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Research Article

Holocene Vegetation Succession and Response to Climate Change on the South Bank of the Heilongjiang-Amur River, Mohe County, Northeast China

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Pollen samples from peat sediments on the south bank of the Heilongjiang River in northern Northeast China (NE China) were analyzed to reconstruct the historical response of vegetation to climate change since 7800 cal yr BP. Vegetation was found to have experienced five successions from cold-temperate mixed coniferous and broadleaved forest to forest-steppe, steppe-woodland, steppe, and finally meadow-woodland. From 7800 to 7300 cal yr BP, the study area was warmer than present, and *Betula, Larix*, and *Picea*-dominated mixed coniferous and broadleaved forests thrived. Two cooling events at 7300 cal yr BP and 4500 cal yr BP led to a decrease in *Betula* and other broadleaved forests, whereas herbs of Poaceae expanded, leading to forest-steppe and then steppe-woodland environments. After 2500 cal yr BP, reduced temperatures and a decrease in evaporation rates are likely to have resulted in permafrost expansion and surface ponding, with meadow and isolated coniferous forests developing a resistance to the cold-wet environment. The Holocene warm period in NE China (7800–7300 cal yr BP) could have resulted in a strengthening of precipitation in northernmost NE China and encouraged the development of broadleaved forests.

1. Introduction

At present, global warming and its possible ecological consequences have become the focus for governments around the world, the scientific community, and the general public [1, 2]. In tackling core issues, it is very important to evaluate the effects of climate change accurately [3]. The Holocene is the most recent geological epoch. The early Holocene experienced increased temperatures, the mid-Holocene was warm and humid, and the late Holocene cooled [4, 5], providing research models for future climate change [6]. Land vegetation is an important part of the global ecological system and responds profoundly to climate change; exploring this relation between vegetation and climate change in critical areas has thus become an important approach in assessing the likely environmental impact of future climate change.

NE China, which has typical land ecosystems (including forests, steppes, and wetland) [7], is located on the eastern margin of the Eurasian continent. The northern Greater Khingan Range (GKR), in the northernmost part of NE China (on the southern margins of the permafrost zone), contains cold-temperate coniferous forest. The permafrost layer is shallow and its temperature stability is relatively low in this area, so the region is highly sensitive to climate change [8–10]. Over the past century, there has been a clear degradation of permafrost in NE China. Its southern boundary has moved northward 20–30 km [11–14]. This has caused a series of ecological and hydrological changes, resulting in wetland and forest degradation and other environmental problems. Permafrost wetlands in the northern GKR have been characterized by original wetland atrophy and new wetland expansion [13, 15, 16].

In recent years, research into the Holocene environment in this area has focused more on climatic and environmental reconstruction [17, 18] and concentrated on the Sanjiang Plains in the northeast [19–21], the Changbai Mountains in

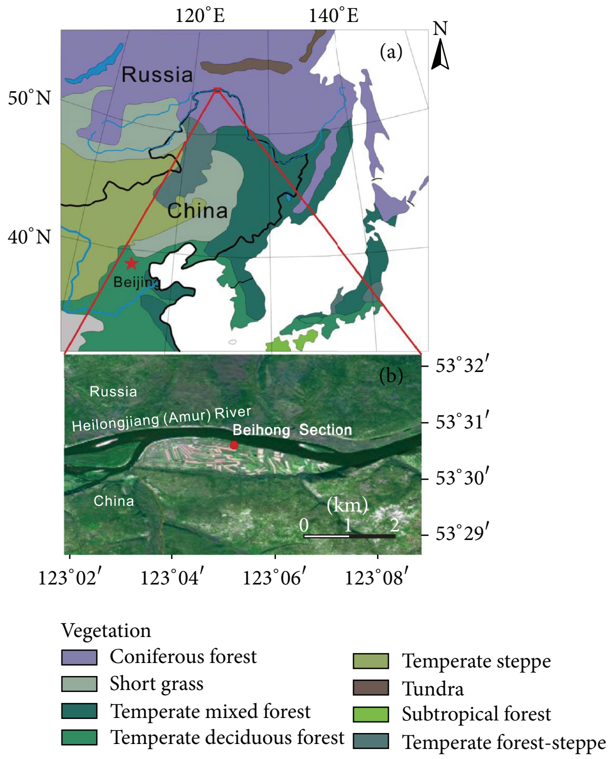

Figure 1: Map of the study area. (a) Red rectangle indicates the study area. (b) Red dot shows the Beihong Section.

the east [22–27], Hulun Lake in the western GKR [28, 29], Dali Lake in the southern GKR [30], Moon Lake in central GKR [31, 32], and so forth. These studies have highlighted a significant warming in the early mid-Holocene, followed by a transition to a dry-cold climate in the late Holocene.

However, a longer and more detailed vegetation history of NE China is still needed to verify vegetation succession interpretative studies and vegetative responses to climate change. There have until now been no other records sufficiently reliable for testing how cold-temperate vegetation on the northern margins of NE China has responded to Holocene climate change. This study is based on pollen records derived from Holocene peat sediments on the south bank of the Heilongjiang River. It aims to reconstruct a vegetation succession history, explore vegetation succession responses to climate change (especially during the Holocene Megathermal), and provide evidence for the evaluation of the possible effects of future climate change.

2. Materials and Methods

2.1. Study Area. The northern GKR (52°32′–53°41′N, 121°15′–125°58′E) (Figure 1) is located in the transition zone between a semihumid and semiarid cold-temperate continental monsoon climate; it is controlled by the cold Siberian-Mongolian High (extremely cold and dry) in winter and is marginally affected by the Pacific High (warm and humid) in summer [7]. Based on the Mohe County meteorological station, mean annual temperature (MAT) is −4.9°C, minimum temperature is −52.3°C, and the ground is frozen for up to eight months per annum. Mean annual precipitation (MAP) is 403 mm, about 80% of which is concentrated in June–September [37, 38]. In the last half century, the interannual rainfall shows fluctuation and changed between 274 mm and 635 mm [39]. The annual evaporation is ~1000 mm.

The Beihong Section (53°30′8.3″N, 123°5′24.5″E, altitude: 280 m a.s.l.), which is located in the north of Beihong Village, on the southern bank of the Heilongjiang River in Mohe County, is dominated by peat sediments from the upper reaches of the Heilongjiang River (Figure 1). The Heilongjiang (Amur) Valley in northern NE China is dominated by taiga vegetation, with *Larix gmelinii* as a typical vegetation type, including *Betula Platyphylla* forest, *Pinus sylvestris* var. *mongolica* forest, *Picea* forest, and Poaceae meadow [7, 40].

The GKR has been directly administered by the central government since the Yuan Dynasty (1206–1368 CE) [41, 42]. Its native inhabitants continued to hunt and gather until the onset of the Opium Wars (1840 CE), when its forests began to undergo large-scale exploitation [7, 43, 44]. Consequently, vegetation succession in the study area has been principally affected by natural factors, with relatively weak human influence during the Holocene. It is the ideal area to study vegetation succession and its responses to climate change.

2.2. Beihong Section Sample and Pollen Analysis. The Beihong Section is 260 cm thick. The sediments are mainly peat and silt. They are delineated as follows: 0–80 cm, dark brown peat layer; 80–220 cm, light gray silty clay; 220–260 cm, gray fine sandy silt.

26 samples taken at 10 cm intervals were prepared for pollen analysis, using conventional acid-alkali treatment and heavy liquid separation [45, 46]; they were then treated by acetolysis [47]. Lycopodium tablets were added to the samples in order to estimate pollen concentrations [48]. 315–646 pollen grains were counted from each sample; pollen percentages and concentrations were calculated based on total land pollen count. TILIA software was used to draw the pollen spectra, in which a CONISS module was used to calculate distances and cluster zoning based on the square root transformation of the pollen percentage data.

Detrended correspondence analysis (DCA) and principal component analysis (PCA) have been widely used in forest ecosystem, shrub communities, meadow grasslands, and other vegetation researches [16, 49, 50]. DCA is a sort of gradient analysis method, which can arrange samples or pollen-taxa in a certain space, and the ordination axes can reflect the ecological gradient to explain the relationship between plant communities and the environment [51]; PCA is a method of statistics to focus on a few comprehensive indexes from a set of variables and was applied to extract main gradient changes in vegetation. DCA and PCA figures were created by CANOCO 4.5 based on samples and the terrestrial pollen percentage data (of percentage >3%). PCA function in SPSS was used to generate the PCA F1 values, extracting more comprehensive information on the environment [22].

2.3. Chronology. Macroremains of leaves and peat selected from the samples were examined to obtain an accurate

Table 1: AMS ^{14}C dating results from the Beihong Section.

Sample	Laboratory code	Depth (cm)	Sample type	^{14}C ages (yr BP)	δ^{13}C (‰VPDB)	Calibrated ^{14}C ages (cal yr BP)
BH-16	378769	75	Macro-remains of leaves	3970 ± 30	−28.8	4524–4401
BH-32	379976	155	Peat	6200 ± 30	−25.4	7179–7000
BH-48	376264	238	Macro-remains of leaves	6770 ± 30		7669–7580

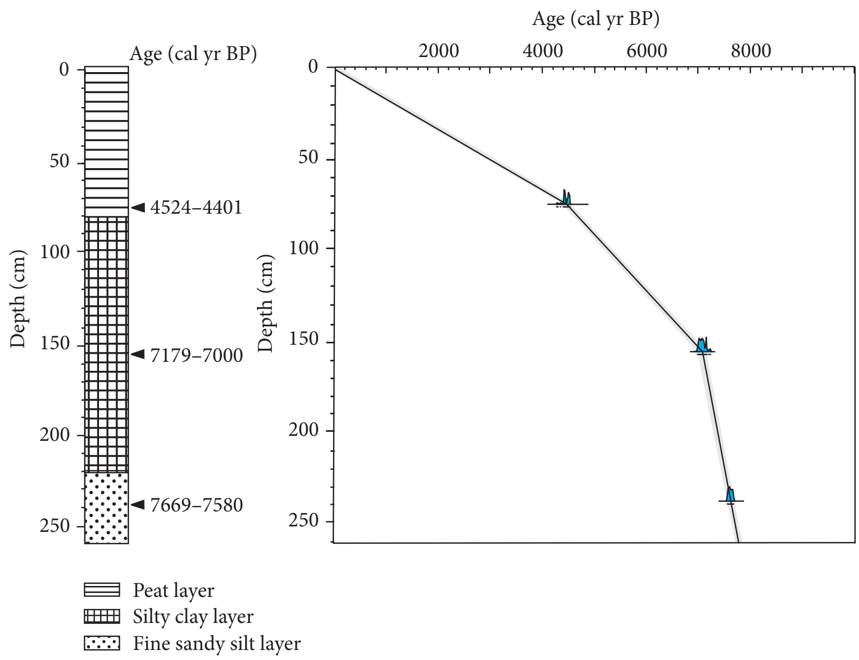

Figure 2: Beihong Section and age-depth model.

age-depth framework. AMS ^{14}C dating was conducted at the Beta Analytic Radiocarbon Dating Laboratory in America, and three AMS ^{14}C ages at depths of 75 cm, 155 cm, and 238 cm were obtained. Radiogenic ^{14}C ages were calibrated to calendar ages based on IntCal13 [52] and an age-depth model was produced using OxCal4.2.4 [35] (Table 1). The Beihong Section shows a positive correlation between age and depth.

A chronosequence for the Beihong Section was established using linear interpolation and extrapolation methods based on three samples. The age of the base (260 cm) was calculated as 7800 cal yr BP; the top consists of modern deposits. Consequently, the Beihong Section presents a historically continuous sedimentary sequence (Figure 2). The sedimentation rate is higher in the lower segment of the section. The average sediment rate is 0.16 cm/yr between 260 cm and 155 cm and falls to an average of 0.02 cm/yr from 155 cm to 0 cm; as a consequence the lower segment of the section has a higher resolution than the upper part.

3. Results

3.1. Pollen Assemblages in the Beihong Section. 53 families and genera of pollen were identified in the Beihong Section (Table 2). They are mainly broadleaved tree pollen (19%–54%) and herb pollen (28%–64%); *Betula* pollen (10%–45%) was the commonest of the broadleaved tree pollen, and Poaceae pollen was the most prominent of the herb pollen, with content ranging from 3% to 36%. Total pollen concentrations exhibited considerable variation, ranging from 2.9×10^2 to 1.9×10^6 grains/g.

Based on chronological changes in pollen percentages, five successions can be recognized from pollen spectra (Figure 3).

In zone 1 (260–190 cm, 7800–7300 cal yr BP), *Betula*, *Larix*, *Picea*, *Alnus*, Cupressaceae, *Pinus*, and other kinds of tree pollen dominate pollen assemblages (55%–66%); of these, broadleaved tree pollen percentages, especially of *Betula* (22%–45%), were extremely high. Coniferous tree pollen content (10%–27%), mainly *Larix* (7%–16%) and *Picea* (2%–7%), was relatively high. Shrub and herb pollen percentages fluctuated from 34% to 45% and were dominated by Liliaceae pollen (1%–19%), with some *Artemisia* (3%–11%), Chenopodiaceae (2%–5%), and Poaceae pollen (3%–16%). Total pollen concentrations (2.9×10^2–2.0×10^4 grains/g) were relatively low.

In zone 2 (190–80 cm, 7300–4500 cal yr BP), spectra were dominated by Poaceae, *Artemisia*, Chenopodiaceae, and other kinds of herb pollen, with their total content ranging from 44% to 50%. Poaceae pollen percentages (9%–28%) clearly increased, whereas Liliaceae pollen content (0–6%)

Table 2: Pollen types in the Beihong Section.

Conifers	*Pinus*, *Picea*, *Larix*, and Cupressaceae
Broadleaved trees	*Quercus*, *Betula*, *Salix*, *Populus*, *Ulmus*, *Alnus*, *Corylus*, *Carpinus*, *Juglans*, *Castanea*, and Aceraceae.
Shrubs and herbs	Ericaceae, *Artemisia*, Chenopodiaceae, Poaceae, Leguminosae, *Thalictrum*, Caryophyllaceae, Compositae, Rosaceae, *Sanguisorba*, Liliaceae, Rubiaceae, *Plantago*, Umbelliferae, *Ephedra*, Polygonaceae, Oleaceae, Cyperaceae, Ranunculaceae, *Tamarix,* Dipsacaceae, and so forth.
Ferns	Polypodiaceae, Athyriaceae, *Selaginella,* and so forth.

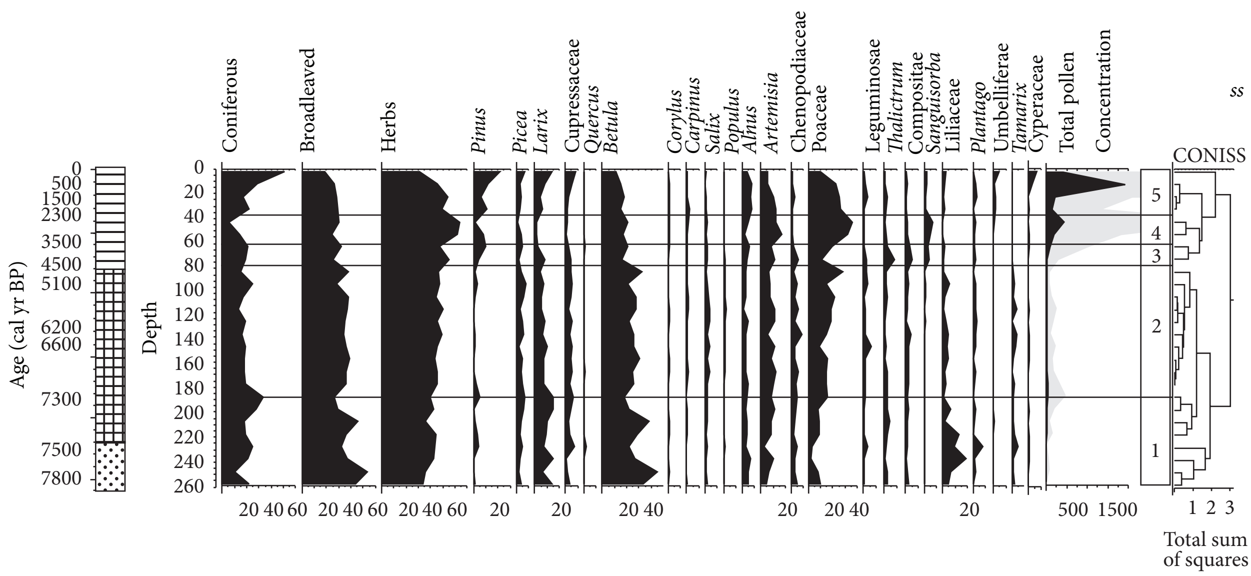

Figure 3: Pollen percentages and concentrations for the Beihong Section (the gray values to the right are magnified tenfold to emphasize changes in concentration).

decreased. In contrast, tree pollen content decreased markedly, with *Larix* (5%–10%), *Betula* (21%–32%), and *Pinus* pollen percentages (0–4%) dropping markedly. Total pollen concentrations (6.7×10^3–4.5×10^4 grains/g) were relatively low.

In zone 3 (80–60 cm, 4500–3500 cal yr BP), this period was characterized by high percentages (48%–55%) of herb pollen, principally *Thalictrum* (3%–9%), Compositae (4%-5%), *Sanguisorba* (3%-4%), and *Artemisia* (8%–11%); Poaceae pollen content (11%–20%) decreased noticeably. Coniferous (19%–21%) and broadleaved tree pollen content (26%–32%) decreased, with *Betula* (17%–20%) and *Picea* pollen percentages (3%–5%) falling markedly. Total pollen concentrations (2.9×10^4–10.0×10^4 grains/g) increased slightly.

In zone 4 (60–40 cm, 3500–2300 cal yr BP), Herb pollen, dominated by Poaceae, *Artemisia,* and *Sanguisorba*, reached its peak values at 62%–64%; among them Poaceae (32%–36%), *Artemisia* (12%–18%), and *Sanguisorba* (5%–7%) pollen markedly increased, while Chenopodiaceae pollen content (about 1%) decreased. Coniferous tree pollen (6%–14%) decreased noticeably, with *Larix*, Cupressaceae, and *Picea* pollen falling to their lowest values, while *Pinus* pollen increased (1%–8%). Total pollen concentrations rose (1.8×10^5–4.3×10^5 grains/g).

In zone 5 (40–0 cm, 2300 cal yr BP-modern), coniferous tree pollen (17%–51%), especially *Pinus* pollen percentages (6%–21%), increased greatly, with some emergence of *Larix* (4%–13%) and *Picea* (3%–6%). Broadleaved tree pollen (29%–19%) decreased, especially *Betula* pollen content (18%–11%), which fell to its lowest value for the entire section. Herb pollen percentages (31%–55%) decreased, but Cyperaceae, *Plantago*, and Umbelliferae content increased to some extent. Total pollen concentrations (1.3×10^5–1.9×10^6 grains/g) increased.

3.2. DCA and PCA Results. Of the 26 samples taken from top to bottom of Beihong Section, 31 families and genera were analyzed using DCA. The first two ordination axes were drawn on a two-dimensional ordination map (Figure 4). The score value of each sample was distributed regularly on the plane composed of the first and second principal axes. Samples from the five pollen assemblages yielded separate, individual clusters, and these clear differences verified the accuracy of the zoning (Figure 3).

According to PCA results for the principal families and genera (Figure 5), the first two principal component axes accounted for 79% of all the variables (the first axis for 69% and the second for 10%). *Pinus*, *Betula*, Chenopodiaceae, and Ericaceae are the four main taxa of the original

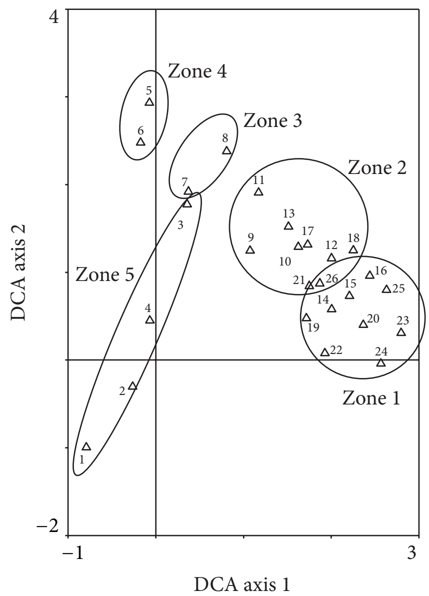

Figure 4: DCA results for 26 representative plant community samples from the Beihong Section.

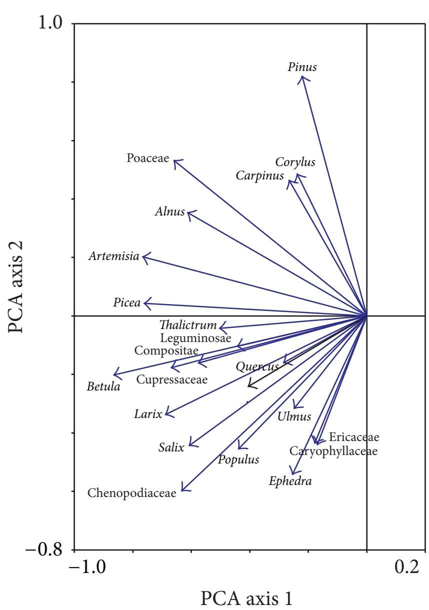

Figure 5: PCA results for principal pollen from the Beihong Section.

data matrix, whose vector lengths represent their degree of effect and significance, while the importance of other taxa decreases accordingly. Relations between the main taxa present a certain regularity. The plants that registered the highest positive scores for the first component axis included Ericaceae, Caryophyllaceae, and other plant types; *Betula*, *Picea*, and other vegetation types yielded the lowest scores. *Pinus* and Poaceae scored the highest positive values on the second component axis; Chenopodiaceae, *Ephedra*, and other vegetation types scored lowest here.

4. Discussion

Stalagmite, ice core, ocean, lake sediment, and other high resolution records show that there was a significant warm period in the mid-Holocene, similar to a scenario encompassing a 1-2°C increase in average global temperatures [5, 53–55]. Marcott et al. suggested that, based on 73 globally discrete records, temperatures during 10000–5000 cal yr BP were 0.7°C warmer than the late Holocene [4]. The reconstruction of the vegetation succession on the southern bank of the Heilongjiang River in northern NE China since 7800 cal yr BP provides an important basis for establishing climate and environment change and their effect on vegetation in a cold-temperate region in the Holocene.

Pollen analysis is the technique most widely used and pollen data are most reliable for the reconstruction of paleovegetation and paleoclimate. Understanding the relation between modern pollen and vegetation is a prerequisite for interpreting fossil pollen records correctly and improving the accuracy of past vegetation type and paleoclimate reconstruction [56–58].

4.1. Pollen Source in Beihong Section. The lithology changed from fine detritus gyttja at the bottom to decomposed peat in the Beihong Section (Figure 2). It may indicate that the environment of sedimentation changed over time and this lithologic transition probably occurred as the site changed from lake to swamp [59].

Source areas and relative pollen representation are shown to depend on basin size [60]. In Beihong Section, 220–260 cm gray fine sandy silt may indicate the enhancement of water-carrying capacity. This may induce a relatively low total pollen concentration because of the poor depositional environment (Figure 3). In addition, surface pollen assemblages in the marsh always includes a large number of regional pollen types usually from aquatic plants [61]; meanwhile, the total pollen concentrations may increase due to favorable depositional environment (Figure 3).

Nevertheless, studies on alluvial pollen show that the differences between alluvial pollen assemblages are the result of different pollen origins [34]. Most studies in different environment of sedimentation show that despite containing some exotic ingredients, the modern pollen assemblages can reflect characteristics of plant community in the immediate area, and the main vegetation zones along the regional can be distinguished by their modern pollen spectra [33, 36, 56–58, 61–65]. Therefore, the transitions of the pollen assemblages of the terrestrial pollen percentage (with the pollen sum excluding aquatics) in Beihong Section are mainly the result of the vegetation succession in the study area.

4.2. Modern Pollen Representation and Climatic Implications. Surface pollen studies have established that there is a relationship among the pollen percentages as well as vegetation type and regional climate [64]. The studies on vegetation and modern pollen distribution show that pollen assemblages are correlated well with the vegetation types in NE China [33, 36, 63].

In addition, *Betula* and *Pinus* pollen is overrepresented. The existence of birch forests was thus indicated only when the *Betula* content exceeded 40%. Pine forest might exist when *Pinus* pollen percentages are more than 30%. Poaceae and *Larix* pollen is of low representative feature. *Larix* pollen contents accounted for only 15% in larch forest [57, 62, 66]. A higher proportion of Poaceae (24%) was the main characteristic of wetland shrub. Poaceae pollen contents are <10% in Poaceae grassland, with *Artemisia* and Chenopodiaceae pollen percentages being more than half of the total. Hence, a high representation of *Artemisia* and Chenopodiaceae was found. Cyperaceae and *Ephedra* appeared in the middle or low relative representation values [33, 57].

Larix gmelinii and *Pinus sylvestris* var. *mongolica* are dominated in cold-temperate zone. The relationship among *Pinus* pollen, temperature, and humidity is more complex. *Pinus* pollen contents rise rapidly with increasing humidity [36]. The distribution of spruce is in cold-temperate zone (average temperature is 0–8°C) in the northern part of NE China; others grow in the cold-wet subalpine zone between 1000 and 2000 m [67]. The abundance of *Picea* pollen generally increases along with the humidity rise [68]. The *Betula* pollen count in topsoil of northern China is affected mainly by annual precipitation and will rise consistent with the increase of the amount of precipitation [67, 68].

Poaceae pollen is abundant in fossil records and is often used as a paleoclimatic indicator [69]. Poaceae pollen always concentrated in low temperature and high humidity area or semiarid warm zone, and its abundance increases with the decrease of temperature, as well as the increase of precipitation in low temperature and high humidity area [67]. The abundances of Chenopodiaceae and *Ephedra* pollen increased with increasing aridity; Compositae and *Plantago* pollens appear at low temperature and high humidity area [67, 68].

4.3. Vegetation Succession in Beihong Area. Based on the pollen assemblages and the modern pollen analysis, the vegetation history in Beihong area has experienced five chronosequences since 7800 cal yr BP.

(1) In 7800–7300 cal yr BP, *Betula* pollen percentage is at the highest level of the section, up to 45%. Larix content (7%–16%) is also relatively high. The pollen assemblage may indicate that the study area developed *Larix* and *Betula* dominated cold-temperate coniferous and broadleaved mixed forest.

(2) In 7300–4500 cal yr BP, herb pollens increase (>44%). Poaceae pollen percentages range from 9% to 28%, while *Betula* (<32%), *Larix* (<10%), *Pinus* pollen (<4%), and other tree pollen contents decreased markedly, suggesting a forest-steppe vegetation type.

(3) In 4500–3500 cal yr BP, herb pollen increases, including *Thalictrum*, Compositae, *Sanguisorba*, and *Artemisia*. Tree pollen percentages decrease markedly, with *Betula* pollen ranging from 17% to 20%. Pollen assemblages indicate steppe-woodland.

(4) In 3500–2300 cal yr BP, pollen records reveal Poaceae (32%–36%), *Artemisia,* and *Sanguisorba* dominated steppe vegetation type.

(5) In 2300 cal yr BP-modern, pollen assemblages indicate that Poaceae, Cyperaceae, and other mesophydrophyte-dominated meadow vegetation developed, along with an expansion in isolated coniferous forests composed largely of *Pinus* pollen (up to 21%). These pollen assemblages are characterized by meadow-woodland vegetation.

4.4. Vegetation Response to Climate Change. Climate change has an important impact on terrestrial ecosystems [70–72]. Similarly, vegetation successions in different regions are a good indicator of climate change and are an important index for revealing the environmental impact of climate change. Fossil pollen diagrams can be assumed to reflect information about natural vegetation dynamics and provide the evidence for the behavior of plant taxa when subjected to major climatic and environmental changes in the past [64].

The vegetation history mainly experienced a clear decrease in *Betula* and other broadleaved trees, while Poaceae-dominated herbs increased in the study area (Figure 3). The pollen samples exhibited five vegetation successions, from coniferous and deciduous mixed forest at the section's base, upward to forest-steppe, steppe-woodland, steppe, and meadow-woodland, transitioning from a forest vegetation cover, resistant to a cold-dry environment to meadow-woodland vegetation and then to cold-wet environs (Figure 4). These vegetation types and the succession process had similar records at high latitudes.

Herbaceous plants, such as Cyperaceae and Poaceae, are the most important components of wetland communities [73]. Alpine vegetation occurs from the treeline to the snow line, whose important taxa include Cyperaceae, Poaceae, Compositae, Ericaceae, Caryophyllaceae, and Rosaceae [74]. The Holocene pollen diagram from eastern Canadian Arctic Island showed that there was virtually no *Betula* pollen present in very cold temperature, while Poaceae pollen with varying amounts of Ericaceae and Caryophyllaceae dominated the pollen assemblages [75]. Vegetation history of the western America in the Holocene shows that the lower subalpine communities are usually closed forests, and upper communities are steppe-woodland and shrublands. Based on the meteorological data of Changbai Mountain, the distribution age of *Betula ermanii* was in the trend of decreasing with elevation rising in the ecotone between *Betula ermanii* and alpine tundra [76]. Therefore, vegetation dominated by *Betula* might reflect a relatively warmer environment than the later meadow-woodland community in Beihong Section.

Consequently, DCA reflected a clear relation between different plant communities as well as between plant communities and the environment. The first axis can reflect the temperature gradients for different plant communities, with ability to resist the cold strengthening leftward along the axis; the second axis can indicate changes in humidity, with a plant community's ability to withstand drought strengthening

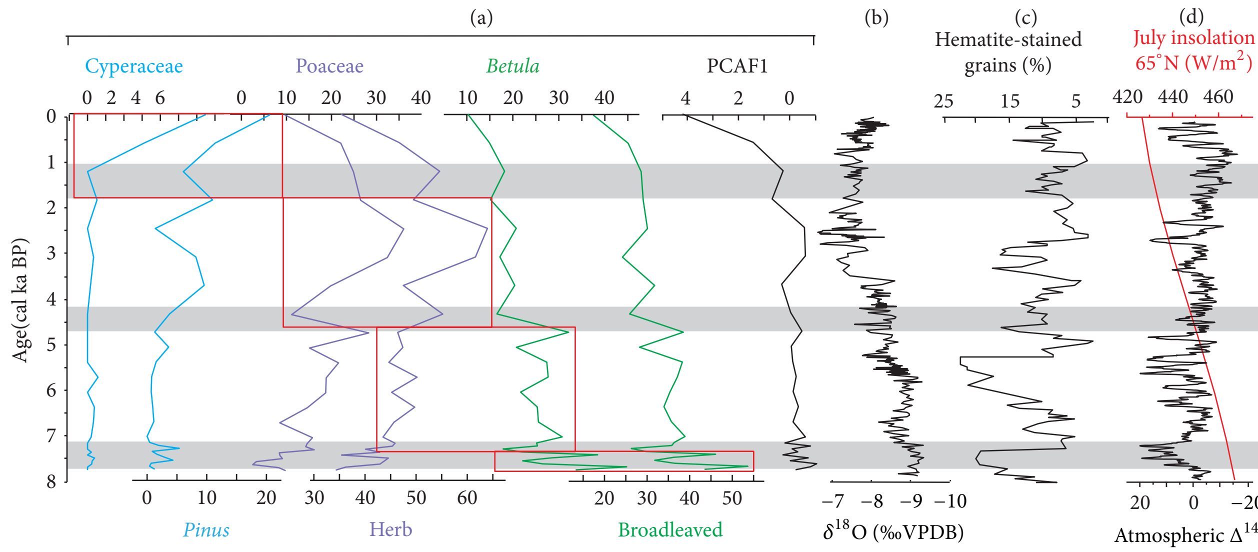

FIGURE 6: Comparison of principal pollen percentages and the PCA F1 curve from the Beihong Section with other selected proxy records. (a) Pollen index from the Beihong Section. From the right to left are the PCA F1 curve, the percentage curves of broadleaved trees, *Betula*, herb, Poaceae, *Pinus*, and Cyperaceae. (b) Dongge Cave D4 [33]. (c) Holocene drift ice record for the MC52-VM29-191 North Atlantic core [34]. (d) Northern Hemisphere July insolation at 65°N [35] and the residual atmospheric Δ^{14}C record (~2000-year moving average) [36]. The lateral gray bands trace the interconnection between climate cooling, drift ice, a weakened EASM, reduced insolation activity, and the principal pollen taxa changes in this study. The red boxes show the main indicator plants of vegetation type conversion.

upward along the axis. The first principal component of PCA reflected temperatures and the second changes in humidity.

The PCA F1 scores of the taxa on the first principal component axis better reflected the pollen percentage variations with temperature; that is, higher values may represent cold and lower values warm climates (Figure 5). The PCA F1 curve thus revealed that temperatures have fluctuated downward decreased since 7800 cal yr BP (Figure 6), in tandem with reductions in insolation in northern hemisphere high latitudes [77].

In order to better reflect the response of vegetation to climate change, the principal pollen percentages and the PCA F1 curve from the Beihong Section were compared with high-resolution climate indices from other regions (Figure 6). Results suggested that the warmest and wettest stage in the Holocene occurred at ~7800–7300 cal yr BP, when MAT and MAP suited the growth of coniferous and broadleaved mixed forest in the study area. After 7300 cal yr BP, a decrease in *Betula* and other broadleaved trees and an increase in Poaceae and other herbs, as well as in *Pinus*, Cyperaceae, and other plants resistant to the cold-wet environs of the late Holocene, correspond to documented cooling events and reduced insolation activity [78].

The Beihong Section shows that the area had developed *Betula*, *Larix*, and *Picea*-dominated coniferous and broadleaved mixed forests, with Liliaceae prevalent in the undergrowth during 7800–7300 cal yr BP. Such vegetation indicates a warm and humid climate and essentially agrees with the findings of many other surveys, such as those conducted at Hulun Lake in the western GKR [29], the Qindeli Section on the Sanjiang Plains [20], Hokkaido Island [79], the Kuril Islands [80], the eastern Siberian Yakutia Lake [61], and Sakhalin [79].

At ~7300 cal yr BP and ~4500 cal yr BP, warmth-loving broadleaved trees clearly decreased in number in the study area, while cold-tolerant herbs increased (Figure 6). Vegetation cover changed from mixed coniferous and broadleaved forest to forest-steppe and steppe-woodland. The two significant cooling events which had a profound impact on vegetation succession are consistent with the significant ice event identified in North Atlantic records [81] and with the weakened East Asian Summer Monsoon (EASM) revealed in stalagmite oxygen isotope records from Dongge Cave [5, 82]. At ~2500–1500 cal yr BP, broadleaved trees, Poaceae, and mesophytes-xerophytes taxa declined, while *Pinus* and Cyperaceae vegetation expanded. Plant type was affected by paludification, indicating that global climate cooling had a profound influence on vegetation.

The cooling event at ~7300 cal yr BP, which resulted in a vegetation succession from mixed coniferous and broadleaved forest to forest-steppe, also appears in pollen records from Moon Lake in the central GKR [31] and the Buguldeika Core from Baikal Lake [83]. The cooling event at ~4500 cal yr BP, which may have global parallels, appears in the pollen records from Erlongwan Maar Lake [84], the Gushantun Bog in Jilin [85], and Hokkaido in Japan [86]. Vegetation shows a succession from forest-steppe to steppe-woodland. The cooling during ~2500–1500 cal yr BP in the Beihong area is also apparent in paleoenvironmental records from Hulun Lake in the western GKR [29], Moon Lake in the central GKR [31], Dali Lake in the southern GKR [30], Jingpo Lake in NE China [24], and Hokkaido Island in Japan [79, 80].

Many studies show that there is a complex interaction of climatic and ecological processes in boreal permafrost formation and degradation [73, 87, 88]. Permafrost is directly influenced by climate; climate and permafrost are among the principal driving forces of vegetation establishment and successional change across Siberia [89, 90]. The investigation of potential vegetation cover progression during the Siberian Bioclimatic Model shows that permafrost is predicted to thaw. The future much warmer and drier climate would be suitable for the forest-steppe ecotone and grasslands rather than forests, and water-stress-tolerant light larch (*Larix dahurica*) taiga will continue to be the dominant zonobiome over eastern Siberia [89].

Accordingly, it can be predicted that falling global temperatures and a weakening EASM gave rise to decreased rates of evaporation and an increase in effective humidity levels in the late Holocene. At the same time, an expansion in permafrost led to precipitation and runoff being unable to seep underground, causing surface ponding, marsh expansion, and peat development [13]. As a result, the vegetation type changed gradually to meadow and swamp-meadow, with isolated areas of cold-wet tolerant coniferous woodland [91] and a severe reduction in warmth-loving broadleaved trees. The long-term data from our studies (especially during the Holocene Megathermal) in the permafrost ecosystem suggest that responses of vegetation to climate warming might be the thaw of permafrost which will be deep enough to sustain the growth of *Betula* and *Larix* dominated taiga in south bank of Heilongjiang-Amur River [89].

5. Conclusions

The pollen records of peat sediments from the southern bank of the Heilongjiang River in northernmost NE China show that the period 7800–7300 cal yr BP was the warmest and wettest stage of the Holocene. At that time, the study area developed *Betula* and *Larix*-dominated mixed coniferous and broadleaved forest. This indicates that increases in temperature and precipitation were conducive to the growth of broadleaved forests in the study area. At ~7300 cal yr BP and ~4500 cal yr BP, two significant cooling events resulted in a reduction in broadleaved forests and an expansion of herbs, with a vegetation succession into forest-steppe and then steppe-woodland. After a decrease in temperatures during ~2500–1500 cal yr BP, the vegetation type changed into meadow, accompanied by the development of "islands" of cold-wet tolerant coniferous forest. In the late Holocene, lower global temperatures and a weakening EASM led to decreases in evaporation and increases in effective humidity; the expansion of permafrost might have hindered the infiltration of precipitation and runoff, causing surface ponding and an expansion in marsh and meadow vegetation.

Conflict of Interests

The authors declare that there is no conflict of interests regarding the publication of this paper.

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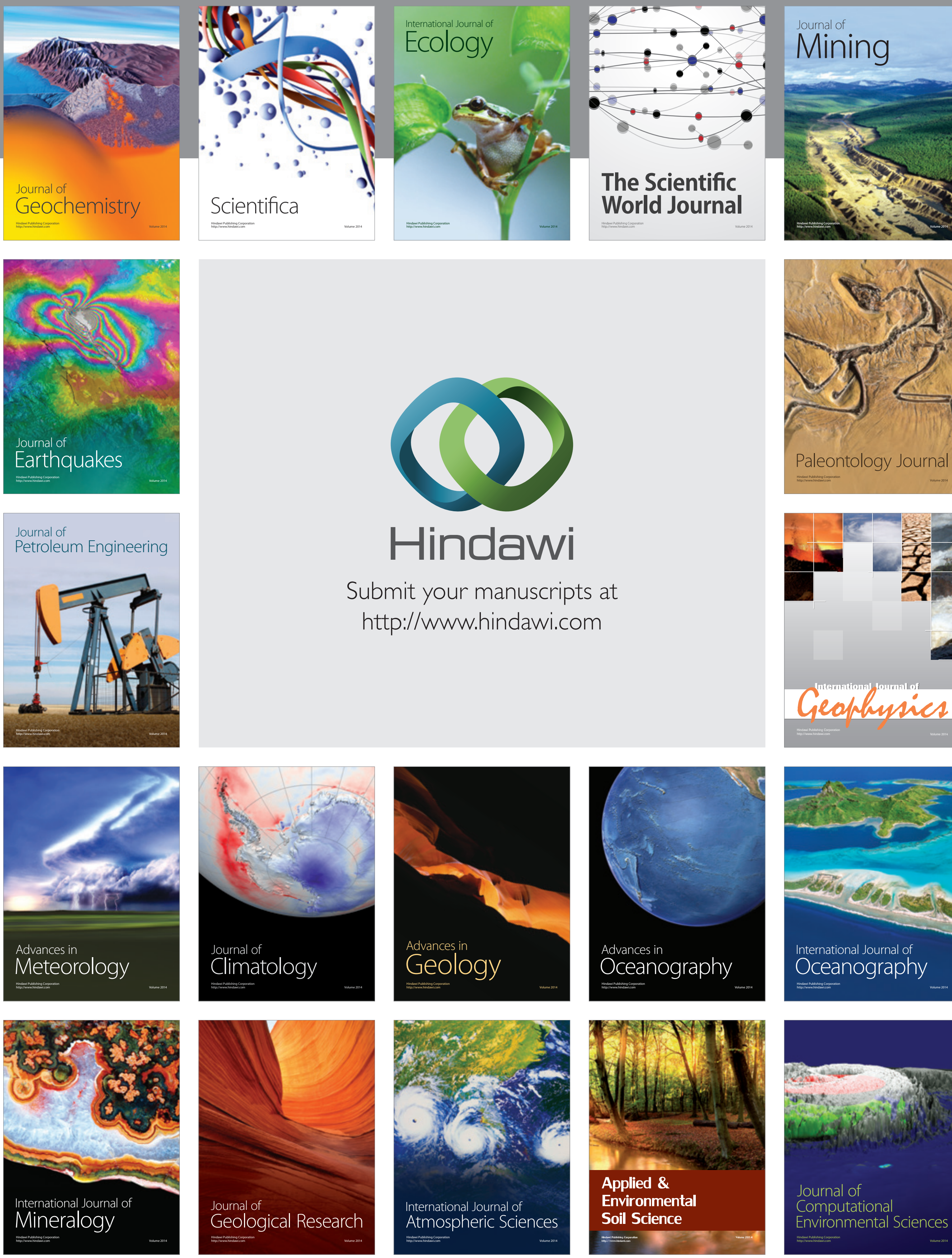

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