Distribution Characteristics of Surface Soil Sporopollen and Their Influencing Factors in the Monsoon Marginal Zones of China: Postprint

Authors: Wu Siqi, Wei Haiqin, Chen Chunzhu, Weiss, Zhao Wenwei, Li Huan, Sun Yi, Jiang Qingfeng, Zhang Xiaojian, Zhao Yan

Date: 2025-02-27T00:00:00+00:00

Abstract

Investigating the distribution characteristics of surface soil pollen and their influencing factors in the monsoon margin area of China contributes to improving the reliability of reconstructing regional vegetation and paleo-monsoon evolution using fossil pollen. Through pollen analysis of surface soil samples from 38 sampling sites (annual precipitation range: 30–650 mm) in the monsoon margin area of China, this study examines the relationship between surface soil pollen assemblage characteristics and climate as well as human activities. The results indicate that: (1) In low-altitude temperate grassland regions with relatively warm and dry climate, the pollen assemblage is dominated by Amaranthaceae and Artemisia, and the Artemisia/Chenopodiaceae ratio (A/C ratio) generally follows the same trend as mean annual precipitation changes. (2) In high-altitude alpine grassland and meadow regions of the monsoon margin area of China with relatively cold and humid climate, the pollen assemblage is dominated by Cyperaceae, Asteraceae, and Poaceae, the average sum of percentages for Artemisia and Amaranthaceae pollen is 25.8%, and the A/C ratio in this region shows no significant correlation with mean annual precipitation. (3) The correlation between total arboreal and shrub pollen percentage and mean annual temperature/temperature of the warmest month is stronger than that with mean annual precipitation. (4) These pollen assemblage characteristics reflect the distribution patterns of vegetation and hydrothermal conditions along altitudinal gradients in the monsoon margin area of China, and Redundancy Analysis (RDA) of pollen data also clearly reveals the distribution of pollen assemblages and major pollen types along gradients of temperature of the warmest month and altitude. Furthermore, the abundant occurrence of fungal spores in the soil surface of alpine regions in the study area reflects environmental characteristics of high grazing intensity accompanied by high soil erosion rates.

Full Text

Distribution Characteristics and Influencing Factors of Surface Soil Pollen in the Marginal Monsoon Region of China

WU Siqi[1], **WEI Haiqin**[2], **CHEN Chunzhu**[1], **WEI Lisi**[1], **ZHAO Wenwei**[1], **LI Huan**[1], **SUN Yi**[1], **JIANG Qingfeng**[1], **ZHANG Xiaojian**[3], **ZHAO Yan**[4]

[1]School of Geographic Science, Nantong University, Nantong 226019, Jiangsu, China
[2]Shanwang National Nature Reserve Management and Conservation Center at Linqu, Weifang 262617, Shandong, China
[3]School of Geography and Ocean Sciences, Nanjing University, Nanjing 210023, Jiangsu, China
[4]Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, Beijing, China

Abstract

Studying the distribution characteristics of surface soil pollen in the marginal monsoon region of China and their influencing factors helps improve the reliability of reconstructing regional vegetation and paleo-monsoon evolution from fossil pollen records. Through pollen analysis of surface soil samples from 38 sampling sites (with annual precipitation ranging from 30–650 mm) in the marginal monsoon region of China, this study investigates the relationships among surface pollen assemblages, climate, and human activities. The results indicate that: (1) In low-altitude temperate steppe regions with relatively warm and dry climates, pollen assemblages are dominated by Amaranthaceae and Artemisia, and the Artemisia/Chenopodiaceae (A/C) ratio generally aligns with trends in mean annual precipitation. (2) In high-altitude alpine steppe and meadow regions with relatively cold and humid climates, pollen assemblages are dominated by Cyperaceae, Asteraceae, and Poaceae. The summed percentages of Artemisia and Amaranthaceae pollen average 25.8%, and no significant correlation exists between the A/C ratio and mean annual precipitation in these regions. (3) The total percentage of tree and shrub pollen shows stronger correlations with mean annual temperature and warmest month temperature than with mean annual precipitation. (4) These pollen assemblage characteristics reflect the distribution patterns of vegetation and hydrothermal conditions along altitudinal gradients in the marginal monsoon region of China. Redundancy analysis (RDA) of the pollen data also clearly reveals the distribution of pollen assemblages and major pollen types along gradients of warmest month temperature and altitude. Additionally, the high abundance of fungal spores on soil surfaces in the alpine region reflects environmental characteristics associated with intensive grazing activity and high soil erosion rates.

Keywords: marginal monsoon region; surface soil pollen; vegetation; climate;

grazing intensity

1.1 Study Area Overview

The marginal monsoon region of China represents a unique ecological and climatic interface between the arid interior and humid coastal areas, serving as a critical ecological transition zone that is highly sensitive to climate change. In recent years, many scholars have used pollen records from this region to explore vegetation and monsoon evolution processes at different timescales [?]. However, due to differences in pollen production, dispersal pathways, dispersal capacity, sedimentation rates, and preservation conditions among various pollen types, the relationship between pollen and vegetation is relatively complex [?]. Therefore, studying the distribution characteristics of surface soil pollen and their influencing factors in the marginal monsoon region provides an important reference for reconstructing paleovegetation and paleoclimate from fossil pollen, thereby offering scientific insights into the vulnerability and resilience of ecosystems in this region.

Numerous scholars have conducted modern process studies of pollen in China' s marginal monsoon region [?]. For example, Li et al. [?] analyzed surface soil pollen from different vegetation types in northern China, noting significant differences in pollen assemblages among vegetation types and variable correlations with vegetation cover, with different pollen types showing varying representativeness. Additionally, studies on surface soil pollen from the Zoige Basin on the Tibetan Plateau, the Loess Plateau, and surrounding deserts have explored relationships between pollen assemblages, vegetation, and climate, identifying annual precipitation as the primary climatic factor influencing surface pollen composition [?]. Herzschuh [?] evaluated the reliability of modern pollen ratios for climate reconstruction on the eastern Tibetan Plateau. While these studies have advanced understanding of pollen-vegetation-climate-human activity relationships in their respective regions, China' s marginal monsoon region is vast with considerable variation in altitude, climate, and vegetation. Systematic research on modern pollen assemblage characteristics and their influencing factors across the entire region remains limited.

Furthermore, natural pastures are widely distributed in China' s marginal monsoon region, with a long history of grazing activity [?]. In addition to some anthropogenic pollen indicator species [?], coprophilous fungal spores in the fungal spore assemblage serve as effective indicators of animal activity and grazing behavior near sampling sites [?]. Among fungal spores, *Sporormiella* and *Sordaria* can indicate the expansion of livestock populations [?, ?]. Existing spore records show that varying degrees of grazing activity have occurred in China' s marginal monsoon region since the mid-to-late Holocene [?, ?]. Therefore, human activity represents another important factor influencing vegetation and pollen assemblages in this region.

This study collected 38 surface soil pollen samples covering the area along the northern margin of the monsoon from northeastern Inner Mongolia to southern Tibet. Using pollen percentage data and climatic parameters, we investigate the distribution characteristics of surface soil pollen and their influencing factors in China' s marginal monsoon region, providing data support for clarifying relationships among surface pollen, vegetation, climate, and human activities, and for improving the accuracy of quantitative paleoclimate reconstruction from fossil pollen.

The northern boundary of China's marginal monsoon region [**?**] extends from the eastern foothills of the Great Khingan Mountains, across the Inner Mongolian Plateau and the eastern Qilian Mountains, to the western Tibetan Plateau, involving four provinces/autonomous regions: Inner Mongolia, Gansu, Qinghai, and Tibet [Figure 1: see original paper]. The terrain gradually rises from east to west, spanning China' s first and second topographic steps, with plateau and mountain landforms dominating. The study area is primarily distributed across two geomorphic units—the Inner Mongolian Plateau and Tibetan Plateau—with a relatively arid climate and precipitation concentrated in June–September.

In the marginal monsoon region, the Inner Mongolian Plateau belongs to the temperate continental arid and semi-arid climate zone, with mean annual precipitation of 30–650 mm and mean annual temperature of -6–9°C. The Tibetan Plateau portion of the marginal monsoon region has mean annual precipitation of 80-360 mm and mean annual temperature of 1–9°C. Significant differences in topography and climate conditions across the marginal monsoon region lead to obvious differentiation of surface vegetation. In the northeastern corner of the Inner Mongolian Plateau near the Great Khingan Mountains, forest-steppe is the main vegetation type, with arboreal species dominated by spruce (*Picea*) and birch (*Betula*). The central Xilingol Plateau is primarily covered by zonal temperate steppe vegetation. Further west, desert-steppe vegetation and temperate desert gradually become dominant. In temperate steppe vegetation, Asteraceae (with *Artemisia* as the most diverse genus) is most abundant, followed by Poaceae, Fabaceae, Amaranthaceae, Ranunculaceae, Rosaceae, Cyperaceae, Brassicaceae, Polygonaceae, and Lamiaceae.

In the Tibetan Plateau region located on the northern boundary of monsoon influence, the main vegetation types are alpine scrub, meadow, and steppe. Cold-resistant Ericaceae and *Dasiphora arbuscula* often form alpine scrub. Various species of *Kobresia* (Cyperaceae), such as *Kobresia pygmaea*, *K. capillifolia*, and *K. prattii*, together with *Polygonum viviparum*, commonly form alpine meadows. Alpine steppe is composed of cold-resistant *Stipa purpurea*, *S. subsessiliflora* var. *basiplumosa*, *Carex moorcroftii*, the small semi-shrub *Artemisia salsoloides* var. *wellbyi*, *A. younghusbandii*, and cushion-shaped *A. minor* [**?**].

1.2 Field Sample Collection

From July to August 2021, we collected 38 surface soil pollen samples along the marginal monsoon region, covering Inner Mongolia, Gansu, Qinghai, and Tibet (Table 1) . The samples represent the main vegetation types in the study area. At each site, surface soil samples within a 0.5 m radius were collected using the five-point method and mixed. During sampling, aerial photography was conducted using an unmanned aerial vehicle to document the plant communities around each site, and GPS was used to record latitude, longitude, and elevation. The sampling sites range from 80.25°–118.2°E and 29.22°–48.2°N, with elevations reaching up to 4890 m and a minimum of 594 m.

1.3 Pollen Analysis

Pollen sample pretreatment was performed on 1–2 g of each sample. First, coarse particles were removed using a 180 m mesh, then one *Lycopodium* spore tablet (approximately 27,636 grains per tablet) was added as a tracer to calculate pollen concentration [?]. Samples were subsequently processed using acid-alkali treatment, acetolysis, and ultrasonic sieving (using a 7 m mesh) for pollen extraction [?]. Processed samples were preserved in glycerin in small test tubes for microscopic identification and counting. Pollen identification was conducted under a 400× microscope, primarily referring to *Pollen Flora of China* [?], *An Illustrated Handbook of Quaternary Pollen and Spores in China* [?], and *Study on Pollen Morphology of Plants from Dry and Semidry Areas in China* [?]. Except for a few samples with extremely low concentrations, each sample contained at least 300 identified terrestrial pollen grains. Spore and pollen percentages were calculated based on the total sum of terrestrial pollen, and Tilia software was used to plot pollen diagrams.

1.4 Data Processing

This study used interpolated climate data from 752 meteorological stations across China (http://data.cma.cn), obtained through thin-plate spline interpolation to derive climate data for the 38 pollen sampling sites [?]. Climate parameters included mean annual precipitation, warmest month precipitation, coldest month precipitation, mean annual temperature, warmest month temperature, and coldest month temperature. Major pollen types appearing in more than 10 samples with maximum percentages greater than 5% were selected from the pollen assemblages to analyze relationships between pollen assemblages and climate parameters. To enhance the signal-to-noise ratio, pollen percentage data were square-root transformed [?]. Detrended correspondence analysis (DCA) yielded an axis 1 gradient length of 2.1, indicating linear response characteristics, so redundancy analysis (RDA) was used to ordinate the pollen data [?]. RDA was employed to explore the contribution of different climate parameters to pollen assemblage distribution characteristics in the marginal monsoon region. In the RDA results, variance inflation factors (VIFs) for climate parameters indicated multicollinearity, requiring elimination and reanalysis.

2.1 Pollen Assemblage and Distribution Characteristics

A total of 56 pollen and spore types were identified in the 38 surface soil samples from the marginal monsoon region. Among these, frequently occurring terrestrial pollen types included *Artemisia*, Cyperaceae, Amaranthaceae, Poaceae, Asteraceae, *Picea*, *Alnus*, *Betula*, *Nitraria*, Brassicaceae, and Polygonaceae [Figure 2: see original paper]. Herbaceous pollen accounted for an average of 93.9% of the total assemblage, ranging from 84.9% to 99.1%. Additionally, fungal spores appeared frequently in some samples, mainly including *Glomus*, *Sordaria*, *Cercophora*, and *Sporormiella*, as well as other fungal spores (0%-109.1%).

Based on altitude, sampling sites were divided into temperate zone sites (samples 1-15, located in Inner Mongolia) and alpine zone sites (samples 16-38, located in Gansu, Qinghai, and Tibet), with distinct pollen assemblage characteristics between groups.

Temperate Zone: Herbaceous pollen absolutely dominates (93.9% on average, range 84.9%-99.1%). *Artemisia* and Amaranthaceae show the highest percentages, averaging 37.6% and 36.4%, respectively. Poaceae averages 11.2%, while Cyperaceae, Caryophyllaceae, and Brassicaceae average 1.0%-2.0%. Sample 4 contains up to 14.5% Polygonaceae pollen. Among arboreal and shrub pollen, *Picea* (0%-8.9%), *Betula* (0%-14.5%), and *Nitraria* (0.2%-9.9%) have relatively high contents. Fungal spore content is relatively low overall.

Alpine Zone: Herbaceous pollen accounts for 94.4% on average (range 62.7%-100%). Cyperaceae shows the highest content, averaging 36.9% (range 0.5%-88.2%). Amaranthaceae (average 13.1%), Asteraceae (average 14.7%), and Poaceae (average 11.2%) also have relatively high percentages, ranging from 0.5%-43.9%, 0%-41.3%, and 0%-41.2%, respectively. Among arboreal and shrub pollen, *Picea* content is relatively high in Tibetan samples (0%-14.3%), followed by Brassicaceae (0.2%-26.1%) and Polygonaceae (0%-22.7%). Fungal spore content is significantly higher than in the temperate zone, including *Glomus* (0%-481.8%), *Sordaria* (0%-125.0%), *Cercophora* (0%-44.2%), and *Sporormiella* (0%-14.9%).

The spatial distribution of major pollen taxa percentages [Figure 3: see original paper] shows significant changes in pollen content from northeast to southwest along the marginal monsoon region. This difference is particularly pronounced between temperate and alpine zones. Compared with the alpine zone, temperate zone surface soils have generally higher *Artemisia* and Amaranthaceae pollen, while Cyperaceae, Poaceae, and Asteraceae pollen show higher percentages at most alpine sites. Tree and shrub pollen content is relatively high near the Great Khingan Mountains and southern Tibet, but appears less frequently in the extensive area between these two regions.

2.2 Analysis of Climate Factors Influencing Pollen Distribution

RDA analysis incorporating climate parameters (mean annual precipitation, warmest month precipitation, coldest month precipitation, mean annual temperature, warmest month temperature, and coldest month temperature) revealed that mean annual temperature, warmest month temperature, and coldest month temperature showed high linear correlations. After removing mean annual temperature and repeating the analysis, all remaining climate parameters had VIF values < 10. RDA with individual climate parameters as sole environmental factors indicated that warmest month temperature explained the highest variance (12.9%), followed by mean annual precipitation (10.8%). Using the five climate parameters (excluding mean annual temperature) as environmental factors, constrained axis permutation ANOVA confirmed that warmest month temperature explained the most variance and was the only parameter with significance level $p < 0.05$, so only warmest month temperature was retained as an environmental factor.

In the RDA results [Figure 4: see original paper], warmest month temperature and altitude are located on Axis 1, with most temperate zone sites distributed in the negative direction of Axis 1. Temperate zone pollen taxa with higher content —*Artemisia*, Amaranthaceae, and *Betula*—are also distributed in the negative direction of Axis 1, indicating relatively warm environments. Most alpine zone sites are distributed in the positive direction of Axis 1, with alpine zone taxa having higher content—Cyperaceae, Asteraceae, and Poaceae—also distributed in the positive direction of Axis 1, indicating relatively cold environments.

3 Discussion

The 38 surface soil samples from the marginal monsoon region show distinct changes in pollen assemblages with increasing altitude. Low-altitude temperate steppe regions have relatively warm and dry climates, with pollen assemblages dominated by Amaranthaceae and *Artemisia*. High-altitude alpine steppe and meadow regions have relatively cold and humid climates, with pollen assemblages dominated by Cyperaceae, Asteraceae, and Poaceae, plus small amounts of Ericaceae pollen. These pollen assemblage characteristics reflect the distribution of vegetation and hydrothermal conditions along altitudinal gradients in the marginal monsoon region. RDA results clearly show the distribution of pollen assemblages and major pollen types along gradients of warmest month temperature and altitude. Although climate parameters other than warmest month temperature failed significance tests in RDA analysis, their influence on pollen assemblages and vegetation cannot be ignored.

Among arboreal pollen, *Picea* pollen shows relatively high percentages at sites near the Great Khingan Mountains and southern Tibet [Figure 3: see original paper], reflecting proximity to *Picea* distribution areas. Since no arboreal vegetation occurs near sampling sites, this also demonstrates the strong dispersal capacity of *Picea* pollen [**?**]. Arboreal pollen such as *Betula*, *Juglans*, *Ulmus*, and *Alnus* appears mainly in temperate steppe, reflecting these trees' preference for warm environments. *Nitraria* pollen occurs primarily in temperate zone samples, with percentage peaks in temperate desert (sample 8, Inner Mongolia) and alpine desert (sample 22, Qinghai) samples, reflecting extremely arid environmental characteristics at these locations [?]. Overall, the total percentage of tree and shrub pollen in the study area correlates more strongly with mean annual temperature and warmest month temperature than with annual precipitation [Figure 5: see original paper].

Among herbaceous pollen, temperate zone *Artemisia* and Amaranthaceae pollen percentages are relatively high, with their sum exceeding 50% in most samples. In arid and semi-arid regions of China, when the sum of *Artemisia* and Amaranthaceae pollen percentages exceeds 50%, the A/C ratio is often used as a semi-quantitative indicator of drought severity [?, ?]. As shown in [Figure 5: see original paper], the monsoon' s northern boundary crosses temperate zones with relatively high temperatures, low annual precipitation, and arid climate. The A/C ratio in surface soils generally aligns with mean annual precipitation trends, consistent with the general pattern that higher aridity corresponds to lower A/C ratios [?]. In alpine regions at the monsoon margin, the sum of *Artemisia* and Amaranthaceae pollen percentages averages 25.8%, and the A/C ratio shows no clear correlation with mean annual precipitation trends in these regions. In the alpine zone at the monsoon margin, pollen assemblages reflect vegetation dominated by alpine steppe and meadow communities composed of Cyperaceae, Asteraceae, Poaceae, *Artemisia*, Polygonaceae, and Brassicaceae, demonstrating plant adaptations to cold conditions. The Artemisia/Cyperaceae (A/Cy) ratio is often used to characterize hydrothermal distribution and variation on the Tibetan Plateau [?], such as the relationship with warmest month temperature [?]. Since temperate zones have far less Cyperaceae pollen than alpine regions, the A/Cy ratio in the former is much higher than in the latter. In alpine regions at the monsoon margin, the correlation between the A/Cy ratio and temperature is not significant, possibly due to the relatively small sample size ($n = 23$).

Fungal spores frequently occur in surface soil samples from alpine regions. Previous studies indicate that fungal spores typically deposit near their sporulation sites, with coprophilous fungal spores particularly limited by animal activity ranges and thus reflecting more local environmental information [?]. *Cercophora*, *Sporormiella*, and *Sordaria* may all indicate the presence of feces near sampling sites [?], while increases in *Sporormiella* and *Sordaria* may indicate expanding livestock populations [?, ?]. *Glomus* commonly appears in newly formed soils, and its abundance is thought to reflect soil erosion rates. Therefore, the high abundance of these fungal spores in surface soils of the alpine region may reflect environmental characteristics of intensive grazing activity accompanied by high soil erosion rates [?, ?]. Pollen records from the marginal monsoon region indicate that grazing activity in the northeastern Tibetan Plateau has gradually intensified since the mid-to-late Holocene [?, ?].

4 Conclusions

(1) Surface soil pollen assemblages in the marginal monsoon region of China show obvious changes with increasing altitude. Temperate zones have relatively high *Artemisia* and Amaranthaceae pollen content, while alpine zones are rich in Cyperaceae, Poaceae, and Asteraceae pollen. These pollen assemblage characteristics can accurately reflect the distribution of vegetation and hydrothermal conditions along altitudinal gradients in the marginal monsoon region.

(2) RDA analysis of the relationship between pollen assemblages and climate factors in the marginal monsoon region shows that warmest month temperature explains the highest variance in pollen data (12.9%), with pollen assemblage variation dominated by warmest month temperature.

(3) Coprophilous fungal spores appear abundantly in surface soils of the alpine region in the marginal monsoon region, reflecting environmental characteristics of intensive grazing activity and high soil erosion rates.

References

[1] Li G Q, Wang Z, Zhao W W, et al. Quantitative precipitation reconstructions from Chagan Nur revealed lag response of East Asian summer monsoon precipitation to summer insolation during the Holocene in arid northern China[J]. Quaternary Science Reviews, 2020, 239: 106365, doi: 10.1016/j.quascirev.2020.106365.

[2] Wen R L, Xiao J L, Fan J W, et al. Pollen evidence for a mid Holocene East Asian summer monsoon maximum in northern China[J]. Quaternary Science Reviews, 2017, 176: 29-35.

[3] Zhang Y R, Li Y Q, Liu L N, et al. No evidence of human disturbance to vegetation in the Zoige Region (north eastern Tibetan Plateau) in the last millennium until recent decades[J]. Palaeogeography, Palaeoclimatology, Palaeoecology, 2022, 589: 110843, doi: 10.1016/j.palaeo.2022.110843.

[4] Shen J, Liu X Q, Wang S M, et al. Palaeoclimatic changes in the Qinghai Lake area during the last 18000 years[J]. Quaternary International, 2005, 136(1): 131-140.

[5] Davis M B, Brubaker L B. Differential sedimentation of pollen grains in lakes[J]. Limnology and Oceanography, 1973, 18(4): 635-646.

[6] Prentice I C. Pollen representation, source area, and basin size: Toward a unified theory of pollen analysis[J]. Quaternary Research, 1985, 23(1): 76-86.

[7] Jackson S T. Pollen representation of vegetational patterns along an elevational gradient[J]. Journal of Vegetation Science, 1991, 2(5): 613-624.

[8] Sugita S. Pollen representation of vegetation in Quaternary sediments: Theory and method in patchy vegetation[J]. Journal of Ecology, 1994, 82(4): 881-

897.

[9] Cao X Y, Tian F, Li K, et al. Lake surface sediment pollen dataset for the alpine meadow vegetation type from the eastern Tibetan Plateau and its potential in past climate reconstructions[J]. Earth System Science Data, 2021, 13(7): 3525-3537.

[10] Chen F H, Xu Q H, Chen J H, et al. East Asian summer monsoon precipitation variability since the last deglaciation[J]. Scientific Reports, 2015, 5: 11186, doi: 10.1038/srep11186.

[11] Zhang J, Huang X Z, Wang Z L, et al. A late Holocene pollen record from the western Qilian Mountains and its implications for climate change and human activity along the Silk Road, northwestern China[J]. The Holocene, 2018, 28(7): 1141-1150.

[12] Wang J L, Huang X Z, Zhang J, et al. Pollen record of humidity changes in the arid western Qilian Mountains over the past 300 years and comparison with tree ring reconstructions[J]. Frontiers in Earth Science, 2020, 8: 562426, doi: 10.3389/feart.2020.562426.

[13] Herzschuh U. Reliability of pollen ratios for environmental reconstructions on the Tibetan Plateau[J]. Journal of Biogeography, 2007, 34(7): 1265-1273.

[14] Chen F H, Dong G H, Zhang D J, et al. Agriculture facilitated permanent human occupation of the Tibetan Plateau after 3600 BP[J]. Science, 2015, 347(6219): 248-250.

[15] Li M Y, Xu Q H, Zhang S R, et al. Indicator pollen taxa of human induced and natural vegetation in northern China[J]. The Holocene, 2015, 25(4): 686-701.

[16] Ma M M, Dong G H, Jia X, et al. Dietary shift after 3600 cal yr BP and its influencing factors in northwestern China: Evidence from stable isotopes[J]. Quaternary Science Reviews, 2016, 145: 57-70.

[17] Li J Y, Zhao Y, Xu Q H, et al. Human influence as a potential source of bias in pollen based quantitative climate reconstructions[J]. Quaternary Science Reviews, 2014, 99: 112-121.

[18] Li F R. The surface pollen assemblages and their relationships with modern vegetation and climate in north China[D]. Lanzhou: Lanzhou University, 2012.

[19] Xu Q H, Li Y C, Yang X L, et al. Quantitative relationship between pollen and vegetation in northern China[J]. Science in China Series D: Earth Sciences, 2007, 50(4): 582-599.

[20] Wei H C, Chongyi E, Duan R L, et al. Fungal spore record of pastoralism on the NE Qinghai Tibetan Plateau since the middle Holocene[J]. Science China Earth Sciences, 2021, 64: 1318-1331.

[21] Zhang Y P, Zhao K L, Zhou X Y, et al. A study of pollen and fungal spores extracted from the feces of domestic herbivores in China and their implications for human behavior[J]. Acta Anthropologica Sinica, 2021, 40(5): 879-887.

[22] Hao X D, Wen C Y. The indicative significance of spores of coprophilous fungi in palaeoecological research[J]. Marine Geology & Quaternary Geology, 2015, 35(1): 175-184.

[23] Chen H, Lü X M, Li S C. A study on topsoil pollens in the east of Qaidam Basin[J]. Geographical Research, 2004, 23(2): 201-210.

[24] Editorial Committee of Vegetation of China. Vegetation of China[M]. Beijing: Science Press, 1995: 917-1034.

[25] Stockmarr J. Tablets with spores used in absolute pollen analysis[J]. Pollen et Spores, 1971, 13: 615-621.

[26] Faegri K, Iversen J. Textbook of pollen analysis[M]. 4th ed. Chichester: John Wiley & Sons, 1989.

[27] Wang F X, Qian N F, Zhang Y, et al. Pollen flora of China[M]. Beijing: Science Press, 1995.

[28] Tang L Y, Mao L M, Li C H, et al. An illustrated handbook of Quaternary pollen and spores in China[M]. Beijing: Science Press, 2016.

[29] Xi Y Z, Ning J C. Study on pollen morphology of plants from dry and semidry area in China[J]. Yunshania, 1994, 11: 119-191.

[30] Hijmans R J, Cameron S E, Parra J L, et al. Very high resolution interpolated climate surfaces for global land areas[J]. International Journal of Climatology, 2005, 25(15): 1965-1978.

[31] Prentice I C. Multidimensional scaling as a research tool in Quaternary palynology: A review of theory and methods[J]. Review of Palaeobotany and Palynology, 1980, 31: 71-104.

[32] Lepš J, Šmilauer P. Multivariate analysis of ecological data using CANOCO[M]. Cambridge: Cambridge University Press, 2003.

[33] Pan Y F, Yan S, Behling H, et al. Transport of airborne *Picea schrenkiana* pollen on the northern slope of Tianshan Mountains (Xinjiang, China) and its implication for paleoenvironmental reconstruction[J]. Aerobiologia, 2012, 29(2): 161-173.

[34] Li W. On dispersal efficiency of *Picea* pollen[J]. Journal of Integrative Plant Biology, 1991, 33(10): 792-800.

[36] Liu H Y, Li Y Y. Pollen indicators of climate change and human activities in the semi arid region[J]. Acta Palaeontologica Sinica, 2009, 48(2): 211-221.

[37] Zhao Y, Liu H Y, Li F R, et al. Application and limitations of the *Artemisia* /Chenopodiaceae pollen ratio in arid and semi arid China[J]. The Holocene,

2012, 22(12): 1385-1392.

[38] El Moslimany A P. Ecological significance of common nonarboreal pollen: Examples from drylands of the Middle East[J]. Review of Palaeobotany and Palynology, 1990, 64(1-4): 343-350.

[39] Li Q, Lu H Y, Zhu L P, et al. Pollen inferred climate changes and vertical shifts of alpine vegetation belts on the northern slope of the Nyainqentanglha Mountains (central Tibetan Plateau) since 8.4 kyr BP[J]. The Holocene, 2011, 21(6): 939-950.

[40] Zhao Y, Herzschuh U. Modern pollen representation of source vegetation in the Qaidam Basin and surrounding mountains, north eastern Tibetan Plateau[J]. Vegetation History and Archaeobotany, 2009, 18: 245-260.

[41] van Geel B. Non pollen palynomorphs[C]//Smol J P, Birks H J B, Last W M, et al. Tracking Environmental Change Using Lake Sediments (vol. 3): Terrestrial, Algal, and Siliceous Indicators. Dordrecht: Kluwer Academic Publisher, 2001: 1-17.

[42] Qin F. Modern pollen assemblages of the surface lake sediments from the steppe and desert zones of the Tibetan Plateau[J]. Science China Earth Sciences, 2021, 64: 425-439.

[43] Huang X Z, Zhang J, Storozum M, et al. Long term herbivore population dynamics in the northeastern Qinghai Tibetan Plateau and its implications for early human impacts[J]. Review of Palaeobotany and Palynology, 2020, 275: 104171, doi: 10.1016/j.revpalbo.2020.104171.

[44] Zhang J, Huang X Z, Wang J L, et al. An inverse relationship between moisture and grazing intensity in an arid mountain basin system[J]. Progress in Physical Geography: Earth and Environment, 2022, 46(2): 310-322.

[45] Zhang J, Huang X Z, Zhang S R, et al. Cycles of grazing and agricultural activity during the historical period and its relationship with climatic and societal changes in northern China[J]. Land Degradation & Development, 2021, 32(11): 3315-3325.

[46] Chen F H, Yu Z C, Yang M L, et al. Holocene moisture evolution in arid Central Asia and its out of phase relationship with Asian monsoon history[J]. Quaternary Science Reviews, 2008, 27(3): 351-364.

[47] Han Y T, Li J Y, Liu J B, et al. Indicative study of pollen on vegetation in western Junger Basin[J]. Arid Land Geography, 2023, 46(5): 773-781.

[48] Cheng B, Chen F H. Pollen analysis of topsoil samples from Shiyang River drainage, northwest China[J]. Journal of Desert Research, 2010, 30(2): 350-356.

[49] Wei H C, Zheng Z, Ma H Z, et al. Pollen distribution patterns of surface soil sample in Qinghai of China and their relationship with vegetation[J]. Arid Land Geography, 2009, 32(6): 932-940.

[50] ter Braak C J F, Prentice I C. A theory of gradient analysis[C]//Begon M, Fitter A H, Ford E D, et al. Advances in Ecological Research. Cambridge: Academic Press, 1988.

Note: Figure translations are in progress. See original paper for figures.