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Drivers of land cover and plant compositional changes in Northeast China since the mid-Holocene: climate versus human activities

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Abstract

After the mid-Holocene, human activities gradually began having a notable impact on land cover and plant compositional changes. Evaluating the extent and spatiotemporal variations of the human versus climate impacts on regional ecosystems is becoming an area of focus of current global change research. The present study uses 478 AMS ¹⁴C dating records collected from 5473 archaeological sites to help evaluate variations in prehistoric population size in Northeast China, which suggest changes in the nature of human activities there since the mid-Holocene. Results indicate that prehistoric human impacts remained at a relatively low level during the ca. 7-4 ka

interval except for two minor fluctuations. Human impacts on ecosystems in the study area gradually intensified after 4 ka when societies entered the Bronze Age. In addition, we used a novel methodological approach on three pollen datasets for reconstructing the land cover and plant compositional changes of the three different studied landscapes (steppe, forest, and steppe-forest ecotone) in Northeast China. Results show that total land cover changes in forests were relatively low (i.e. stable) over the studied time period owing to their comparatively higher plant diversity whereas significant fluctuations occurred in the steppe and the steppe-forest ecotone. By comparing these results with regional climate records, climate change was found to dominate plant changes during two periods--before ca. 6 ka and after ca. 0.8 ka. In addition, during ca. 6-4 ka BP, even though climate still played the most significant role in vegetation changes, anthropogenic impacts on plant changes were revealed for the steppe-forest ecotone. During 4-2.3 ka BP, the anthropogenic impacts on plants gradually increased and became the dominant driving force, especially for the forest and steppe-forest ecotone during ca. 2.3-0.8 ka BP. These varied impacts of human activity and climate change on vegetation among the study areas can be related to human migration trends and human subsistence patterns.

Key words: land cover change; ancient population size; pollen analysis; Holocene; Northeast China

1. Introduction

Intensified human impacts leading to transformations within the terrestrial ecological environment have long been considered a consequence of the industrial era, emerging over recent centuries (Dinerstein et al., 2019; Hansen et al., 2020). For instance, in northeastern China, the natural vegetation was largely transformed into agricultural land, pastoral land, and built-up areas, especially over the past 100 years (Liu et al., 2005b; Wang et al., 2022). The development of interdisciplinary research, including palaeoecology, archaeology, humanities, and others, provides a long-term perspective on ecosystem change and the potential influences of land use and climate on those changes (e.g. Marquer et al., 2023). At present, it is widely recognized that human societies could have shaped the natural environment over the long term, especially by altering the patterns of plant diversity, landscapes, and even ecosystem processes through the Holocene

(Stephens et al., 2019; Rick et al., 2020; Ellis et al., 2021). However, the nature, extent, and temporal trajectory of the impact of human activities on ecosystem and plant diversity are region-specific, therefore a need exists for further investigation of the long-term trends at regional scales.

Pollen is a key proxy for assessing past vegetation changes over centuries to millennia. Recently, Holocene vegetation cover and plant composition reconstruction studies have been conducted around the world where the resultant landscape is considered to be the direct result of human activities along with climate changes (Gaillard et al., 2010; Kaplan et al., 2011; Marquer et al., 2017, 2023; Li et al., 2020; Githumbi et al., 2022; Shi et al., 2022). Early studies generally attributed Holocene vegetation dynamics in China to changes in climate and placed little emphasis on, or even ignored, human impacts (Herzschuh et al., 2010; Wanner et al., 2010; Tian et al., 2016; Niu et al., 2022). Indeed, vegetation has been sensitive to climate throughout the Holocene even in the late Holocene when human activities became strong enough to change global landscapes. Depending on the region, climate can still affect vegetation changes especially during important climate events, such as Little Ice Age and Warm Medieval Period (Marquer et al., 2017; Magnan et al., 2018; Qi et al., 2023). Recent scholarly endeavors have also sought to assess the importance of human activity on plant dynamics, positing that in regions such as East Asia and Europe--cradles of early human cultures and having diverse practices ranging from agriculture to pastoralism--ancient anthropogenic activities likely exerted a significant impact on plant succession (Zhao et al., 2017; Marchant et al., 2018; Poska et al., 2022). However, it is crucial to underscore that these influences were not uniform, but rather exhibited marked temporal and spatial variability. These variations may have been particularly pronounced within some regions, potentially attributable to region-specific differences in natural environmental factors, population density, and technological advances.(Klein et al., 2011; Berger et al., 2019; Roberts et al., 2019; Sun et al., 2022b).

In East Asia, China, with a dense population and intensive human activities, has long been recognized as one of the world's centers of civilization (Lu & Teng, 2000; Bellwood et al., 2007; Chen et al., 2020; Dong et al., 2020; Ma et al., 2020). In central China, early agricultural activities

can be traced to 10000 cal BP as evidenced by millet domestication (Lu et al., 2009). Since then, adaptability of humans to a changing environment has gradually increased, promoting the gradual extension of human occupation from lower to higher elevations (Chen et al., 2015; Yang et al., 2022). In southern China, after the mid-Holocene, the succession and evolution of natural vegetation have been significantly altered by rice development, especially as it led to a decrease in both land cover and arboreal diversity (Cheng et al., 2018; Zheng et al., 2021). In northern China, dramatically increasing populations associated with dryland agricultural practices and the use of fire for heating and food processing severely depleted the mountain forests from 6000 cal BP (Ren et al., 2000, 2007; Dong et al., 2013; Tan et al., 2020). Because Northeast China is a relatively independent region enclosed on three sides by mountains, it developed its own ancient culture and civilizations (Shelach, 2000; Jia et al., 2016). Few studies, however, have been conducted regarding the comparative extent to which human activities and climate change influenced vegetation cover in Northeast China.

Over the preceding decades, researchers working in Northeast China have systematically extracted copious pollen records from diverse profiles, encompassing lakes, maar lakes, peatlands, and aeolian sand-paleosols (Supplementary Table S3). The predominant foci of these investigations have been the extraction and analysis of the most discerning climate signals, predicated upon vegetation data as represented by pollen. Noteworthy examples include the utilization of pollen records from Xiaolongwan and Sihailongwan to investigate periodic oscillations of climate and paleoprecipitation variations, respectively (Stebich et al., 2015; Xu et al., 2019). However, scant attention has been devoted to the inherent intricacies of plant diversity or compositional alterations. Furthermore, quantitative examination of vegetation cover changes was not addressed in these studies. These antecedent investigations, however, furnish a robust foundation upon which the present research is premised.

In this study, we first utilized three high-resolution pollen records after cautious selection to reconstruct Holocene land cover for two different landscapes (steppe and forest) in Northeast China by using a new MAT-REVEALS approach proposed by Sun et al. (2022a). Second, Holocene plant composition and diversity changes for these regions were reconstructed based on

the pollen records. Third, we compiled 478 AMS ^{14}C dating records from 5473 archaeological sites to evaluate the extent to which the vegetation changes could be related to human activities. Finally, we compared those results with regional climate records.

The goal of this study is to assess the relative influences of climate and human activities on Holocene vegetation dynamics in Northeast China. Results provide key insights into the impacts of human subsistence strategies on plant composition and land cover during the Neolithic, Bronze Age, and historical periods and thus offer a deeper understanding of the ancient human-landscape relationships in Northeast China.

2. Regional setting

Northeast China (39°40'N – 53°30'N, 115°05'E – 135°02'E) is flanked by the Changbai Mountains on the east, the Lesser Khingan Mountains on the northeast, and the Greater Khingan Mountains on the west; together these mountains enclose the Northeastern Great Plain (Fig. 1). Influenced by the East Asian monsoon, the modern climate of the region has four distinct seasons with a long cold and dry winter and a short warm and humid summer. Average annual temperatures range north to south from -4°C to 11°C and average annual precipitation ranges east to west from 1,000 mm to 350 mm (Niu et al., 2022). Between the surrounding mountains and the central plain lies an ecotone that changes gradually downslope from forest to steppe (Gao et al., 2022). The encompassing mountains primarily host a temperate mixed conifer-hardwood forest characterized by a preponderance of *Pinus koraiensis* and *Quercus mongolica*. This arboreal ensemble is complemented by a diverse assemblage of other broadleaved deciduous taxa, including *Carpinus cordata*, *Phellodendron amurense*, *Acer pictum*, *Fraxinus mandshurica*, *Betula pendula*, *Juglans mandshurica*, *Ulmus davidiana*, and *Tilia amurensis*. The coniferous component of the forest extends beyond *Pinus koraiensis* to incorporate species such as *Pinus densiflora*, *Abies nephrolepis*, and *Picea jezoensis* (Stebich et al., 2009; Xu et al., 2019). At present, the central plain is largely occupied by farmland that is primarily planted with corn. Additional common crops include rice, sorghum, foxtail millet (*Setaria italica*), other miscellaneous grains, and adzuki beans (*Vigna angularis*). The indigenous vegetation mainly consists of meadow-steppe plants dominated by *Spita baicalensis*, *Filifolium sibiricum*, and *Leymus chinensis*. Marsh vegetation

commonly grows around the low-lying marshes, lakes (pools), floodplains, and other lowlands, with dominant species including *Phragmites australis*, *Carex lehmanii*, and *Deyeuxia langsdorffii* (Niu et al., 2022; Niu et al., 2023).

3. Materials and methods

3.1. Pollen archives and chronology

After compiling all published pollen records from Northeast China (Supplementary Table S3) these four criteria were used to select suitable datasets for the present study:

1. The selected pollen records had to exhibit continuity and possess a high sample resolution below 100 years to ensure their transformation into a time window of no less than 300 years for comprehensive land cover reconstruction;
2. Pollen records used in this study had to feature a minimum of three dates to establish a robust chronological framework;
3. Geographical locations of pollen records had to align with the regions encompassed by the collected archaeological sites, complemented by radiocarbon ages to facilitate an analytical assessment of the relative impacts of climate and human activities on plant changes;
4. Elevation of the pollen records were not to exceed 550 meters above sea level (a.s.l.) because ancient human settlements in Northeast China were predominantly confined to areas below that elevation (Jia et al., 2018; Liu et al., 2022; Wang et al., 2022).

Applying the aforementioned criteria, only the Dabusu, Shuangyang, and Gushantun pollen datasets met the specified conditions (Table 1).

Lake Dabusu (DBSL, 44°49'48.4"N, 123°40'27.2"E; 27 m a.s.l.) is a closed alkaline lake that lies on the Qian'an highland, which is located in the central part of the Northeastern Great Plain in northeastern China; the Dabusu peatlands (DBSP) are found on the northern shore of the lake. In 2016, a 3.0 m peat core was obtained from the center of the Dabusu peatlands. After constructing an age-depth model based on AMS ¹⁴C dates, high-resolution pollen records were extracted from the peat core. Detailed dating information and pollen records for this profile can be found in Niu et al. (2022).

The Gushantun peatlands (GSTP, 42°18'22.1"N, 126°16' 57.7"E, 506 m a.s.l.) lie to the west of the Changbai Mountains in the Longgang Volcanic Field. A 7.5-m peat sediment core was extracted in 2009 using an Eijkelkamp peat sampler. Ten bulk organic samples were AMS radiocarbon dated at Peking University while pollen analyses were conducted at 1-cm intervals. The pollen records and ages derived from this profile have been previously published (Gao et al., 2018; Meng et al., 2023).

The Shuangyang peatlands (SYP, 43°36' 79"N, 125°33'4"E, 230 m a.s.l.) were formed in a partially enclosed depression in a forest-grassland ecotone valley, located in the middle of the Northeastern Great Plain and Changbai Mountains. A 3.26-m long peat core was obtained in 2010 and five bulk organic samples were subjected to AMS ^{14}C dating. While the detailed profile and dating information have already been published (Li et al., 2017), the pollen records extracted from the SYP profile have not yet been published (see Supplementary Table S2).

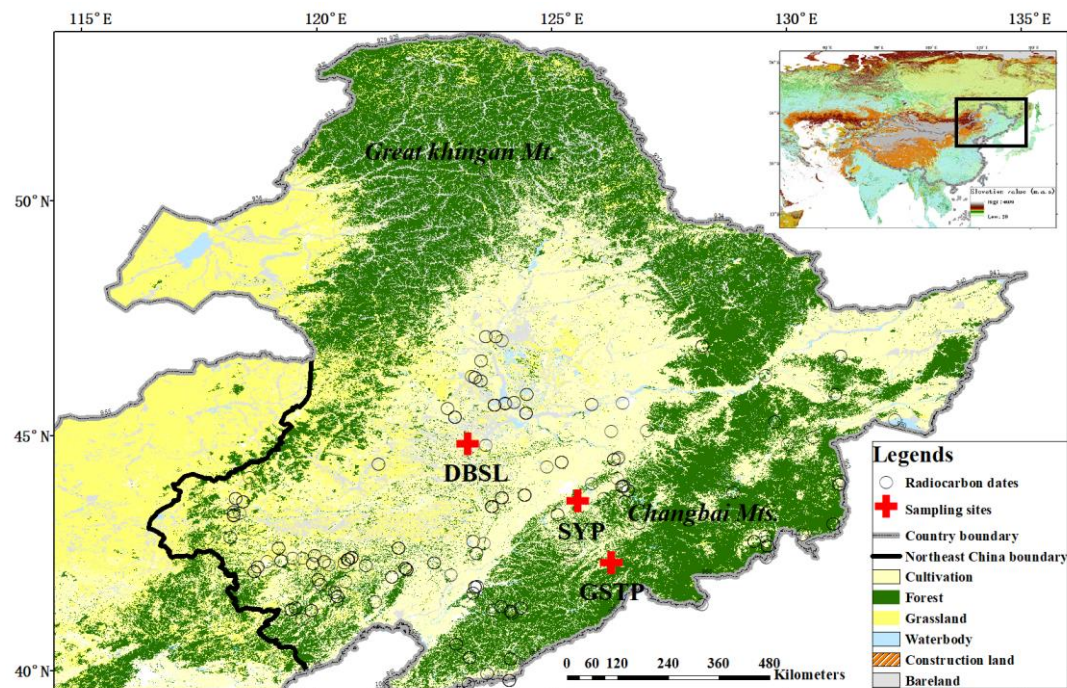


Fig. 1. Location of sampling sites and radiocarbon ages from Neolithic and Bronze Age archaeological sites in Northeast China.

3.2. Regional land cover reconstruction

This study applied the combined MAT-REVEALS approach proposed by Sun et al. (2022a) to the pollen data records extracted from the DBSP, GSTP, and SYP profiles to reconstruct the actual

land cover changes in these three regions since the mid-Holocene. The REVEALS model transformed the pollen assemblages into their corresponding relative cover of the individual plant taxa while the MAT techniques add information on bare ground cover into the REVEALS reconstructions. The MAT approach was used to correct the REVEALS estimations; total plant cover can be determined as the percentage of individual plant taxa cover plus the percentage of bare ground cover, summing to 100%. The detailed procedures of the MAT-REVEALS approach and the REVEALS model settings are given in the Supplementary Materials (Text S1, Fig. S1, Table S1).

3.3. Indices of plant compositional change

Two indices of plant compositional change--rate of compositional change and evenness--were calculated based on the REVEALS estimates. In addition, one plant diversity-related index, palynological richness, was established based on all pollen types. The rate of compositional change holds the potential to distinguish phases of stability and change in vegetation (Jacobson and Grimm, 1986). The evenness index provides a quantitative measure of the numerical equality observed among different plant taxa in terms of their abundance (Magurran, 2021). Fluctuations in palynological richness may serve as partial indicators of plant diversity changes (Birks et al., 2016). Rarefaction analysis was applied to the whole pollen counts to calculate the palynological richness (Marquer et al., 2017; see Supplementary Fig. S7). These three indices were calculated using the “vegan” package in R (Oksanen et al., 2017) and following the procedure described in Marquer et al. (2017).

3.4. Data collection and analyses of archaeological sites and climate

Locational information for 5473 archaeological sites was gathered from the third national cultural relics censuses of Heilongjiang, Jilin, and Liaoning provinces and from previous studies. After careful selection (for detailed selection criteria see Text S2), we compiled 478 AMS ^{14}C dating records from these archaeological sites and summed their probability distributions in order to reconstruct the prehistoric population size. The $\delta^{14}\text{C}$ summed probability analysis was performed using the “IntCal” and “rcarbon” packages of R (Wang et al., 2014).

We systematically gathered all published climate records pertinent to Northeast China (Supplementary Table S4). To ensure the selection of the most suitable climate records for this study, we established three criteria:

1. To facilitate a robust comparison with plant changes, the chosen climate records must exhibit continuity and have high sample resolution that below 100 years;
2. For the purpose of establishing a usable chronological framework, pollen records must feature a minimum of three numeric ages. Additionally, the climate records should extend over at least 7500 years, allowing for comprehensive comparison with plant changes;
3. Given our earlier assertion regarding the predominant distribution of ancient human settlements below 550 m a.s.l., the selected locations for pollen records used in climate reconstruction must exceed this elevation threshold.

Adhering to these stringent criteria resulted in the selection of six climate records from Northeast China (Table 1). Each of the six records from the collected data was linearly interpolated at 100-year intervals and the interpolated data were then converted to *Z*-scores based on Zhou et al. (2023). The average of the six *Z*-score served as a representative depiction of climate changes in Northeast China. For comparison an EASM (East Asian Summer Monsoon) index was compiled based on results of multiproxy analyses from 11 lakes in central Asia (Chen et al., 2008) and stalagmite $\delta^{18}\text{O}$ records from Nuanhe and Lianhua caves in Northern China. In order to evaluate the relative contributions of climate and human activities on land cover and plant composition during the mid-Holocene in these regions, variation partitioning was performed using the *varpart* () function in the “vegan” package of R (Oksanen et al., 2020), as previously used by Marquer et al. (2017).

Table 1. Selected pollen and climate records spanning since the late Pleistocene in Northeast China used in this study.

Site No.	Site name	Abbrev.	Long (°E)	Lat (°N)	Elev (m a.s.l.)	Core type	Dating method	No. of dates	Time period (cal BP)	Core depth (cm)	Sample resolution (yr)	Proxies used	Reference
Selected pollen records for plant reconstruction													
1	Dabusu	DBSP	123.22	44.83	27	peat	¹⁴ C	7	7340	300	34	Pollen	Niu et al., 2022
2	Shuangyang	SYP	125.56	43.61	230	peat	¹⁴ C	5	6485	326	81	Pollen	Niu et al., 2023
3	Gushantun	GSTP	126.28	42.3	506	peat	¹⁴ C	10	12970	750	17	Pollen	Meng et al., 2023
Selected climate records													
1	Gushantun	GSTP4	126.28	42.31	506	Peatland	¹⁴ C	9	11165	750	151	Grain size	Li et al., 2014
2	Hani	HN	126.51	42.23	900	Peatland	¹⁴ C	6	13280	350	88	Grain size	Li et al., 2014
3	Jingbohu	JBL	129.04	43.99	350	Lake	¹⁴ C	7	9300	890	10	Grain size	Hou et al., 2006
4	Sihailongwan	SHLW	126.6	42.28	797	Lake	¹⁴ C	40	12000-150	437-18	56	Pollen	Stebich et al., 2015
5	Xiaolongwan	XLW	126.36	42.3	655	Lake	¹⁴ C	10	9210	387	24	Pollen	Xu et al., 2019
6	Moon lake	ML	120.87	47.51	1190	Lake	¹⁴ C	21	21000	886	24	TOC, TN, $\delta^{13}\text{C}_{\text{org}}$	Liu et al., 2010

4. Results and discussion

4.1. Regional land cover and plant composition changes since the mid-Holocene

Three pollen records were used to reconstruct land cover changes since the mid-Holocene for the Northeastern Great Plain, the Changbai Mountain region, and the forest-grassland ecotone in the study area. Based on the modern vegetation map around the sampling sites and their basin types and sizes, it was inferred that pollen influxes at present into the DBS lake, SY peatlands, and GST peatlands are mainly derived from areas within a 20-50 km radius from these sampling sites (Niu et al., 2023). To reconstruct regional land cover changes, fern spores, Cyperaceae, and *Typha* pollen, which originate mostly from the local vegetation, were excluded from all pollen records.

Situated at the edge of the region influenced by the EASM, the present climate of the study area varies from the more humid Changbai Mountains in the east to the drier Songnen grasslands in the west, and the vegetation gradually changes across this transect to the west from temperate coniferous-broadleaved mixed forest to steppe. The pollen-based regional vegetation reconstructions also show these differences (Fig. 2). Since the mid-Holocene, vegetation that grew in the GST region mainly comprised broadleaved trees, including *Quercus*, *Tilia*, and *Juglans*, with a combined average land cover of 46.1%. Coniferous trees were dominated by *Pinus*, with an average cover of 10.1%. Herb cover occupied less than 8% of the area and mainly consisted of *Artemisia*, Asteraceae, Poaceae, and Chenopodiaceae. The total land cover of the GST region fluctuated rather narrowly between 71.3% and 79.7%. Land cover varied between 49.9% and 77.2% in the SY region and between 45.7% and 65.1% in the DBS region. The land cover proportions of different vegetation types and even individual species, however, display notable differences. In the SY region, the average tree cover was approximately 51.9%, which was much higher than the herb cover, while the DBS region shows the opposite, with average herb cover reaching 45.2% and trees occurring occasionally. Regarding tree cover, compared to the GST region where broadleaved trees dominated, the proportions of broadleaved trees and coniferous trees were approximately equal for both the SY and DBS regions. For herb cover, understory grasses were likely distributed throughout the GST region; drought-tolerant plants such as *Artemisia*,

Chenopodiaceae, and *Ephedra* probably grew widely in the SY region; and Poaceae was the dominant taxon for the DBS region. Additionally, palynological diversity in the DBS and GST regions had mean values that were much higher than those in the SY region, which had a mean value of 6.4, indicating that pollen-based related plant diversity in the SY region was only moderate. The relatively unstable vegetation structure in the SY region is also attributed to the region's lower plant diversity, as evidenced by the higher mean value of compositional change than in the other two regions. Because relative tree abundance is more constant than relative grass abundance, the GST region had the highest mean value for vegetation evenness, 0.79, followed by the SY and DBS regions at 0.77 and 0.59, respectively.

During ca. 7.5-4 ka, total vegetation cover in the GST region was generally maintained at the highest level (average cover 76.8%) in the study period with a gradually decreasing trend until ca. 4.5 ka when total vegetation cover increased slightly due to the abrupt expansion of *Betula* trees. Broadleaved trees were widely distributed in both the GST and SY regions, dominated by *Tilia* and *Quercus*. Notably, *Juglans* trees were relatively abundant in both the GST and SY regions but were rare in the DBS region. Coniferous trees were absent in the GST region, but they were present in the SY and DBS regions. *Ephedra* dominated the herb cover in the SY region and was apparently much lower in percentage than tree cover. Poaceae dominated the DBS region, which had with few *Ephedra* plants but more Chenopodiaceae and *Artemisia* plants. Palynological diversity was comparable between the GST and SY, with mean values of 12.23 and 12.28, respectively, and was notably higher than it was in the DBS region, where the mean value was 8.1. The pace of compositional changes in the SY and DBS regions were approximately equivalent, with mean values of 0.046 and 0.044, respectively, and both were much faster than the pace of compositional change in the GST region, which had a mean value of 0.038. Mean evenness values near 0.80 for the GST and SY regions were much higher than the 0.58 mean value for the DBSP region. Notably, evenness steadily decreased in the SY region while increasing in the GST and DBS regions.

In the period of ca. 4-2.3 ka, land cover in the SY region continuously increased from 61.9% to 72.9% because of the rapid increase in broadleaved tree cover even though both herb cover and

coniferous cover did not change. The pattern of transformation from trees to herbs can also be seen in the GST region where only the *Quercus* tree cover gradually increased. Poaceae expanded slightly in the DBS region resulting in a slight increase in total herb cover. Palynological diversity was slightly lower in the DBSP and SY regions compared to the preceding time interval, but the GST region's palynological diversity did not change. As a result, the GST region had the highest plant diversity, followed by the SY and DBS regions. The rates of compositional change revealed a variety of trends in the three regions. They increased in SY, decreased in GST, and barely changed in DBS, making SY the region with the lowest stability of the vegetation structure, followed by DBS and GST. Although their fluctuation trends varied, the mean evenness values in the three regions showed little change from the previous time interval. While decreasing somewhat in the GST and DBS regions, evenness suddenly surged in the SY region in the ca. 4-2.3 ka interval.

From ca. 2.3 ka to the present, land cover near the GST and DBS regions has experienced a continuously decreasing trend. Coniferous trees in the GST region increased slightly compared to the preceding period, while all broadleaved tree cover except for *Carpinus* decreased, resulting in the total vegetation cover declining to 63.1%. Herb cover, especially Poaceae cover, appears to have decreased in the DBS region along with the slight decrease in tree cover, contributing together to the reduction in total vegetation cover. Notably, for the SY region, total tree cover initially underwent an abrupt decrease but then recovered slightly and has maintained the higher level through the present. Coniferous tree cover grew slightly with an expansion of *Pinus* while all the broadleaved trees decreased except for *Salix*, which increased. Compared to the previous time interval, in the SY region palynological diversity continuously decreased to its lowest level; palynological diversity in the GST and DBS regions did not change in the latest time period from what it had been in ca. 4-2.3 ka. The rate of compositional change in the SY region climbed to its highest level which was notably higher than the rates in the GST and DBS regions, both of which underwent a decreasing trend. Evenness remained constant in the GST region, gradually decreased in DBS region, and increased slightly in the SY region.

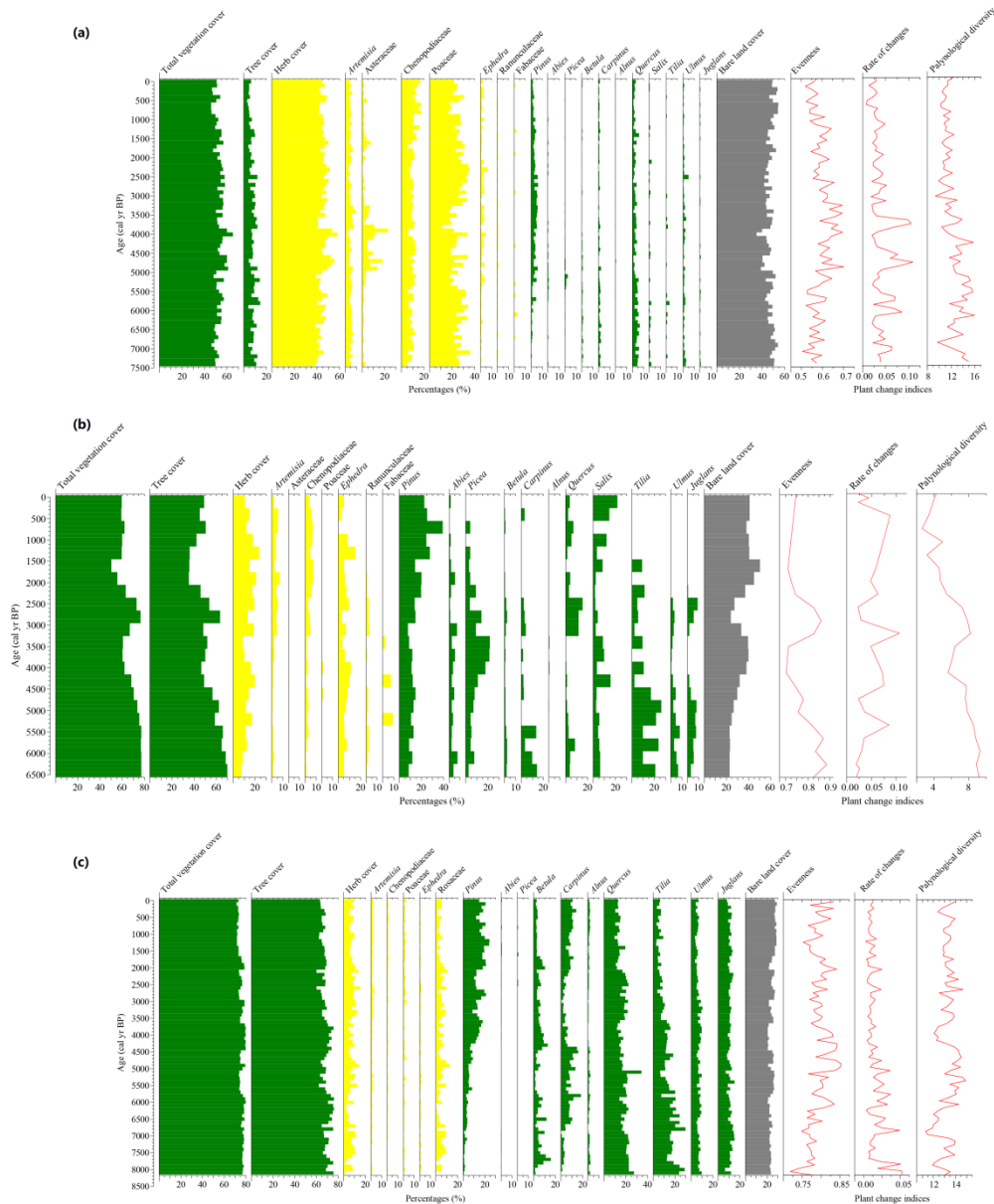


Fig. 2. Holocene land cover and plant composition changes in the (a) DBS region, (b) SY region, and (c) GST region.

4.2. Changes in prehistoric population size and intensity of human activity

Selected AMS¹⁴C chronological data from the region's archaeological sites were used to reconstruct changes in the prehistoric population size during 7500-2100 cal BP. Rick (1987) proposed that larger prehistoric population size in Northeast China was related to more intensive human activities, which resulted in greater accumulations of cultural carbon that have higher possibilities for detection, excavation, and dating by modern archaeologists. Within a large area, summed probability distributions based on radiocarbon dates from a certain number of

archaeological sites have been shown to be reliable proxies for prehistoric population changes worldwide (Gamble et al., 2005; Shennan, 2009; Crema & Bevan, 2021) and it is the first time this method has been used in northeastern China. Although some researchers argue that taphonomic and investigative methods may bias the population size estimates, there is increasing agreement that if these biases are controlled by careful selection, and if the number of available dates is sufficiently large, an important demographic signal can still be discerned (Bevan et al., 2017). It is generally suggested that the $\delta^{14}\text{C}$ summed probability requires a minimum dataset volume of 200 to 500 depending on the size of the study area. In this study, 478 AMS ^{14}C dating records were used to ensure the reliability of the reconstructed population size.

The $\delta^{14}\text{C}$ summed probability results show that the human population of northern China was at a relatively low level during the Neolithic but increased abruptly when human society entered the Bronze Age (Fig. 4). Previous work has suggested that the population of northern China showed an overall increasing trend during the Holocene (Teng, 2017). It has been postulated that in warm and humid periods, the population growth rate was relatively fast, whereas during cold and dry climate periods, the population growth rate was slow or declining (Tallavaara et al., 2012). Evidence from the present study, however, indicates that population size fluctuated in a consistent fashion with climate change only during the Neolithic period. It shows that the population increased steadily during the Bronze Age even during periods of significant cooling, which might be a manifestation of increased productivity that allowed humans to adapt to climate change and maintain population growth (Chen et al., 2011).

The population size differences between the Neolithic and Bronze Age can also be demonstrated by the distributions of archaeological sites, and they both can partly reflect the intensity of prehistoric human activity (Fig. 3). During the Neolithic period, the total number of archaeological sites is 1111, whereas the number of archaeological sites representing the Bronze Age is 4362. The large increase in archaeological sites may partly represent greater preservation of Bronze Age sites but is also consistent with an increase in population accompanying the improvement of human activities. Moreover, the distribution of the archaeological sites can also roughly reflect human migration patterns during the two periods. More than two-thirds of the Neolithic

archaeological sites are located in the Northeastern Great Plain with one-third distributed in the Changbai Mountains. During the Bronze Age, archaeological sites located in the Changbai Mountains comprise 46% of the total, suggesting that a large number of prehistoric humans moved to the wetter and warmer region in adapting to the harsh climate conditions.

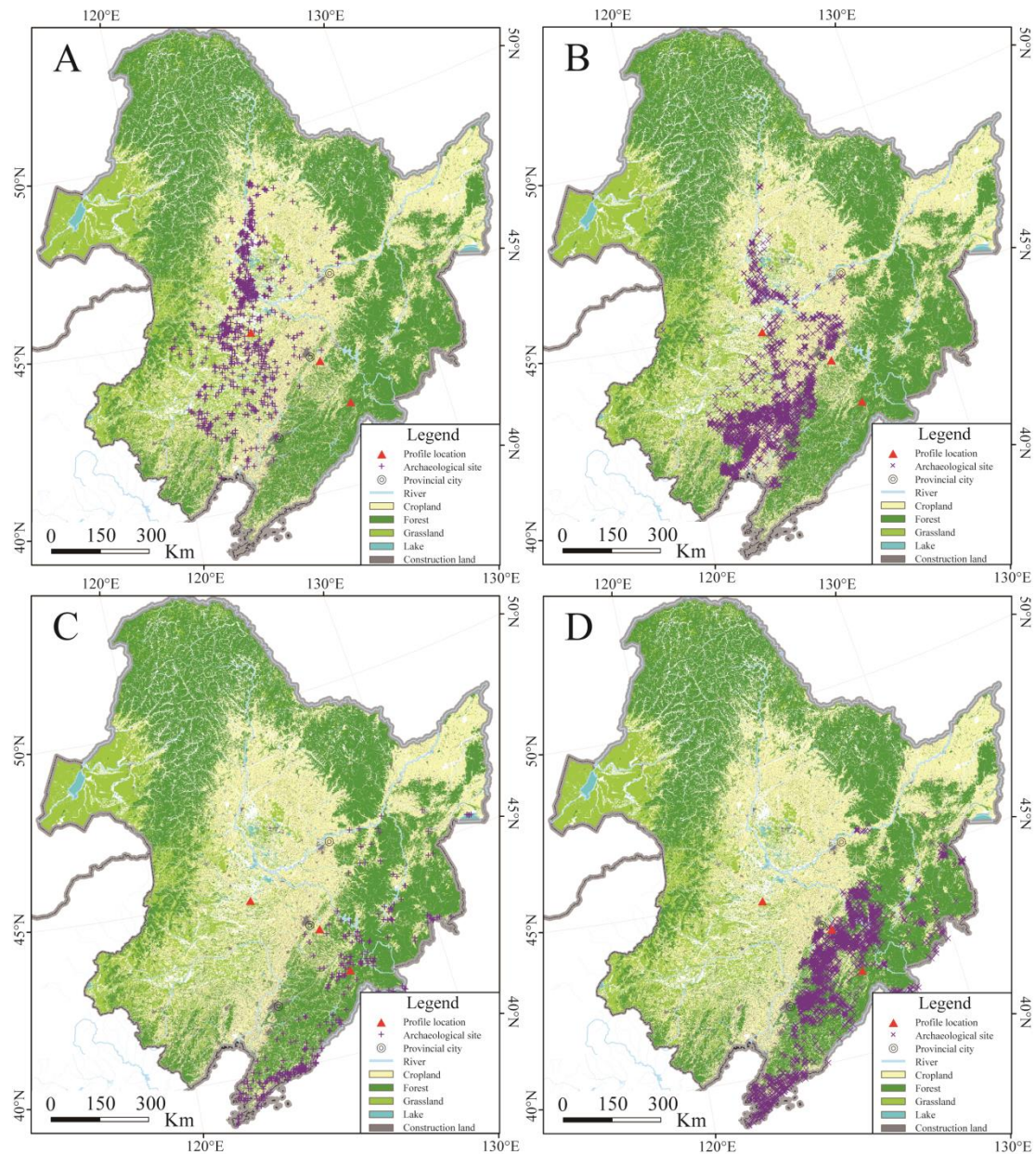


Fig. 3. Maps of the spatiotemporal distribution of archaeological sites in the (A) Northeast Great Plain during the Neolithic, (B) Northeast Great Plain during the Bronze Age, (C) Changbai Mountain region during the Neolithic, and (D) Changbai Mountain region during the Bronze Age.

4.3. Spatiotemporal climate- and human disturbance- related vegetation changes

Archaeological cultural time periods used in this paper are those defined for the Songhua River basin (Wang, 2019). That work specifies that multiple prehistoric cultures flourished in the GST, SY, and DBS regions since the mid-Holocene, including the Lower Zuojiashan culture (7000-6000 cal BP) (Chen & Xu, 1985; Zhao, 2011), Upper Zuojiashan culture (6000-5000 cal BP) (Chen & Zhao, 1989), Angangxi culture (5000-4000 cal BP) (Zhu & Zheng, 2008), Xiaolaha culture (4000-3500 cal BP) (Yu et al., 1998), Gucheng culture (3500-3000 cal BP) (Zhu, 2009), and Xituanshan culture (3000-2300 cal BP) (Zhao, 2009). Moreover, during the historical period, many indigenous dynasties controlled these regions including the Gaogouli (2100-1300 cal BP) (Hua, 2015), Bohai (1300-1100 cal BP) (Liu et al., 2005a), Liao (1100-800 cal BP) (Han, 2004), Jin dynasty (800-700 cal BP) (Pang et al., 1993), Yuan (700-600), Ming (600-300), and Qing (300-50) dynasties (Luan, 2006). Therefore, it is considered likely that part of the vegetation changes (plant cover and composition) experienced by these regions since the mid-Holocene should be the result of human activities.

This study compares vegetation changes, climate changes (Bond et al., 2001; Chen et al., 2008; Cosford et al., 2009; Wen et al., 2010; Wu et al., 2011;), $\delta^{14}\text{C}$ summed probability records, and the rise and decline of Chinese culture phases. Generally, vegetation changes were controlled by climate as can be seen in the outcomes from the variation partitioning with the climate variable explaining 14%, 21%, and 10% of the vegetation change, especially since the mid-Holocene to 1900 cal yr BC in DBS, SY, and GST regions, respectively (Supplementary Materials Fig. S2). Climate change and human activities together also explained greater variations of vegetation change compared to variations explained by human activities alone; human activities may have amplified somewhat the impacts of climate change on vegetation. However, for different regions in different periods, the influences of climate change and human activities on vegetation varied.

During 7.5-6.0 ka, the region was dominated by a strong EASM, which can bring more precipitation and is associated with a warm and humid climate. This mild climate may have promoted the Lower Zuojiashan cultural prosperity, which resulted in a population increase. Vegetation cover showed a slight increase in this interval except for in the DBS region. The other two regions were occupied by stable land cover and plant composition, indicating that human

activities had little influence on plant changes while climate was the dominant factor affecting plant growth. This notion is supported by the partitioning variation results, which show that the climate variable alone explains 12%, 47%, and 19% of the vegetation changes in DBS, SY, and GST regions, respectively (Supplementary Materials Fig. S2).

During 6.0-4.0 ka, the influence of the EASM gradually weakened and the climate became cold and arid including both the IRD 3 and 4.2 ka cooling events. For the SY region, vegetation cover, evenness, and palynological diversity decreased slightly along with an increase in the rate of composition change in response to the climate change. Tree cover also fluctuated accompanied by population fluctuations resulting from the Upper Zuojiashan and Angangxi cultures emerging and diminishing, suggesting anthropogenic disturbance of vegetation. This notion is also supported by the variation partitioning results which show that human activities alone explain 5% of vegetation changes (Supplementary Materials Fig. S2). In the DBS and GST regions, however, human activities had little influence on vegetation change and climate remained the primary driving force affecting vegetation successions. More specifically, for the GST region, drought-tolerant vegetation expanded, as indicated by the increase in *Carpinus* cover. For the DBS region, the declining tree cover is replaced by continuously increasing herb cover resulting in total vegetation cover increases (Fig. 2).

During 4.0-2.3 ka, the EASM fluctuated at a low level and the climate was generally cold and humid. Human societies entered the Bronze Age and population increased rapidly, as shown by the increased $\delta^{14}\text{C}$ probability records and the increase in number of archaeological sites (Figs. 3 & 4). The harsh climate conditions led to swift cultural dislocations and human impacts on vegetation changes increased rapidly indicated by the partitioning variation results (Supplementary Materials Fig. S2). Climate-induced vegetation changes commonly represented by the changes of the tree species or vegetation types while human-induced vegetation changes commonly represented by the land cover and tree cover changes (Li et al., 2020; Sun et al., 2022b; Text S3). More specifically, driven by climate, broadleaved tree cover decreased, especially for cold-intolerant *Tilia*, and coniferous tree cover increased in the GST region. The gradual decrease in total tree cover was likely driven by human activities. For the SY region, climate change

contributed to the decrease in drought-tolerant *Salix* plants and the increase in cold-tolerant trees such as *Abies* and *Picea*. Human activities also appear to have played a significant role in terms of vegetation change in the SY region: in concert with the flourishing of the Xituanshan culture, the rate of change of plant composition increased while total tree cover decreased significantly together with the pollen-based plant diversity index (Fig. 4). For the DBS region, a cold and wet climate resulted in the expansion of the Poaceae and *Pinus* cover (Fig. 2). In addition, the slightly decreased total vegetation cover might be related to agricultural and pastoral activities (Fig. 4).

During 2.3-0.8 ka, the influence of the EASM gradually decreased and the climate maintained cold and dry conditions. Human societies entered the historical period, and some indigenous dynasties were also established in the Changbai Mountains, which resulted in intensified human activities in the GST and SY regions. Vegetation cover and plant diversity in the SY and GST regions declined to their lowest levels resulting from the abrupt decrease in tree cover accompanying the prosperity of the Gaogouli and Bohaiguo dynasties. During this period, many cities, such as Guonei, Wandushan, and Longtanshan, were constructed (Wei, 2011). Building these cities probably intensified deforestation, and human activities may have surpassed climate as the dominant factor influencing vegetation growth. In contrast, climate change might still have been the dominant factor affecting plant changes for the DBS region. This hypothesis is supported by the abrupt rise in Chenopodiaceae cover in the DBS region, controlled by the weakened EASM. This phenomenon, however, was not observed in the GST or SY regions (Figs. 2 & 4).

After 0.8 ka, the EASM strengthened somewhat, and the climate became warm and humid. Human impacts on vegetation changes are not obvious during the collapse of the last indigenous dynasty (Jin) and climate regained dominance over vegetation cover changes within the three regions (Fig. 4). In response to climate change, the extent of broadleaved trees expanded while that of coniferous trees contracted in both the SY and GST regions resulting in the few changes of total vegetation cover. As the DBS region adapted to the mild climate conditions, Poaceae cover increased contributing to a slight increase in both herb and total vegetation cover (Fig. 2). Plant diversity and evenness of the plant composition in these regions also exhibited a slight increase. After the demise of the Jin dynasty, the three regions were ruled by a central regime from

the Yuan to the Qing dynasty and the historical documentary evidence indicates that the population of the three regions remained at a very low level during this period due to population migration, endless war, and limitations by the policy of Northeast China (Huang, 2002; Li & Wang, 2004).

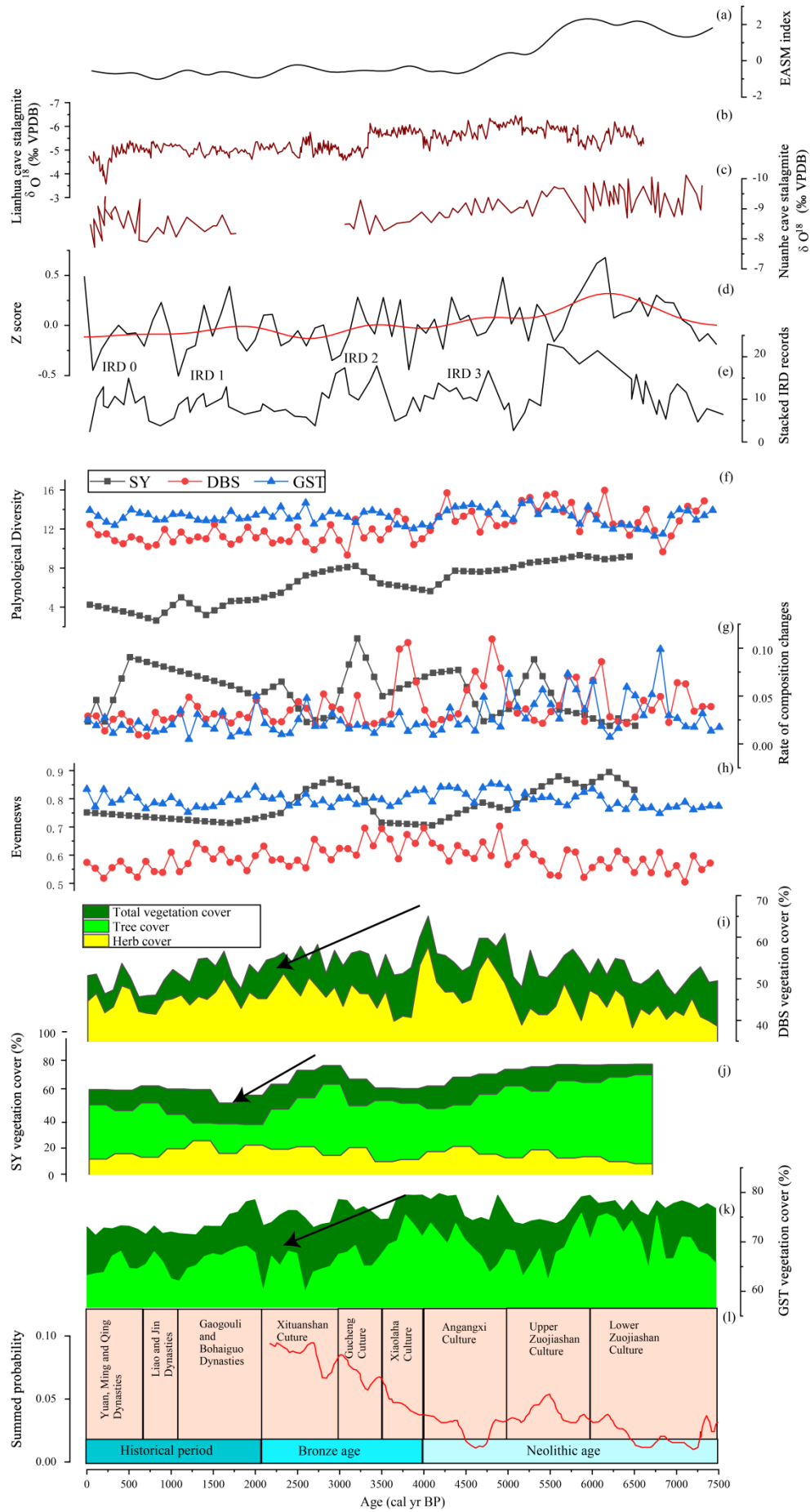


Fig. 4. Changes in land cover, climate, and human activity in the DBS, SY, and DBS regions since the mid-Holocene. (a) The EASM index (Chen et al., 2008); (b) Stalagmite $\delta^{18}\text{O}$ records from Nuanhe Cave, northeastern China (Wu et al., 2011); (c) Stalagmite $\delta^{18}\text{O}$ records from Lianhua Cave, northern China (Cosford et al., 2009); (d) Z-score calculated based on the selected climate records in Northeast China; (e) Holocene stacked IRD events in the North Atlantic (Bond et al., 2001); (f) Pollen-based plant diversity; (g) Pollen-based rate of plant compositional change; (h) Pollen-based plant evenness; (i) Reconstructed vegetation cover in the DBS region; (j) Reconstructed vegetation cover in the SY region; (k) Reconstructed vegetation cover in the GST region; (l) $\delta^{14}\text{C}$ summed probability reflecting the population size and cultural sequences.

4.4. Region-specific differences in human activity since the mid-Holocene

Vegetation changes, especially for vegetation cover within the region with intense human activities, are undoubtedly an important indicator of human activity. However, the extent and impact of human activity on vegetation change depend on variable patterns of resource utilization, subsistence strategies, and natural vegetation types (Ellis et al., 2021). The DBS and GST regions belong to dissimilar morphological units: the different landscapes and resources might result in different human subsistence strategies. The SY region, which is located in a more fragile environmental zone transitional between steppe and forest, allows the changes in grasses and trees to be easily detected under either the changes in climate or human activities.

During the Neolithic period, approximately between 7500 and 4000 cal BP, similar subsistence strategies are apparent for both steppe and forest regions. Fishing, hunting, and gathering were the main activities supporting human subsistence (Zhao, 2007). More specifically, fishing was the most common behavior for humans living in steppe regions as shown by human settlement locations, which were mostly in the vicinity of the lakes and rivers, and by the large proportions of clam shells and fish bones. For ancient humans living in the forest region, hunting was more common than fishing, as shown by the excavation of large numbers of arrowheads made of stones and bones, and by bone spears and wild animal bones. These subsistence strategies have few impacts on plants and could explain plant changes being mainly controlled by climate rather than human activities for both regions.

During the Bronze Age, between approximately 4000 and 2300 cal BP, the cultivation of crops spread from southern to northeastern China through the Korean Peninsula. A large number of

agricultural societies emerged in the forest region earlier than in the grasslands and this resulted in the different subsistence strategies of the two regions (Huang, 1993). Archaeological sites from forest regions have yielded many agricultural tools and domesticated cereal grains, including Broomcorn and foxtail millet, showing that human subsistence was primarily dependent on agriculture (Liu, 1983; Wang & Zhang, 2016). In contrast, humans living in steppe regions mainly retained a typical fishing and hunting culture with limited livestock raising and little agricultural activity. This is evidenced by the large number of advanced tools for fishing and hunting, along with domestic animal bones, excavated from the archaeological sites situated on the steppes (Li, 2008). The vegetation cover of the GST and DBS regions also illustrate the difference in human subsistence strategies of the two regions. Vegetation cover reduction in the GST and SY regions could be related to deforestation activities undertaken for agricultural purposes, and an increase in agricultural activities might also have resulted in the abrupt increase of Asteraceae cover in the DBS region (Li et al., 2008).

During the historical period (2300 cal BP- the present), frequent changes of indigenous dynasties occurred in the forest region until the collapse of the Jin dynasty. Growing population and an increase in social complexity led to population aggregation and establishment of large cities (Li, 2006; Jin & Xiao, 2016). This was accompanied by a decrease in the agricultural population of the grassland region, which for a long interval became dominated by a few nomadic groups (Zhang, 2009). This can explain the phenomenon of anthropogenic land cover being more obvious in the GST and SY regions than in the DBS region.

5. Conclusions

This study applied the MAT-REVEALS approach to three pollen records from Northeast China to reconstruct the actual land cover changes of the DBS, SY, and GST regions since the mid-Holocene and further evaluated plant composition changes. The distribution of archaeological sites and selected $\delta^{14}\text{C}$ summed probability results were used to reconstruct the relative size of human populations and the intensity of human activity for the study area.

The extent of total vegetation cover in the GST and DBS regions was relatively stable while this variable fluctuated considerably in the SY region probably because of its relatively lower plant diversity. Trees comprised the largest amount of vegetation cover in the GST region, whereas herbs occupied the least amount of cover. Similarly, tree cover dominated the SY region, which had relatively low proportions of herb cover. Herbs dominated the DBS region with relatively low proportions of tree cover. Prehistoric human activities remained at a relatively low level during ca. 7-4 ka in the Neolithic and gradually intensified after 4 ka when human societies entered the Bronze Age.

The impact of human activity and climate change on land cover and plant composition varied spatially and temporally in the study region. Climate change predominantly influenced the vegetation cover and plant composition changes after ca. 0.8 ka and before ca. 6 ka. Climate continued as the main driving force affecting plant changes in the ca. 6-4 ka BP interval in the three study areas. Together with climate change, human activities began to affect vegetation cover and plant composition during 4-2 ka BP. Human activities dominated vegetation cover changes in the GST and SY regions during ca. 2-0.8 ka BP while climate remained the dominant factor for plant changes in DBS region. These differences between regions can be related to human migration trends and varied human subsistence patterns.

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