Liu, W., & Yang, H. (2014). Chinese cave records and the East Asia summer monsoon. *Quaternary Science Reviews*, 83, 115–128. <https://doi.org/10.1016/j.quascirev.2013.10.021>
- Lu, H., Zhang, J., Liu, K.-B., Wu, N., Li, Y., Zhou, K., Ye, M., Zhang, T., Zhang, H., Yang, X., Shen, L., Xu, D., & Li, Q. (2009). Earliest domestication of common millet (*Panicum miliaceum*) in East Asia extended to 10,000 years ago. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 7367–7372. <https://doi.org/10.1073/pnas.0900158106>
- Ma, Z., Guo, J., Li, W., Cai, Z., & Cao, S. (2020). Regional differences in the factors that affect vegetation cover in China. *Land Degradation and Development*, 32(5), 1961–1969. <https://doi.org/10.1002/ldr.3847>
- Martin, C. A., Proulx, R., Vellend, M., & Fahrig, L. (2021). How the relationship between vegetation cover and land-cover variance constrains biodiversity in a human dominated world. *Landscape Ecology*, 36, 3097–3104. <https://doi.org/10.1007/s10980-021-01312-9>
- Miehe, G., Miehe, S., Bach, K., Kluge, J., Wesche, K., Yang, Y., & Liu, H. (2011). Ecological stability during the LGM and the mid-Holocene in the alpine steppes of Tibet? *Quaternary Research*, 76, 243–252. <https://doi.org/10.1016/j.yqres.2011.06.002>
- Miehe, G., Miehe, S., Böhner, J., Kaiser, K., Hensen, I., Madsen, D., Liu, J., & Opgenoorth, L. (2014). How old is the human footprint in the world's largest alpine ecosystem? A review of multiproxy records from the Tibetan Plateau from the ecologists' viewpoint. *Quaternary Science Reviews*, 86, 190–209. <https://doi.org/10.1016/j.quascirev.2013.12.004>
- Miehe, G., Miehe, S., Kaiser, K., Reudenbach, C., Behrendes, L., Duo, L., & Schlütz, F. (2009). How old is pastoralism in Tibet? An ecological approach to the making of a Tibetan landscape. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 276, 130–147. <https://doi.org/10.1016/j.palaeo.2009.03.005>
- Miehe, G., Schless, P.-M., Seeber, E., Babel, W., Biermann, T., Braendle, M., Chen, F., Coners, H., Foken, T., Gerken, T., Graf, H.-F., Guggenberger, G., Hafner, S., Holzapfel, M., Ingris, J., Kuzyakov, Y., Lai, Z., Lehnert, L., Leuschner, C., ... Wesche, K. (2019). The *Kobresia pygmaea* ecosystem of the Tibetan highlands – Origin, functioning

- and degradation of the world's largest pastoral alpine ecosystem: *Kobresia* pastures of Tibet. *Science of the Total Environment*, 648, 754–771. <https://doi.org/10.1016/j.scitotenv.2018.08.164>
- Mipam, T.-D., Zhong, L.-L., Liu, J.-Q., Mieke, G., & Tian, L.-M. (2019). Productive overcompensation of alpine meadows in response to Yak grazing in the Eastern Qinghai-Tibet Plateau. *Frontiers in Plant Science*, 10, 925. <https://doi.org/10.3389/fpls.2019.00925>
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H., Szoecs, E., & Wagner, H. (2019). *vegan: Community ecology package, version 2.5-4*. <https://cran.r-project.org/web/packages/vegan/index.html>
- Pailler, D., & Bard, E. (2002). High frequency paleoceanographic changes during the past 140,000 years recorded by the organic matter in sediments off the Iberian Margin. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 181, 431–452. [https://doi.org/10.1016/S0031-0182\(01\)00444-8](https://doi.org/10.1016/S0031-0182(01)00444-8)
- Pang, R., Xu, Q., Ding, W., & Zhang, S. (2011). Pollen assemblages of cultivated vegetation in central and southern Hebei Province. *Journal of Geographical Sciences*, 21(3), 549–560. <https://doi.org/10.1007/s11442-011-0863-4>
- Peres-Neto, P., & Jackson, D. (2001). How well do multivariate data sets match? The advantages of a Procrustean superimposition approach over the Mantel test. *Oecologia*, 129, 169–178. <https://doi.org/10.1007/s004420100720>
- Piao, S., Yin, G., Tan, J., Cheng, L., Huang, M., Li, Y., Liu, R., Mao, J., Myneni, R. B., Peng, S., Poulter, B., Shi, X., Xiao, Z., Zeng, N., Zeng, Z., & Wang, Y. (2015). Detection and attribution of vegetation greening trend in China over the last 30 years. *Global Change Biology*, 21(4), 1601–1609. <https://doi.org/10.1111/gcb.12795>
- Prentice, I. C. (1980). Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Review of Palaeobotany and Palynology*, 31, 71–104. [https://doi.org/10.1016/0034-6667\(80\)90023-8](https://doi.org/10.1016/0034-6667(80)90023-8)
- Qu, S., Wang, L., Lin, A., Yu, D., Yuan, M., & Li, C. (2020). Distinguishing the impacts of climate change and anthropogenic factors on vegetation dynamics in the Yangtze River Basin, China. *Ecological Indicators*, 108, 105724. <https://doi.org/10.1016/j.ecolind.2019.105724>
- R Core Team. (2019). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.
- Reimer, P. J., Baillie, M. G. L., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Bronk Ramsey, C., Buck, C. E., Burr, G. S., Edwards, R. L., Friedrich, M., Grootes, P. M., Guilderson, T. P., Hajdas, I., Heaton, T. J., Hogg, A. G., Hughen, K. A., Kaiser, K. F., Kromer, B., ... Weyhenmeyer, C. E. (2009). IntCal09 and Marine09 radiocarbon age calibration curves, 0–50,000 years cal BP. *Radiocarbon*, 51(4), 1111–1150. <https://doi.org/10.1017/S0033822200034202>
- Ren, G. (2007). Changes in forest cover in China during the Holocene. *Vegetation History and Archaeobotany*, 16, 119–126. <https://doi.org/10.1007/s00334-006-0075-5>
- Rolls, R. J., Chessman, B. C., Heino, J., Wolfenden, B., Grown, I. O., Cheshire, K. J. M., Curwen, G., Ryan, D., & Butler, G. L. (2021). Consequences of hydrological alteration for beta diversity of fish assemblages at multiple spatial scales. *Science of the Total Environment*, 798, 149170. <https://doi.org/10.1016/j.scitotenv.2021.149170>
- Schlütz, F., & Lehmkuhl, F. (2009). Holocene climatic change and the nomadic Anthropocene in Eastern Tibet: Palynological and geomorphological results from Nianbaoyeze Mountains. *Quaternary Science Reviews*, 28, 1449–1471. <https://doi.org/10.1016/j.quascirev.2009.01.009>
- Shi, Y., Jin, N., Ma, X., Wu, B., He, Q., Yue, C., & Yu, Q. (2020). Attribution of climate and human activities to vegetation change in China using machine learning techniques. *Agricultural and Forest Meteorology*, 294, 108146. <https://doi.org/10.1016/j.agrfor.2020.108146>
- Simpson, E. H. (1949). Measurement of diversity. *Nature*, 163(4148), 688. <https://doi.org/10.1038/163688a0>
- Tarasov, P. E., Nakagawa, T., Demska, D., Österle, H., Igarashi, Y., Kitagawa, J., Mikhova, L. M., Bazarova, V. B., Okuda, M., Gotanda, K., Miyoshi, N., Fujiki, T., Takemura, K., Yonenobu, H., & Fleck, A. (2011). Progress in the reconstruction of Quaternary climate dynamics in the Northwest Pacific: A new modern analogue reference dataset and its application to the 430-kyr pollen record from Lake Biwa. *Earth-Science Reviews*, 108(1–2), 64–79. <https://doi.org/10.1016/j.earscirev.2011.06.002>
- ter Braak, C. J. F., & Verdonschot, P. F. M. (1995). Canonical correspondence analysis and related multivariate methods in aquatic ecology. *Aquatic Sciences*, 57, 255–289. <https://doi.org/10.1007/BF00877430>
- Tian, F., Cao, X., Dallmeyer, A., Lohmann, G., Zhang, X., Ni, J., Andreev, A., Anderson, P. M., Lozhkin, A. V., Bezrukova, E., Rudaya, N., Xu, Q., & Herzschuh, U. (2018). Biome changes and their inferred climatic drivers in northern and eastern continental Asia at selected times since 40 cal ka BP. *Vegetation History and Archaeobotany*, 27, 365–379. <https://doi.org/10.1007/s00334-017-0653-8>
- Tian, F., Cao, X., Dallmeyer, A., Ni, J., Zhao, Y., Wang, Y., & Herzschuh, U. (2016). Quantitative woody cover reconstructions from eastern continental Asia of the last 22 ka reveal strong regional peculiarities. *Quaternary Science Reviews*, 137, 33–44. <https://doi.org/10.1016/j.quascirev.2016.02.001>
- Wang, C., Lu, H., Zhang, J., Gu, Z., & He, K. (2014). Prehistoric demographic fluctuations in China inferred from radiocarbon data and their linkage with climate change over the past 50,000 years. *Quaternary Science Reviews*, 98, 45–59. <https://doi.org/10.1016/j.quascirev.2014.05.015>
- Wang, N., Liu, L., Zhang, Y., & Cao, X. (2022). A modern pollen data set for the forest-meadow-steppe ecotone from the Tibetan Plateau and its potential use in past vegetation reconstruction. *Boreas*. <https://doi.org/10.1111/bor.12589>
- Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters*, 19(5), 510–518. <https://doi.org/10.1111/ele.12582>
- Wang, X., Li, Y., Xu, Q., Cao, X., Zhang, L., & Tian, F. (2010). Pollen assemblages from different agricultural units and their spatial distribution in Anyang area. *Chinese Science Bulletin*, 55(6), 544–554. <https://doi.org/10.1007/s11434-009-0480-0>
- Wang, Y., Heberling, G., Görzen, E., Mieke, G., Seeber, E., & Wesche, K. (2017). Combined effects of livestock grazing and abiotic environment on vegetation and soils of grasslands across Tibet. *Applied Vegetation Science*, 20, 327–339. <https://doi.org/10.1111/avsc.12312>
- Wei, H., Chongyi, E., Duan, R., Zhang, J., Sun, Y., Hou, G., & Gao, J. (2021). Fungal spore record of pastoralism on the NE Qinghai-Tibetan Plateau since the middle Holocene. *Science China Earth Sciences*, 64, 1318–1331. <https://doi.org/10.1007/s11430-020-9787-4>
- Wu, L., Wang, X., Zhang, G., & Xiao, X. (2008). Vegetation and climate evolution since the Holocene recorded by pollen-charcoal assemblages from lacustrine sediments of Chaohu Lake in Anhui Province. *Journal of Palaeogeography*, 10(2), 183–192 (in Chinese with English abstract).
- Xiao, X., Yao, A., Hillman, A., Shen, J., & Haberle, S. G. (2020). Vegetation, climate and human impact since 20 ka in central Yunnan Province based on high-resolution pollen and charcoal records from Dianchi, southwestern China. *Quaternary Science Reviews*, 236, 106297. <https://doi.org/10.1016/j.quascirev.2020.106297>
- Xu, Q., Chen, F., Zhang, S., Cao, X., Li, J., Li, Y., Li, M., Chen, J., Liu, J., & Wang, Z. (2017). Vegetation succession and East Asian summer monsoon changes since the last deglaciation inferred from high-resolution pollen record in Gonghai Lake, Shanxi Province, China. *The Holocene*, 27(6), 835–846. <https://doi.org/10.1177/0959683616675941>

- Yang, S., Zheng, Z., Huang, K., Zong, Y., Wang, J., Xu, Q., Rolett, B. V., & Li, J. (2012). Modern pollen assemblages from cultivated rice fields and rice pollen morphology: Application to a study of ancient land use and agriculture in the Pearl River Delta, China. *The Holocene*, 22(12), 1393–1404. <https://doi.org/10.1177/0959683612449761>
- Yang, X., Wan, Z., Perry, L., Lu, H., Qang, Q., Zhao, C., Li, J., Xie, F., Yu, J., Cui, T., Wang, T., Li, M., & Ge, Q. (2012). Early millet use in northern China. *Proceedings of the National Academy of Sciences of the United States of America*, 109, 3726–3730. <https://doi.org/10.1073/pnas.1115430109>
- Yao, F., Ma, C., Zhu, C., Li, J., Chen, G., Tang, L., Huang, M., Jia, T., & Xu, J. (2017). Holocene climate change in the western part of Taihu Lake region, East China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485, 963–973. <https://doi.org/10.1016/j.palaeo.2017.08.022>
- Yin, L., Dai, E., Zheng, D., Wang, Y., Ma, L., & Tong, M. (2020). What drives the vegetation dynamics in the Hengduan Mountain region, southwest China: Climate change or human activity? *Ecological Indicators*, 112, 106013. <https://doi.org/10.1016/j.ecolind.2019.106013>
- Yue, Y., Zheng, Z., Rolett, B. V., Ma, T., Chen, C., Huang, K., Lin, G., Zhu, G., & Cheddadi, R. (2015). Holocene vegetation, environment and anthropogenic influence in the Fuzhou Basin, southeast China. *Journal of Asian Earth Sciences*, 99, 85–94. <https://doi.org/10.1016/j.jseaes.2014.12.004>
- Zhang, D. (2013). *The surface pollen assemblages and their relationships with climate in the middle and lower reaches of the Talung Zangbo River* (Master thesis). Southwestern University (in Chinese with English abstract).
- Zhang, K., Zhao, Y., Zhou, A., & Sun, H. (2010). Late Holocene vegetation dynamic and human activities reconstructed from lake records in western Loess Plateau, China. *Quaternary International*, 227, 38–45. <https://doi.org/10.1016/j.quaint.2010.04.019>
- Zhao, C., Yan, Y., Ma, W., Shang, X., Chen, J., Rong, Y., Xie, T., & Quan, Y. (2021). RESTREND-based assessment of factors affecting vegetation dynamics on the Mongolian Plateau. *Ecological Modelling*, 440, 109415. <https://doi.org/10.1016/j.ecolmodel.2020.109415>
- Zhao, L., Ma, C., Leipe, C., Long, T., Liu, K.-B., Lu, H., Tang, L., Zhang, Y., Wagner, M., & Tarasov, P. E. (2017). Holocene vegetation dynamics in response to climate change and human activities derived from pollen and charcoal records from southeastern China. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 485, 644–660. <https://doi.org/10.1016/j.palaeo.2017.06.035>
- Zheng, Z., Ma, T., Roberts, P., Li, Z., Yue, Y., Peng, H., Huang, K., Han, Z., Wan, Q., Zhang, Y., Zhang, X., Zheng, Y., & Satio, Y. (2021). Anthropogenic impacts on Late Holocene land-cover change and floristic biodiversity loss in tropical southeastern Asia. *Proceedings of the National Academy of Sciences of the United States of America*, 118(40), e2022210118. <https://doi.org/10.1073/pnas.2022210118>
- Zhu, Z., Feinberg, J. M., Xie, S., Bourne, M., Huang, C., Hu, C., & Cheng, H. (2017). Holocene ENSO-related cyclic storms recorded by magnetic minerals in speleothems of central China. *Proceedings of the National Academy of Sciences of the United States of America*, 114(5), 852–857. <https://doi.org/10.1073/pnas.1610930114>
- Zong, Y., Chen, Z., Innes, J. B., Chen, C., Wang, Z., & Wang, H. (2007). Fire and flood management of coastal swamp enabled first rice paddy cultivation in east China. *Nature*, 449, 459–462. <https://doi.org/10.1038/nature06135>

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