

# Does palynological diversity reflect floristic diversity? A case study from Northeast China

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**Abstract** Fossil pollen data can provide important information of past vegetation diversity, on the basis of established relationship between modern palynological and floristic diversity. However, current studies on modern pollen assemblages in China have not examined this relationship yet. Herein, we report a case study from Northeast China, aiming to investigate the representation of modern palynological diversity to regional floristic diversity. A total of 87 sets of modern pollen and vegetation data from various vegetation types were applied to assess modern palynological diversity and floristic diversity in Northeast China, and the relationship between palynological and floristic diversity was studied using spatial pattern comparison and correlation analysis. Moreover, to reduce representation bias related to pollen production and dispersal, we calibrated pollen data using the Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) model with Pollen Productivity Estimates (PPEs) and Fall Speeds of Pollen (FSP). The results show that the spatial variations of palynological and floristic richness among vegetation types are similar, and have a good positive correlation ( $r=0.41$ ,  $p<0.01$ ). However, palynological evenness presents a different spatial pattern from floristic evenness, with a weaker positive correlation ( $r=0.21$ ,  $p>0.05$ ). The calibration on pollen data using REVEALS model minimized the differences in spatial patterns between palynological and floristic diversity, and improved the correlations between them (richness,  $r=0.50$ ,  $p<0.01$ ; evenness,  $r=0.33$ ,  $p<0.01$ ). Our study indicates that palynological richness in Northeast China could reflect regional floristic richness in general, and the calibration with REVEALS model is recommended for reconstructing past floristic diversity from pollen data.

**Keywords** Northeast China, Modern palynological diversity, Floristic diversity, Richness and evenness, Community dissimilarity index, REVEALS model

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## 1. Introduction

Biodiversity is vital for maintaining the stability and sustainability of ecosystems (Balvanera et al., 2006; Cardinale et al., 2012). Global warming and precipitation pattern alterations exacerbated by human activity, have significantly

affected biodiversity in recent decades (Araujo and Rahbek, 2006; Wei et al., 2014). Studies on past biodiversity can provide insights into the mechanisms of biodiversity dynamics at different spatiotemporal scales, and hence a basis for future biodiversity protection. However, the scarcity of long-term diversity studies limits the understanding of biodiversity responses to climate change in the past and providing convincing predictions in the future (Jaramillo et al.,

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2006; Reitalu et al., 2015).

As a direct and reliable indicator of past vegetation composition, fossil pollen can also be used to retrieve information of past floristic diversity (Birks and Line, 1992; Odgaard, 1999). To ensure the reliability of floristic diversity reconstructed by pollen data, investigating the relationship between modern palynological and floristic diversity is indispensable. Many studies have revealed that modern palynological diversity is positively associated with contemporary floristic diversity, such as richness in southern Estonia (Meltsov et al., 2011), northern Europe (Reitalu et al., 2019), Serra da Estrela (Connor et al., 2021), Storbreen (Pardoe, 2021); the Shannon-Wiener index and Simpson's index in Storbreen and Grjøtbreen (Pardoe, 2021). Nevertheless, other studies have pointed out that palynological richness and Shannon-Wiener index in Bolivia and Ghana (Gosling et al., 2018), and evenness in southern Estonia (Meltsov et al., 2011), have no correlation with the corresponding floristic diversity. The relationship between palynological and floristic diversity is still debated, and further studies in various regions are essential.

To date, studies on modern pollen assemblages have been conducted extensively in China (Liu et al., 1999; Li et al., 2005; Ma et al., 2008; Zhao and Herzsuh, 2009; Lu et al., 2011; Zhao et al., 2012; Zheng et al., 2014; Xu et al., 2016; Cui et al., 2019; Geng et al., 2019; Li et al., 2020; Shen et al., 2021; Cao et al., 2021; Chen et al., 2021). However, little attention has been devoted to modern palynological diversity (Li et al., 2005; Pan et al., 2010; Li, 2018; Wang et al., 2022) and the research on the relationship between modern palynological and floristic diversity is still vacant in China. The lack of modern investigation has hampered the wide application of palynological diversity as a proxy for floristic diversity in paleo-ecological research.

To explore whether palynological diversity could reflect regional floristic diversity, we select Northeast China as the study region, which is ideal for studying the relationship between modern palynological and floristic diversity, owing to its diverse vegetation types and relatively clear zonal distribution of flora (Zhou et al., 2010). Herein, we present the first assessment of palynological diversity representation to floristic diversity in China using 87 pairs of modern pollen assemblages and detailed vegetation survey data from different vegetation types of Northeast China, as well as the available calibration method to improve the representation of palynological diversity. The aims of this study are to (1) investigate the basic features of modern palynological and floristic diversity in Northeast China, (2) compare the spatial patterns and analyze the relationship between palynological and floristic diversity, and (3) verify the validity of calibrating pollen data to improve the representation of palynological diversity.

## 2. Materials and methods

### 2.1 Study region

The study region is located in Northeast China, ranging from 40.9°N to 52.0°N in latitude and from 115.0°E to 129.6°E in longitude. The region lies in cold-temperate and mid-temperate zones from north to south, and crosses semi-arid, semi-humid, and humid zones from west to east (Shi et al., 2022). The climate of this region is affected by the Eastern Asian monsoon, and is characterized by distinct seasonality with simultaneous rain and heat. According to meteorological data (1981–2010) from the National Meteorological Information Center (<http://data.cma.cn/site/index.html>), the mean annual precipitation (MAP) generally exhibits a gradient that increases from 205 mm in the west to 765 mm in the east, and the rain falls mainly in June, July and August. The mean annual temperature (MAT) of this region varies from  $-4.0^{\circ}\text{C}$  in the north to  $10.2^{\circ}\text{C}$  in the south.

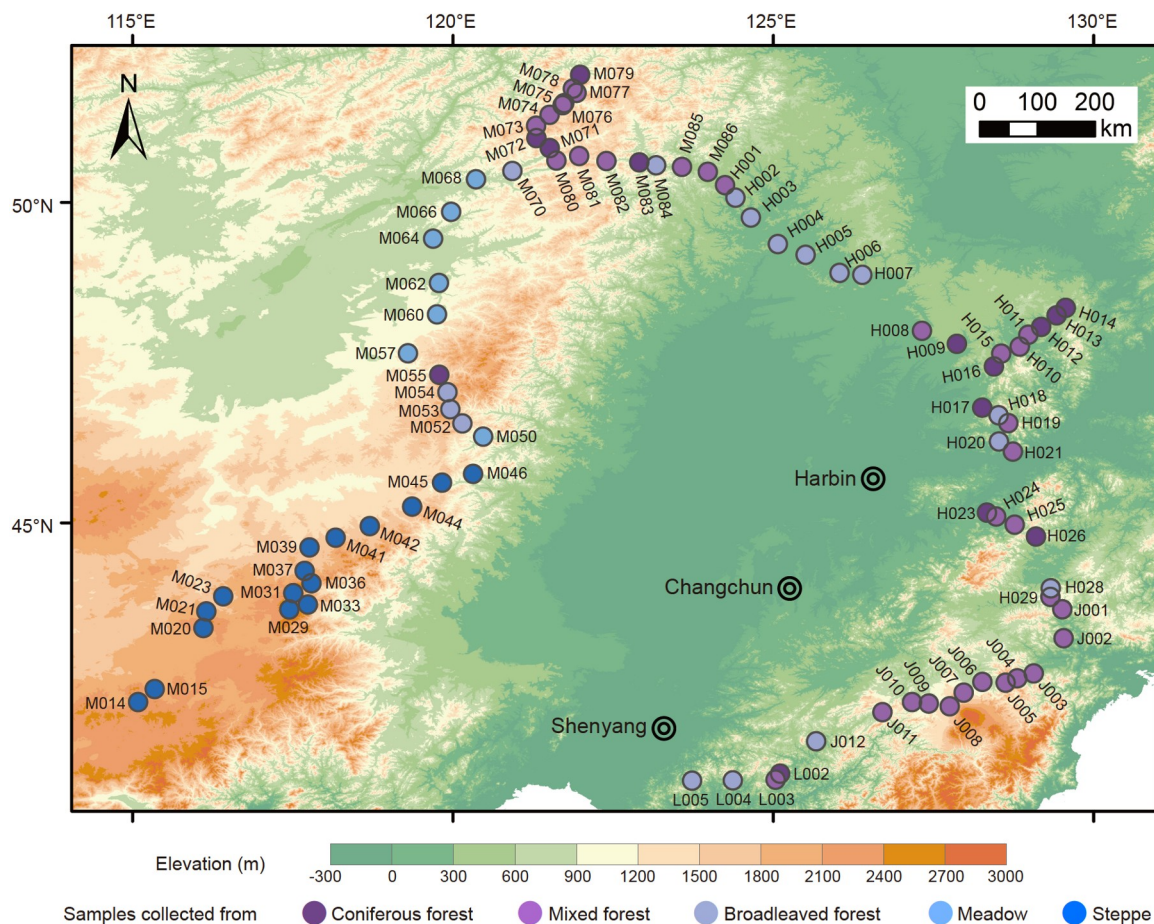
The vegetation in Northeast China shows clear zonation (Hou, 2001). Forests are mainly distributed in the east of the study region and can be classified as cold temperate coniferous forests (coniferous forest for short hereinafter), conifer-broadleaved mixed forests (mixed forest for short), and broadleaved deciduous forests (broadleaved forest for short) from north to south. The western part of the study region is mainly covered by grasslands, including meadows and temperate steppes.

### 2.2 Modern pollen sampling and vegetation survey

In September 2017, 87 modern pollen samples were collected from Northeast China at 20–40 km intervals, which contained 64 moss samples from forest regions (15 samples from coniferous forests, 32 samples from mixed forests, and 17 samples from broadleaved forests), seven topsoil samples from meadows, and 16 topsoil samples from steppes (Figure 1).

We recorded the plant taxa and their coverages in the field around the pollen sampling sites within a range of 30 m × 30 m in the meadow and steppe zones, and a larger range of 50 m × 50 m in the forest zones. Most plant taxa were identified to the species level, and a small number of taxa were recognized at the genus or family levels (Appendix A, <https://link.springer.com>). The coverages of recorded plant taxa were optically estimated in tree, shrub and herb layers separately, and were classified into 10 grades from 5% to 95%. To balance the overlap of vegetation from the three layers, the coverage of each plant taxon was divided by three to obtain the plant abundance used for the diversity estimate.

Detailed information on vegetation and pollen data of the 87 samples had been described by Cui et al. (2019) and Geng et al. (2019). The abundances of major taxa in vegetation compositions and pollen assemblages were presented in



**Figure 1** The locations of the modern pollen sampling sites in study region.

**Figure 2.** The main dominating plant taxa of coniferous forests include *Larix* and *Picea*. The most abundant plant taxa in mixed forests are *Larix*, *Pinus koraiensis*, *Betula platyphylla*, *Quercus mongolica* and other species in *Quercus*. The broadleaved forests are primarily composed of *B. platyphylla* and *Quercus* plants. Cyperaceae and Poaceae are the main dominating plant taxa in meadows. And the temperate steppe vegetation are primarily consist of *Stipa capillata* and other grass (**Figure 2a**). The pollen assemblages from coniferous, mixed and broadleaved forests are similar, and they all contain high percentages of *Betula*, *Pinus*, *Quercus* and *Artemisia* pollen. The major pollen taxa in meadow samples are *Artemisia*, Cyperaceae and Poaceae, while *Pinus* also contributes significant numbers for the pollen assemblages. *Artemisia* and Chenopodiaceae are the most abundant pollen types in the steppe pollen assemblages, followed by Cyperaceae and Poaceae (**Figure 2b**).

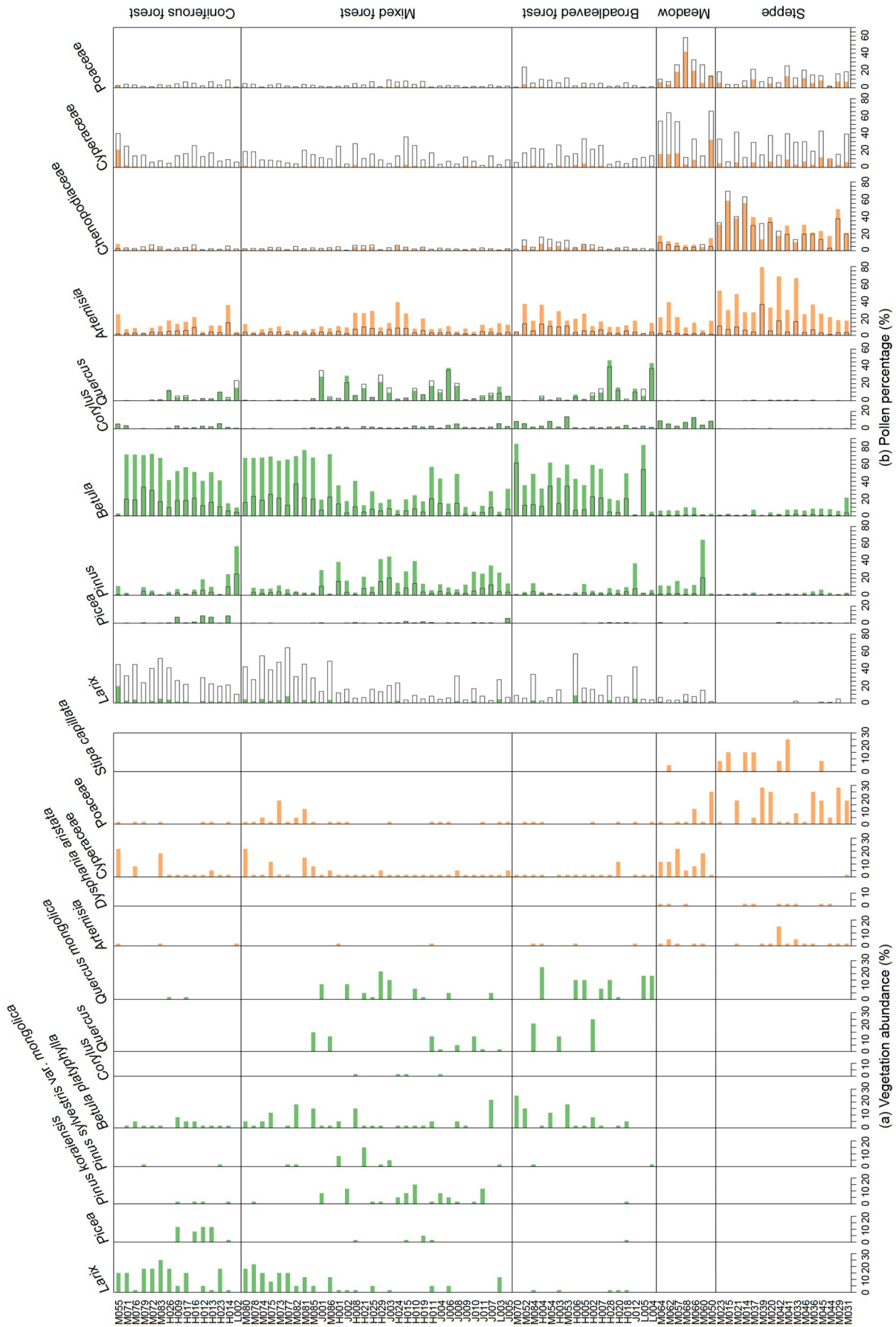
### 2.3 Diversity estimate

Richness and evenness were used to evaluate the diversity of vegetation and pollen. Richness, referring to the number of taxa in one unit (e.g., sampling site, community), describes

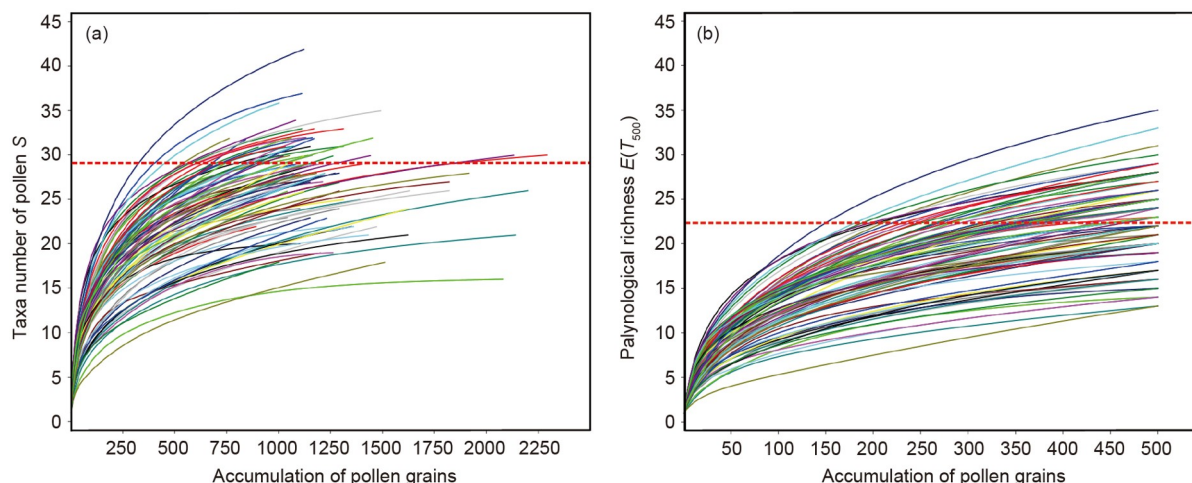
the quantity characteristics of the recorded taxa (Gaston, 1996; Odgaard, 1999). The evenness was estimated using the Simpson evenness index ( $E_{1/D}$ ), which could reflect the abundance distribution of taxa recorded in one unit (Smith and Wilson, 1996). In addition, to provide broader insight into biodiversity change, community dissimilarity among 87 sites was assessed using the Whittaker index (Whittaker, 1960, 1972).

The floristic richness was determined by counting the taxa recorded at each site. The floristic evenness was calculated with plant abundances using the “Diversity indices” function in software PAST3 (Hammer et al., 2001). Pairwise community dissimilarity among 87 sites was evaluated with the “betadiver” function in the R package “vegan” (Dixon, 2003). Then, a dimension reduction was performed and the dissimilarity results were presented with Principal coordinate analysis (PCoA) using the “cmdscale” function in R (Gower, 1966). The formulas for calculating floristic richness, evenness and community dissimilarity index are attached in Appendix B.

Palynological diversity was assessed with terrestrial pollen. However, the total number of terrestrial pollen in 87 samples varied from 698 to 2,301 (**Figure 3a**). In this case,



**Figure 2** The abundances of major taxa in vegetation compositions (a), original pollen assemblages (b), presented by colored bar, and calibrated pollen assemblages (b), presented by empty bar. The samples in each vegetation type are arranged by precipitation. The original data were obtained from Cui et al. (2019) and Ceng et al. (2019).



**Figure 3** Rarefaction curves for the pollen taxa number  $S$  (a) and palynological richness  $E(T_{500})$  (b) with accumulation of pollen counted in pollen assemblages. Different samples are represented by differently colored curved lines. The red dotted line indicates the median value of each sample group.

inter-sample diversity comparison is not rational because the number of taxa increases with the pollen sum (Figure 3a), and the distribution of taxa abundances may also change when the pollen sum increases. To remove the estimated bias of palynological diversity caused by different count sizes and ensure fair diversity comparison among sites, the terrestrial pollen count size of each sample was rarefied to 500 fixed grains by rarefaction analysis (Birks and Line, 1992) (Figure 3b). Palynological richness was estimated as the expected taxa number of the resampled 500 grains pollen, applying the “rarefy” function in the R package “vegan”. The abundances of resampled pollen, which were obtained using the “rrarefy” function in the same package, were employed to estimate the palynological evenness in PAST3. Dissimilarities among the 87 pollen assemblages were measured pairwise in the same manner as for vegetation. The corresponding calculation formulas are presented in Appendix B.

#### 2.4 Calibration of palynological diversity

To minimize the representation bias of palynological diversity induced by different productivities and dispersal abilities of pollen taxa, the original pollen data were calibrated with the Regional Estimates of Vegetation Abundance from Large Sites (REVEALS) model in the Landscape Reconstruction Algorithm (LRA) (Sugita, 2007). The model estimated vegetation abundances of sampling sites from pollen data based on parameters of pollen productivity estimates (PPEs) and fall speeds of pollen (FSP), and then pollen counts were calibrated according to estimated vegetation abundances. The PPEs and FSP values were obtained from the compilation of Li et al. (2018) in China. Note that these two parameters were not available for all pollen taxa found in the modern pollen assemblages of this study. A total of 28 pairs of PPEs and FSP were accessible and applied to cali-

brate pollen counts of corresponding taxa, with pollen counts of other taxa remaining unchanged. Then, a new set of calibrated palynological richness and evenness values were recalculated following the same procedures as section 2.3.

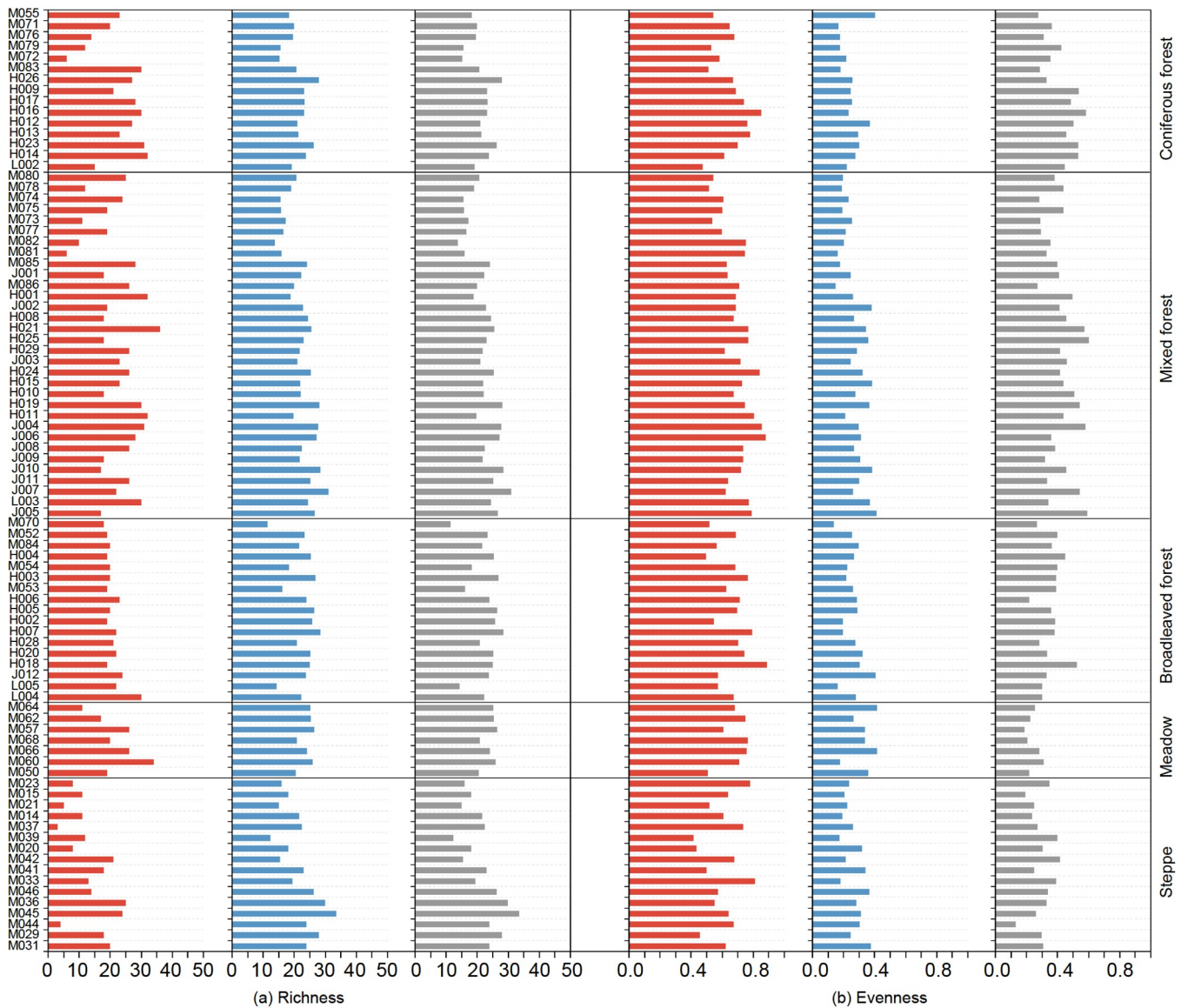
### 3. Results

#### 3.1 Palynological and floristic diversity

The palynological richness of modern pollen assemblages in Northeast China varied from 11.4 to 33.4, with a median of 22.4 (Figure 4, Table 1). The floristic richness ranged from 3 to 36, with a median of 20 (Figure 4, Table 1). The overall spatial pattern of palynological richness was similar to that of contemporary floristic richness. Along the gradient of vegetation types from coniferous forest to steppe, palynological and floristic richness both increased towards mixed forest and then decreased towards steppe, with a sharp upward trend in the more humid part of the steppe zone (Figure 5). Notably, the decrease of floristic richness from broadleaved forest to steppe was more remarkable than that of palynological richness (Figure 5). There was a significantly positive correlation ( $r=0.41$ ,  $p<0.01$ , Figure 6a) between the palynological and floristic richness.

The palynological evenness ranged from 0.14 to 0.42, with a median of 0.26, and the floristic evenness varied between 0.42 and 0.89, with a median of 0.68 (Figure 4, Table 1). The floristic evenness presented an upward trend from coniferous forest to mixed forest, followed by a downward trend from broadleaved forest to steppe (Figure 5). In contrast to floristic evenness, the palynological evenness showed an overall increasing trend in the steppe (Figure 5). The palynological evenness was also positively correlated to floristic evenness, but the relevance was weak ( $r=0.21$ ,  $p>0.05$ , Figure 6b).

According to the community dissimilarity index of vege-



**Figure 4** Floristic diversity (red bars), palynological diversity (blue bars) and calibrated palynological diversity (gray bars) of samples from various vegetation types, including richness (a) and evenness (b). The samples in each vegetation type are arranged by precipitation.

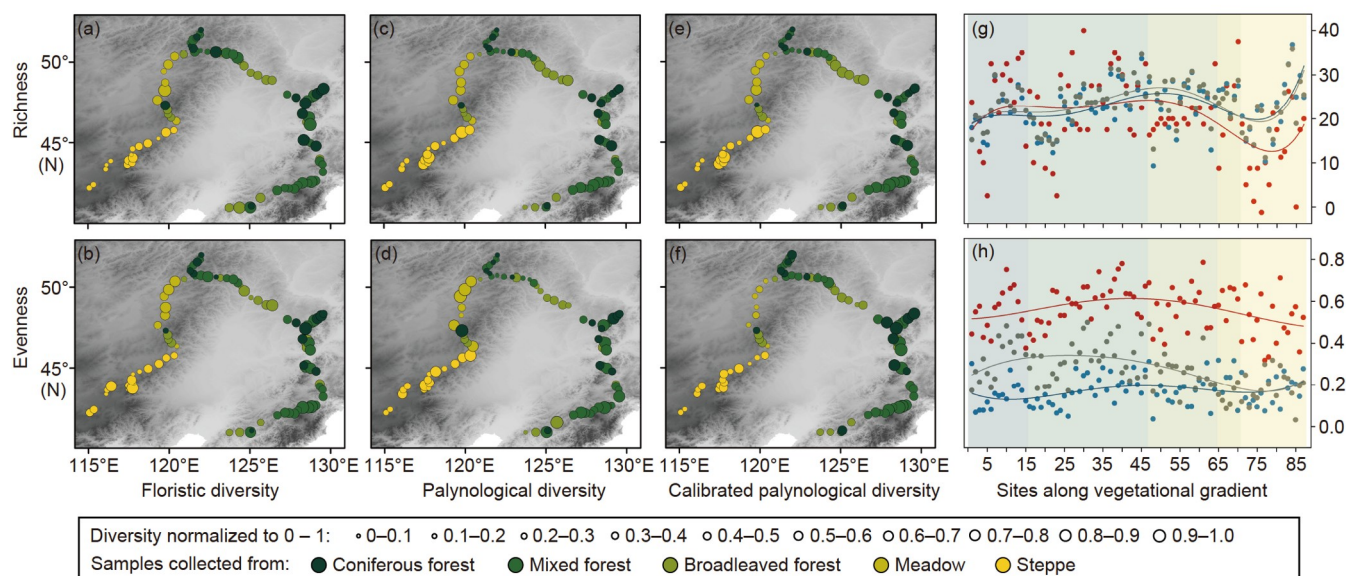
tation (Figure 7a), the samples from coniferous forests, mixed forests, and broadleaved forests were distinctly separated from those from steppes and meadows. However, samples from different forests could not be distinguished, and samples from non-forest types were grouped together. Unlike in vegetation, dissimilarity analysis based on pollen assemblages showed that the samples from meadows were clustered with samples from forests, but were broadly distinct from steppe samples. Steppe samples can generally be distinguished from samples from other vegetation types (Figure 7b).

### 3.2 Calibrated palynological diversity

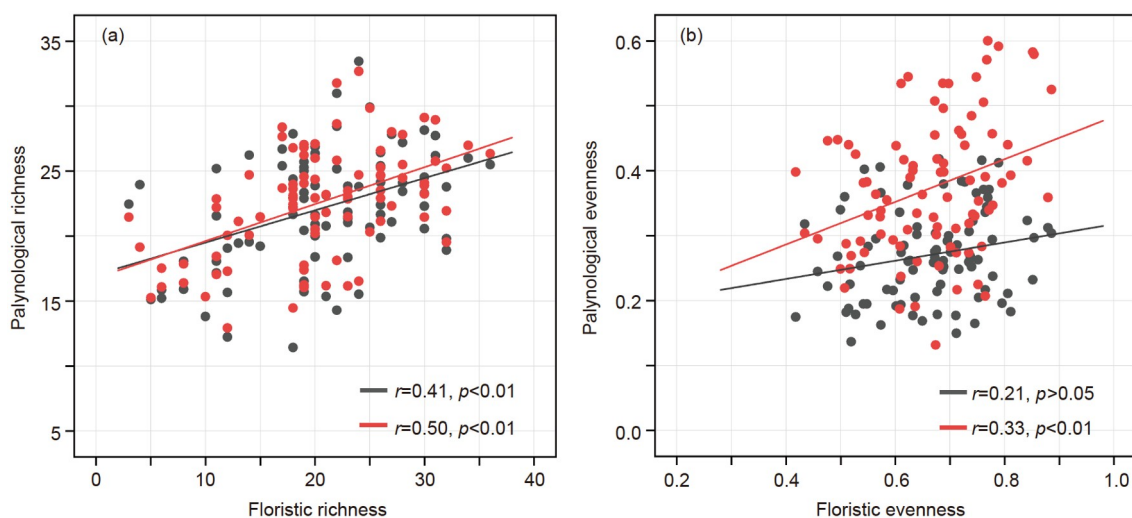
Calibrating pollen data with REVEALS model led to a

higher palynological richness in the forest regions and a lower palynological richness in the non-forest regions (Figures 5 and 8). The calibrated palynological richness ranged from 12.9 to 32.7, with a median of 22.9 (Figure 4, Table 1). The spatial pattern of palynological richness changed slightly after calibration, and its declining trend from broadleaved forest to steppe was more significant (Figure 5). The calibrated palynological richness had a stronger positive correlation with floristic richness than the one based on original pollen data ( $r=0.50$ ,  $p<0.01$ , Figure 6a).

After calibration, the palynological evenness increased greatly in the forest regions and slightly in the steppes, but decreased in the meadows (Figures 5 and 8). The calibrated palynological evenness varied from 0.13 to 0.60, with a median of 0.36 (Figure 4, Table 1). The spatial pattern dif-



**Figure 5** Spatial patterns of floristic diversity, palynological diversity and calibrated palynological diversity are displayed as: (a)–(f) spatial variation maps based on the diversity data normalized to 0–1; (g)–(h) trend chart with scatter and polynomial fitting ( $n=5$ ) showing the changes of floristic diversity (red circle), palynological diversity (blue circle), and calibrated palynological diversity (gray circle) along the vegetational gradient. The vegetation zones in different colors are coniferous forest, mixed forest, broadleaved forest, meadow and steppe successively. Samples in each vegetation type are arranged by precipitation.



**Figure 6** Relationships between floristic and palynological diversity for richness (a) and evenness (b). The black dots and fitting lines indicate the correlation between floristic and palynological diversity, while the red ones indicate the correlation between floristic and calibrated palynological diversity.

ferences between the palynological evenness and floristic evenness reduced to some extent after calibrating. A more marked decrease trend in palynological evenness was observed from broadleaved forest to steppe (Figure 5). The calibrated palynological evenness had a significantly positive correlation with the floristic evenness ( $r=0.33$ ,  $p<0.01$ , Figure 6b).

The calibration had little influence on community dissimilarity among pollen assemblages in Northeast China (Figure 7c). The PCoA results based on calibrated pollen data displayed a similar distribution in PCoA axes 1 and 2 as

the original pollen data. The pollen samples from the meadows were still scattered among the forest samples and were distinct from the steppe samples (Figure 7c).

## 4. Discussion

### 4.1 The representation of palynological diversity to floristic diversity

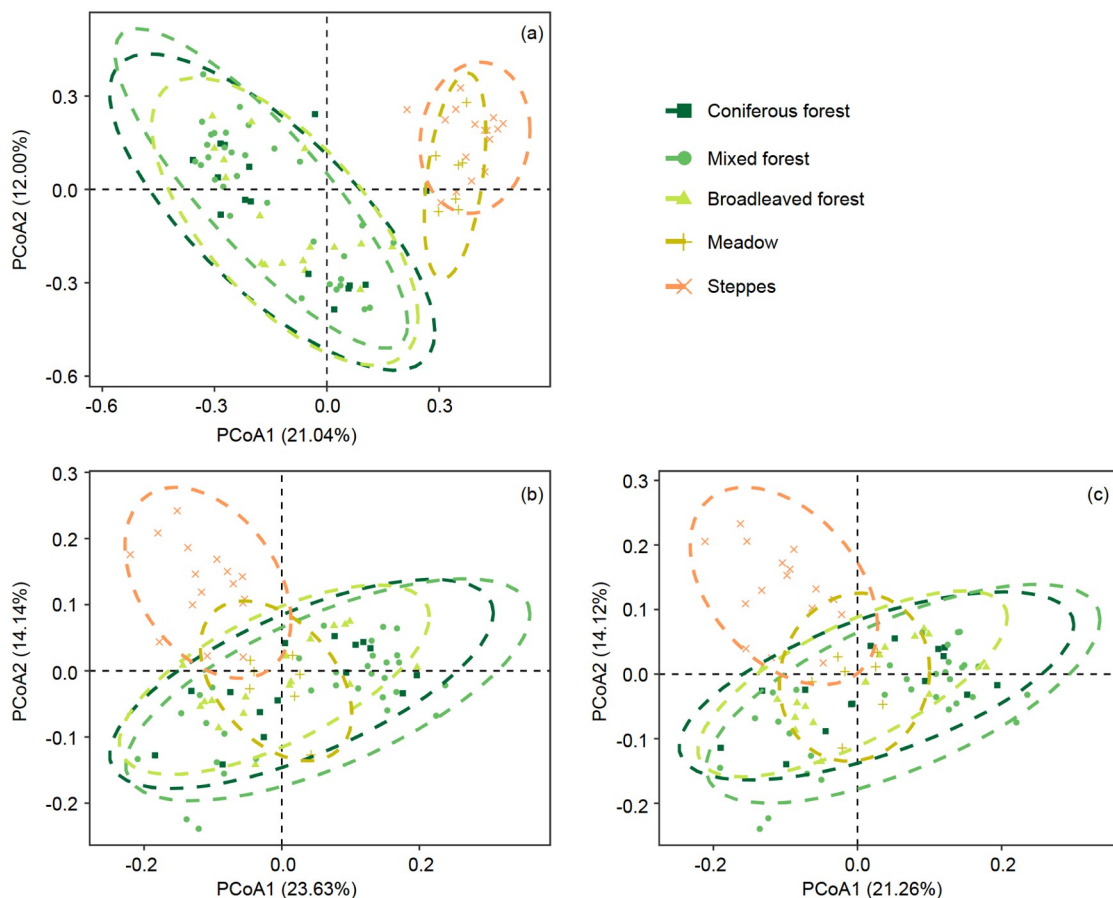
The palynological richness in Northeast China had a similar spatial pattern and a significantly positive correlation

**Table 1** Variation ranges and median values of floristic diversity, palynological diversity, and calibrated palynological diversity

Vegetation types	Floristic richness		Palynological richness		Calibrated palynological richness	
	Variation range	Median	Variation range	Median	Variation range	Median
Coniferous forest	6–32	23	15.2–27.8	21.1	16.2–28.0	21.5
Mixed forest	6–36	23	13.8–31.0	22.2	15.3–31.8	23.3
Broadleaved forest	18–30	20	11.4–28.4	23.8	14.5–28.6	24.6
Meadow	11–34	20	20.4–26.4	25.2	17.4–27.0	23.5
Steppe	3–25	12.5	12.2–33.4	22	12.9–32.7	21.3
Total	3–36	20	11.4–33.4	22.4	12.9–32.7	22.9

Vegetation types	Floristic evenness		Palynological evenness		Calibrated palynological evenness	
	Variation range	Median	Variation range	Median	Variation range	Median
Coniferous forest	0.48–0.85	0.67	0.17–0.40	0.25	0.27–0.58	0.45
Mixed forest	0.51–0.88	0.71	0.15–0.41	0.27	0.27–0.60	0.42
Broadleaved forest	0.49–0.89	0.68	0.14–0.41	0.27	0.22–0.53	0.36
Meadow	0.51–0.76	0.71	0.18–0.42	0.34	0.19–0.31	0.22
Steppe	0.42–0.81	0.62	0.17–0.38	0.25	0.13–0.42	0.30
Total	0.42–0.89	0.68	0.14–0.42	0.26	0.13–0.60	0.36



**Figure 7** Community dissimilarity among 87 sites for vegetation (a), pollen (b), and calibrated pollen data (c).



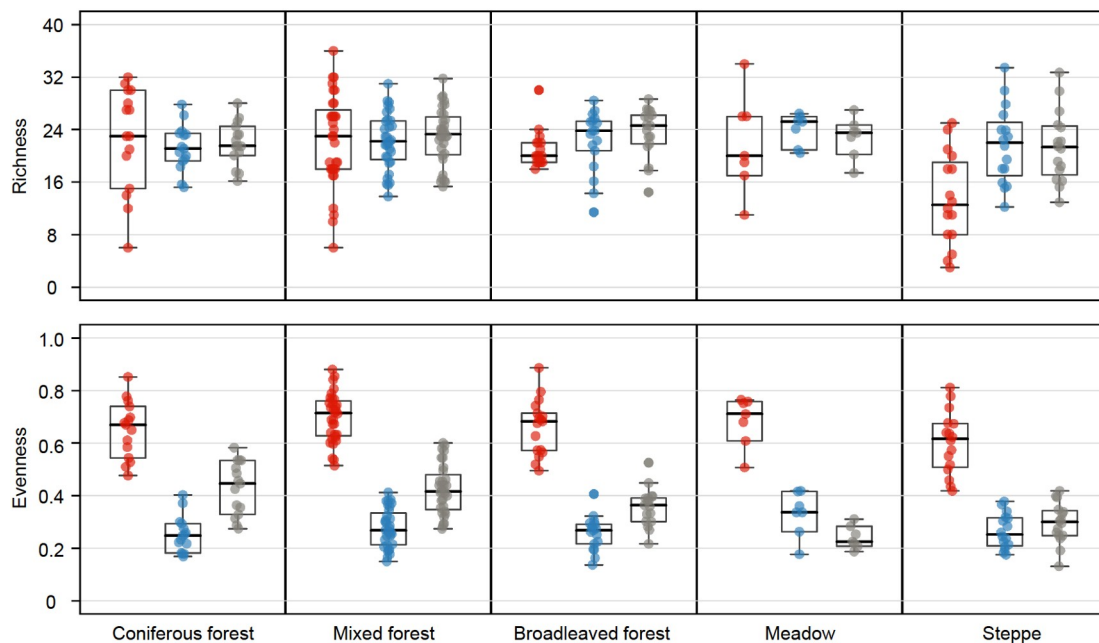
( $r=0.41$ ,  $p<0.01$ ) with corresponding floristic richness, demonstrating that regional palynological richness could be used to indicate the temporal change of floristic richness. However, a minor difference in spatial patterns between modern palynological and floristic richness should be noted, that is, a slight downward trend in palynological richness against a marked downward trend in floristic richness from broadleaved forest to steppe (Figure 5). Such pattern differences are mainly attributed to inconsistent representation of palynological richness in various vegetation types. The palynological richness in coniferous forests and mixed forests ranged between 13.8 and 31.0, and would underrepresent floristic richness (range, 6–36). Meanwhile, the palynological richness in broadleaved forests, meadows and steppes varied from 11.4 to 33.4 and would overrepresent floristic richness (range, 3–34) (Figure 8, Table 1). This has implications for reconstructing past floristic richness based on fossil pollen data in Northeast China. The paleo-floristic richness of samples, which represents a period dominated by coniferous forests or mixed forests, would be underestimated by palynological richness, whereas the floristic richness of samples reflecting broadleaved forests, meadows, or steppes would be overestimated by palynological richness. Generally, the floristic richness change through time could be detected by fossil pollen, but inconsistent representation of palynological richness would lead to minor estimate biases in the period when vegetation transitions between coniferous forest, mixed forest, and broadleaved forest, meadow, steppe.

The palynological evenness was unstable in terms of representing regional floristic evenness owing to the sig-

nificant spatial pattern differences and weak correlation ( $r=0.21$ ,  $p>0.05$ ) between them. The palynological evenness in Northeast China (range, 0.14–0.42) was much lower than floristic evenness (range, 0.42–0.89) (Figure 8, Table 1). In addition, the weak relationship between palynological and floristic evenness indicates that some other factors rather than floristic evenness should have decisive effects on the palynological evenness in Northeast China. A previous study in southern Estonia have also revealed a weak relationship between regional palynological evenness and floristic evenness, suggesting the uncertainty of using palynological evenness to interpret past floristic evenness (Meltsov et al., 2011).

The overall patterns of community dissimilarity among sites were different between vegetation and pollen in Northeast China, which affects the application of pollen data for reconstructing floristic community composition change through time. Vegetation communities from meadows and steppes were similar, but were obviously different with those from forests. However, pollen assemblages from meadows were similar with those from coniferous forests, mixed forests and broadleaved forests, but were different with those from steppes. The results indicate that pollen-based community dissimilarity through time would underestimate the floristic community composition change between forests and meadows, but overestimate the change between meadows and steppes.

In addition to indicating floristic diversity, palynological diversity is also potential to reveal changes in environmental factors and human activity intensity. Previous research have



**Figure 8** Boxplots showing the differences among floristic diversity (red circle), palynological diversity (blue circle), and calibrated palynological diversity (gray circle) in various vegetation types.

indicated that soil condition, climate variable and anthropogenic land-use change are important factors affecting regional floristic diversity (Mattison and Norris, 2005; Dong et al., 2019), which would also impact the palynological diversity theoretically. The complex relationship between floristic and palynological diversity limits the further exploration of how these factors influence palynological diversity, although some studies in Northeast China have revealed that variations in modern pollen assemblages are related to climate variables and human activity (Zhang et al., 2010; Li et al., 2012; Cui et al., 2019; Geng et al., 2019). More studies on modern palynological diversity are needed in the future to investigate the relationships among floristic diversity, palynological diversity and external changes derived from environmental factors and human activity.

#### 4.2 Factors affecting the representation of palynological diversity

In theory, palynological diversity could reflect the spatial and temporal changes of floristic diversity, as plants are the sources of pollen. Nevertheless, the relationship between palynological and floristic diversity is influenced by factors from regional vegetation structure, pollen production, dispersal and preservation, and research designs such as vegetation survey and pollen analysis (Weng et al., 2006; Goring et al., 2013; Odgaard, 2013; Birks et al., 2016; Väli et al., 2022), which lead to representation biases in palynological diversity.

Floristic richness is overestimated or underestimated by palynological richness in Northeast China, which is commonly found in the studies on modern palynological and floristic richness relationships worldwide (Meltsov et al., 2011; Felde et al., 2016; Gosling et al., 2018; Connor et al., 2021). In this study, the underestimation of palynological richness have primarily resulted from following two issues. First, low-productivity pollen types were less likely to be recorded, especially when pollen taxa with high pollen productivity accounted for a significant proportion of the pollen assemblage. Second, the identification resolution of pollen (mostly identified to genera or family) was lower than that of plant (mostly identified to species and genera) (Appendix A), which resulted in the loss of pollen richness. Conversely, the overestimation of palynological richness might be caused mainly by exotic pollen from areas beyond the vegetation survey range, which would also contribute to the pollen assemblages at sampling sites. Notably, the probability of low-productivity pollen types being recorded and the quantity of input exotic pollen were different among the 87 sites, which caused inconsistent representation of palynological richness in various vegetation types. The pollen percentages of high-productivity pollen taxa in the non-forest regions (dominated by *Artemisia*) were lower than those in the forest regions

(dominated by *Pinus* and *Betula*) (Figure 2). Consequently, more low-productivity pollen taxa could be detected in the pollen assemblages from meadow and steppe zones, and the underestimation to floristic richness would be weaker. In addition, the input of exotic pollen would be stronger in meadow and steppe areas owing to less hindrance from tree canopy, which would further enhance the overestimation of palynological richness to floristic richness.

An overall underestimation of palynological evenness was revealed in this study and previous studies (Meltsov et al., 2011). There are two main reasons for the underestimation of palynological evenness in Northeast China. First, high-productivity pollen types facilitate an uneven distribution of pollen abundances. Second, the abundance of one pollen taxon could be the summation of pollen derived from more than one plant taxon owing to the lower identification of pollen, therefore, the distribution of pollen abundances would be more uneven than that of plant.

In terms of community dissimilarity, it seems that the different influences of exotic arboreal pollen on pollen assemblages from meadows and steppes resulted in the observed community dissimilarity pattern (Figure 7b). Arboreal pollen from the surrounding forests plays a more important role in the pollen assemblages of meadow sites than steppe sites in Northeast China (Cui et al., 2019). Consequently, pollen assemblages from meadows displayed a higher similarity with those from forests, but their compositions were diverse from pollen assemblages from steppes.

#### 4.3 Methods to improve the representation of palynological diversity to floristic diversity

Calibrating pollen data with REVEALS model was proved effective in minimizing biases induced by pollen production and dispersal, which improved the palynological diversity representation to floristic diversity in our study. The over- and under- estimation of palynological richness generally reduced after calibration; thus, the richness pattern differences between pollen and vegetation were narrowed (Figures 5 and 8). The calibrated palynological evenness showed an overall increase and a spatial pattern with higher similarity to floristic evenness (Figures 5 and 8). Additionally, the correlations between palynological and floristic diversity improved after calibration (richness,  $r=0.50$ ,  $p<0.01$ ; evenness,  $r=0.33$ ,  $p<0.01$ ), especially for that between palynological and floristic evenness which appeared to be statistically significant (Figure 6). A similar result was reported by Felde et al. (2016), in which the correlation between palynological and floristic richness in south-central Norway increased after calibrating pollen data with REVEALS model. Nevertheless, only 28 out of 89 pollen taxa in the studied pollen assemblages had PPEs and FSP data, and those of some major taxa

were not available, including *Picea* and *Corylus*. This meant the pollen data of this study were partially calibrated, and the effect of calibration based on REVEALS model was limited owing to insufficient calibration parameters. More studies on pollen productivity are required for the complete calibration of palynological diversity in the future.

In addition, transforming plant types into pollen equivalents to calculate floristic diversity could reduce the identification difference between plant and pollen. This method has been proven useful for improving the correlation between floristic and palynological diversity (Felde et al., 2016; Connor et al., 2021). However, Reitalu et al. (2019) argued that the correlation between floristic and palynological richness in northern Europe decreased when plant taxa were converted to pollen equivalents. These conflicting results put forward skepticism regarding the effectiveness of this calibration method. In addition, such calibration is performed on modern vegetation data rather than pollen data, which would be unavailable for long-term biodiversity reconstruction from fossil pollen. Improving the taxonomic resolution of pollen identification is another practical way to promote the correlation between floristic and palynological diversity. This can be achieved by the usage of scanning electron microscopy for pollen identification and the progress in pollen morphology studies.

## 5. Conclusion

Palynological richness in Northeast China reliably reflected regional floristic richness, which was supported by the similar spatial patterns and significantly positive relevance between them. However, palynological evenness cannot clearly indicate floristic evenness in the study region owing to the existing pattern differences and the weak association between them. The variety of pollen productivities among pollen taxa, the inconsistent identification resolution between pollen and plant, and the influence of exotic pollen from areas beyond the vegetation survey range, were the main contributors to the relationship biases between palynological and floristic diversity in Northeast China.

Using REVEALS model calibrate pollen data effectively improved the representation of palynological diversity to floristic diversity, representing as narrowed differences in spatial patterns and improved correlations between calibrated palynological and floristic diversity.

Our results provide a basis for the application of palynological richness and evenness in Northeast China and fill the research gap in the relationship between modern palynological diversity and floristic diversity in China. Meanwhile, this study provides some implications for the available calibration methods to improve the representation of palynological diversity.

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