

# Spatial influence of the Asian Summer Monsoon on pollen assemblages of the Tibetan Plateau and its potential implication for the interpretation of fossil pollen records

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## ABSTRACT

The direction and intensity of Asian Summer Monsoon (ASM) circulation in the Tibetan Plateau (TP) region strongly influence pollen dispersal patterns; however, this spatial effect has been rarely quantified. In this paper, we explore the relative importance of this directional spatial effect. Specifically, we construct a wind connectivity diagram for modern pollen sample sites according to the prevailing monsoon direction, and extract latent spatial variables representing the directional process of the ASM, using the method of asymmetric eigenvector maps. We fit redundancy analysis models using both spatial variables and local climate factors, and conduct variation partitioning to quantify the effect of directional spatial effect by the ASM. Taking into account the joint effect with local climate, the directional spatial process induced by the ASM significantly explains the variation of pollen assemblages on the TP. The effect is detected in pollen groups with contrasting functional types and dispersal modes; for example, the composition of arboreal pollen and non-arboreal pollen are both significantly affected by the ASM, yet best explained by models assuming different monsoon directions. Anemophilous pollen shows a higher percentage of variation explained by the ASM than non-anemophilous pollen. Our results indicate that directional processes induced by the monsoon is an important influence on pollen assemblages in the TP and support the idea that deposition patterns of pollen, especially arboreal pollen is a useful proxy for studying monsoon evolution. A similar approach can also be applied to paleomonsoon simulations using fossil pollen records. The role of directional dispersal in affecting fossil pollen composition and abundance by prevailing winds deserves further investigation when undertaking Quaternary paleoenvironmental reconstructions using pollen.

## 1. Introduction

Pollen assemblage data is frequently used to reflect vegetation composition and to reconstruct past climate. This is based on the condition that pollen assemblages accurately represent local or regional vegetation (Xu et al., 2016). However, as a major driver of pollen dispersal, wind intensity and direction can have a confounding effect on pollen assemblage by bringing exotic pollen (Liu et al., 2022; Prentice, 1985). Directional dispersal caused by prevailing wind has been reported to shape invertebrate metacommunity (Bertin et al., 2015; Epele et al., 2021; Horváth et al., 2016). Likewise, the prevailing monsoon winds may have a strong effect on shaping pollen assemblages in monsoon-dominated regions, because ample studies have reported long-

distance transportation of pollen by monsoon (Cour et al., 1999; Dai and Weng, 2011; Yu et al., 2001; Zhao et al., 2019).

Vegetation and climate of the Tibetan Plateau (TP) is heavily affected by the Asian Summer Monsoon (ASM), originating from the south and east to the plateau (i.e., South Asian Summer Monsoon and East Asian Summer Monsoon) (Li et al., 2020; Zhao et al., 2020). This coevolution of vegetation, climate and monsoon also cannot be separated from the uplift of TP (An et al., 2001, 2011; Liu and Dong, 2013; Zhang et al., 2018a). The interior of TP is cold and arid, characterized with alpine shrubland, meadow and steppe. Desert occurs in the northwest part, while the heavy precipitation brought by the ASM shaped forest vegetation in the southern and eastern margins of the TP (Lu et al., 2011; Yu et al., 2001). Extensive studies have been made on pollen assemblages

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on the TP and their associations with vegetation and climate, and it is found that pollen is a good indicator of modern vegetation in general (Herzschuh, 2007; Lu et al., 2011; Yu et al., 2001; Zhang et al., 2018b). Fossil pollen is also used to reconstruct past vegetation and climate on the TP (Hou et al., 2017; Zhao et al., 2020). However, many researchers have found exotic arboreal pollen in unforested area of the TP, and it is generally agreed that this kind of pollen is carried by monsoon winds for a long distance from the southern and eastern forests of the plateau (Cour et al., 1999; Herzschuh, 2007; Lu et al., 2011; Lu et al., 2010; Yu et al., 2001; Zhang and Li, 2017). The long-distance transport of tree pollen by the ASM can have two important implications: 1) Non-local pollen carried by monsoon winds can bias the estimation of pollen productivity and pollen-based reconstruction of vegetation and climate (Liu et al., 2022; Ortu et al., 2006). 2) The relative abundance of tree pollen is highly coupled with the ASM pathway and it is proposed that arboreal pollen can be a potential indicator of the evolution of direction and intensity of the ASM (Li et al., 2020; Li et al., 2021; Zhang and Li, 2017; Zhao et al., 2019).

Although many previously mentioned studies have discovered relationships between pollen and local climate, studies quantitatively investigating the relationship between pollen assemblages and the ASM are still rare and the significance of monsoon on large-scale pollen spatial distributional pattern is not fully understood. For example, Li et al. (2020) illustrated that the spatial pattern of tree pollen abundance is closely related to the pathway of the ASM, and the monsoon dominated the distribution patterns of tree pollen. The contribution of the ASM on variation of the whole pollen composition of TP has been unquantified yet. On the other hand, local climate factors, like mean annual precipitation have an important influence on pollen composition on the TP (Lu et al., 2011; Shen et al., 2006). Thus, the ASM can affect pollen composition indirectly via affecting local climate (e.g., bringing rainfall), or directly via dispersing pollen through wind current. The relative contribution of these two different effect types on the variation of pollen assemblages is unclear. To our knowledge, no study has tested if the ASM affects pollen of different functional types (arboreal pollen, AP vs. non-arboreal pollen, NAP) and pollen dispersal type (anemophilous vs. non-anemophilous) differently on the whole TP. It is known that the ASM can lead to long distance dispersal of AP, yet to what extent does it affect pollen of vegetation in the interior TP, mostly NAP, is not sure. Many arboreal pollen taxa have special adaptation to wind dispersal, like air sac, and forests are mostly distributed at the southern to eastern part of the TP, where the ASM primarily rules the climate (Zhao et al., 2020). Thus, we hypothesize that the ASM should have a stronger influence on the relative abundances of AP and anemophilous pollen than those of other pollen. Testing this hypothesis will help us better understand relations between monsoon and pollen composition.

In this study, we utilized the asymmetric eigenvector maps (AEM), a spatial filter method to extract spatial variables representing the directional spatial effect caused by monsoon. AEM has been used for modelling directional ecological processes, like water current or wind on organism metacommunity composition or genetic structure in various studies (Bertin et al., 2015; Blanchet et al., 2010; Liu et al., 2013b; Pollice et al., 2020; Xuereb et al., 2018). Then we fitted redundancy analysis models using AEM spatial variables together with local climate factors against pollen composition data. We further partitioned the variation of pollen assemblages on the basis of model components. By doing so, we can disentangle the unique spatial effect of the ASM with its joint effect with local climate. We aimed at answering these questions: 1) Does ASM significantly affect the pollen assemblages on the TP? 2) How much is the contribution of pure spatial component of the ASM compared to local climate in shaping pollen composition? 3) Is AP indeed more strongly affected by the ASM than NAP? 4) Similarly, is anemophilous pollen more strongly affected by the ASM than non-anemophilous pollen? Finally, based on our results, we also discussed the potential implication of the AEM approach in interpreting fossil pollen record for the Quaternary.

## 2. Material and methods

### 2.1. Pollen data

We used the modern surface pollen assemblage data of China compiled by Chen et al. (2021). The dataset contains modern pollen records of 4497 sampling sites in China between 1960 and 2020. We selected 1235 sampling sites located in the TP, excluding sampling sites beyond the modern Asian summer monsoon limit (Chen et al., 2008), because we want to focus on studying the effect of the ASM. Pollen assemblages were represented as percentage by taxa in dataset. We choose taxa appeared in at least 10% of total sampling sites. To reduce the chance of sample contamination, taxa with percentage lower than 0.5% in a sample was considered non-existent. Many genera and their corresponding families occur simultaneously in the original data set. In this case, we combined these genera with appropriate families (for example, genus *Polygonum* was combined with family Polygonaceae), except for *Artemisia*, which was not combined with Asteraceae, as Chinese researchers usually list it separately from other genera in the Asteraceae (Yu et al., 2001). Then, we recalculated pollen percentage for the combined taxa. A total of 32 taxa were used after taxa combination (Table 1). As we used wind data with a resolution of 0.5° (see Wind data below), we aggregated sampling sites within the same 0.5° grid by averaging the relative abundance of pollen and used the coordinate of grid center as the coordinate of the aggregated site. 227 aggregated sites were used in the final analysis (Fig. 1).

### 2.2. Wind data

Wind speed and direction data was downloaded from the Global Forecasting System via the R package *rwind* (Fernández-López and Schliep, 2019). In this data set, wind velocity of eastward and northward wind is recorded 8 times a day since 6th May 2011. The data resolution

**Table 1**

A list of pollen taxa, number of aggregated sites they occurred, and mean relative abundance.

Taxon	No. of sites	Mean relative abundance (%)
<i>Abies</i>	86	1.3
<i>Alnus</i>	51	0.3
Apiaceae	75	0.5
<i>Artemisia</i>	220	13.7
Asteraceae	207	4.9
<i>Betula</i>	131	3.3
Brassicaceae	134	2.6
Caryophyllaceae	119	1.1
<i>Castanea</i>	28	0.2
Chenopodiaceae	190	7.7
<i>Corylus</i>	47	0.2
Cupressaceae	96	1.0
Cyperaceae	219	29.3
<i>Ephedra</i>	88	0.7
Fabaceae	156	1.5
Gentianaceae	48	0.3
<i>Hippophae</i>	54	0.3
Lamiaceae	77	0.5
Liliaceae	23	0.2
<i>Nitraria</i>	55	0.4
<i>Picea</i>	137	3.7
<i>Pinus</i>	182	6.5
Poaceae	209	6.4
Polygonaceae	173	2.9
<i>Potentilla</i>	44	0.3
<i>Quercus</i>	67	1.4
Ranunculaceae	209	3.7
<i>Rhododendron</i>	51	1.0
Rosaceae	165	2.2
<i>Salix</i>	91	1.7
<i>Tsuga</i>	50	0.5
<i>Veronica</i>	26	0.2

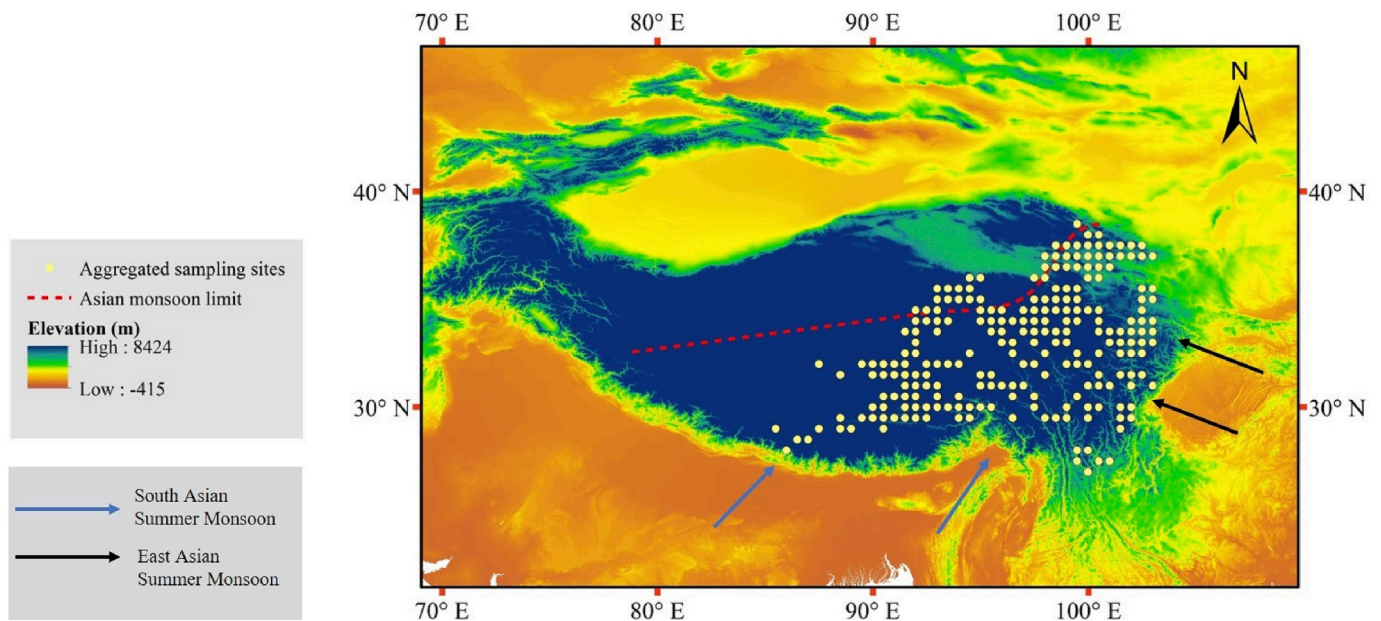


Fig. 1. Topographic map showing aggregated pollen sample sites.

is 0.5 degree (~50 km). We downloaded summer wind data of June–August for the TP from 2011 to 2021 to calculate wind speed and direction.

Movement cost via wind dispersal between sampling sites was produced using wind speed and direction data (see Fernández-López and Schliep (2019) for calculation details). For each time snapshot of wind data, a conductance (1/movement cost) layer to move between all grids was calculated using the *rwind* package and the least cost distance between sampling sites was calculated with the *costDistance* function in the *gdistance* R package (van Etten, 2017). An averaged connectivity matrix between pairs of sampling sites was calculated by averaging all connectivity values (the reciprocal of least cost distance) among sites of different sampling times. The connectivity values measure the ease of wind dispersal between sampling sites and the connectivity matrix was used to extract spatial variables in subsequent steps.

### 2.3. Environmental variables

Three climatic variables were selected to model the variation of pollen assemblages including mean annual temperature (MAT), mean annual precipitation (MAP) and mean temperature of July ( $T_{\text{July}}$ ). They are known to have an important effect on pollen community found in previous studies (Herzschuh et al., 2010; Huang et al., 2018; Lu et al., 2011; Shen et al., 2006; Zhang et al., 2010). Climate data was downloaded from the WorldClim database (Fick and Hijmans, 2017) (<https://www.worldclim.org/>) with a resolution of 2.5 min and rescaled to the same resolution with the wind data using the ArcGIS 10.7 software.

### 2.4. Data analysis

We used the method of asymmetric eigenvector maps (AEM) to investigate the directional spatial effect of ASM which comes from south-east/south to the TP. AEM builds a connection diagram among sampling sites, which is represented by a site×edge matrix (Blanchet et al., 2008; Pollice et al., 2020). A fictitious source site representing ‘source’ of the ASM was assumed to be connected with the most upstream (e.g., southernmost) sampling site by an edge. This design is used to account for the directionality in ecological process. Connections between sampling sites were characterized by the existence of edges. If calculated wind connectivity between two sites was higher than the top 25% quantile of all connectivity values, we decided there was an edge

connecting these two sites. We applied this threshold of connectivity for computational reason, as a large number of edges makes construction of site×edge matrix in next step computation too intensive. If an edge could link a site to the fictitious source site directly or indirectly via other edges, then the corresponding entry in the site by edge matrix is numbered ‘1’, otherwise the value will be ‘0’. To account for strength of wind connectivity, we also assigned wind connectivity values as weight to the binary site by edge matrix. Edges go against the hypothesized direction (going ‘upstream’) are excluded when building the matrix. Finally, a Singular Vector Decomposition (SVD) was applied on the site by edge matrix and the resulted eigenvectors are latent spatial variables representing the underlying directional ecological process. These variables are used as explanatory variables in further analysis. To test the effect of different monsoon directions, we applied this method with three fictitious source sites with different wind directions (south-180°, southeast-135° and east-90°). See Blanchet et al. (2008) for full details of the AEM approach.

To investigate spatial effect of the ASM and compare it with other local environmental variables on pollen composition for different taxa groups, we performed the redundancy analysis (RDA) for each pollen group. The percentages of pollen data were response variables and square root transformed prior to RDA in order to stabilize their variances. The first RDA model was conducted using environment variables only. The second one contains AEM variables only. As the AEM approach usually produces a large number of variables, we followed Blanchet et al. (2010) to apply variable selections. First, we selected AEM variables representing positive autocorrelations by calculating Moran’s I index and fitted a global RDA model using these variables. If this model was significant, we then did a forward selection using two stopping criterions: either the variable was not significant at a level of 0.05 or the accumulated adjusted R square of the model reached the value of the global model. The forward selection was with 999 permutations. Then the model with selected variables was used. If the RDA model with AEM variables is significant, a third model was fitted with both environment variables and selected AEM variables to see if combining AEM variables and environmental variables would improve model performance. To compare the relative contribution of environmental and AEM variables, we applied variance partitioning on the combined model and partitioned the total amount of explained variance into three components: 1) solely explained by the environmental variables; 2) solely explained by the AEM variables, representing pure spatial effect by monsoon; 3)

explained by the environmental and AEM variables jointly.

We first fitted RDA models for all taxa. To investigate how monsoon affects taxa with different functional types and pollen dispersal mode differently, we repeated the same analysis for AP vs. NAP taxa and anemophilous vs. non-anemophilous taxa separately. The model with a south monsoon source is referred to as ‘the south model’ in further discussions. Correspondingly, the models with a southeast monsoon source and east source are referred to as ‘the southeast model’ and ‘the east model’. AEM was calculated with the *adespatial* R package (Dray et al., 2021) and RDA analysis was carried out with the *vegan* R package (Oksanen et al., 2020).

### 3. Results

The RDA models of AEM spatial variables were significant for all pollen taxa groups. Additionally, combining climatic variables and selected AEM variables consistently improved model performance compared to using only one set of variables (Table 2). The improvement of model performance was also observed across three different wind directions. Among the three directions, model performances are relatively similar. The models assuming a southern source have the best performance for all taxa except the AP group, for which the model with a southeastern source has the best performance and the non-anemophilous pollen, for which the southeastern model has equal performance with the southern model (Table 2). We will present and discuss results based on the combined models with the southern source, except in the cases of AP and non-anemophilous pollen.

When analyzed with all taxa, seven AEM variables were selected. In the combined model, the first two RDA axes explained 14.4% and 9.7% of total variance respectively. Meanwhile, they explained 82% of total variance constrained by explanatory variables. It appears that taxa with different habitats and functional groups are affected by different AEM variables (Fig. 2). The figure shows that most AP taxa, including *Abies*, *Pinus*, *Betula* and Cupressaceae, are positively correlated with AEM variable V5, while negatively correlated with V1. On the other hand, taxa associated with alpine steppe and desert habitats, like Chenopodiaceae, *Nitraria* and *Ephedra*, are positively correlated with V1. Cyperaceae, Ranunculaceae and Polygonaceae, typical taxa of alpine grassland, are positively correlated with the AEM variables V3 and V2. The spatial distributions of AEM variables V1–3 have obvious spatial patterns from south to north (Fig. 3).

Variation partitioning shows that both climatic and AEM variables have significant unique contributions in all five cases (Fig. 4). When all taxa modeled together, environmental variables have equal unique

contribution as AEM variables. However, there is a larger portion of variance that cannot be separated between environmental and spatial variables, which reflects the close association between the ASM and climate in the TP. Five and eight AEM variables were selected for the best AP and NAP models respectively. The model with southeastern source has the best performance for AP, and does have a higher unique contribution of spatial variables than the model with the same source for NAP. However, the best model for NAP has a 9% unique contribution of spatial variables. The common contribution by the climate and AEM variables in case of AP is the highest compared to those in cases of other pollen groups (18%, Fig. 4). Six and seven spatial variables were selected in the models with the southern source for anemophilous and non-anemophilous pollen. The model for anemophilous pollen has a higher contribution of AEM variables than the model for non-anemophilous pollen (8% vs. 5%).

### 4. Discussion

#### 4.1. General effect of the ASM on pollen assemblages

Wind-induced dispersal has been found to shape community structure and genetic structure of many organisms and also a main driver of pollen dispersal (Epele et al., 2021; Kling and Ackerly, 2020, 2021). The prevailing wind direction can shape pollen deposition pattern, potentially reflecting the wind direction and deposition. Our results clearly showed that the ASM influences pollen assemblages of the TP, regardless of different pollen dispersal modes or plant functional types. According to model comparisons (Table 2), inclusion of spatial variables representing directional dispersal of summer monsoon always significantly improved RDA model results in all five cases. The improvement suggests the ASM impacts the overall pollen assemblages, not only the AP taxa. Previous studies have examined the relationship between the ASM and AP by coupling the relative abundance of AP with monsoon-dominant precipitation isohyet and streamline of the ASM (Zhang and Li, 2017; Li et al., 2020). Furthermore, Zhang et al. (2023) found that there was a significant correlation between wind connectivity and pollen compositions in the southeastern TP. Our findings are generally in agreement with those works that the ASM dominates spatial distribution of the AP. However, we provided more straightforward quantitative evidence and evaluation on influence of the ASM by accounting for the directional effect with the AEM. Moreover, we discovered that the ASM has a significant effect not only on AP, but also on NAP and the whole pollen assemblages. We also compared contributions of the ASM and commonly used climatic variables on explaining pollen assemblage’s variations. Studies on the pollen-climate relationship have shown that MAT, MAP and July temperature are the most important climatic variables affecting pollen assemblages on the TP (e.g., Shen et al., 2006; Zhao and Herzschuh, 2009; Lu et al., 2011; Wei and Zhao, 2016). However, our results clearly showed that apart from the above commonly-used climate variables, the directional spatial process driven by the ASM also has a significant and non-negligible impact on pollen assemblages. For example, the AEM spatial variables uniquely explained ~7% of variations of the whole pollen assemblages, roughly equal to variation uniquely explained by local climatic variables (Fig. 4).

We chose TP as the study area because its significance of determining regional and global climate. However, similar study can be taken to examine effect of other important atmospheric circulation systems, like the Westerlies, on pollen assemblages in any regions. The ASM probably has comparable effect on pollen assemblages in eastern and northern China, which are also heavily affected by it. In fact, directional spatial effect of prevailing winds on the variation of pollen composition is likely to be prevalent in other monsoon-dominated regions, like Northern American and Australian monsoon-dominated areas. Given its impact on pollen assemblages, monsoon-driven pollen dispersal probably also contributes to the large-scale genetic pattern of plants (Kling and Ackerly, 2021).

**Table 2**

Comparison of adjusted  $R^2$  values of RDA models with different assumed monsoon source. Best models are marked in bold.

Monsoon source	Taxa	Climate	AEM	Climate+AEM
South	All	0.19	0.19	<b>0.26</b>
	AP	0.25	0.18	0.28
	NAP	0.16	0.20	<b>0.25</b>
	Anemophilous Pollen	0.22	0.23	<b>0.30</b>
	Non-anemophilous Pollen	0.14	0.14	<b>0.19</b>
Southeast	All	0.19	0.17	0.26
	AP	0.25	0.25	<b>0.33</b>
	NAP	0.16	0.10	0.19
	Anemophilous Pollen	0.22	0.15	0.26
	Non-anemophilous Pollen	0.14	0.15	<b>0.19</b>
East	All	0.19	0.09	0.22
	AP	0.25	0.15	0.30
	NAP	0.16	0.07	0.19
	Anemophilous Pollen	0.22	0.11	0.26
	Non-anemophilous Pollen	0.14	0.07	0.18

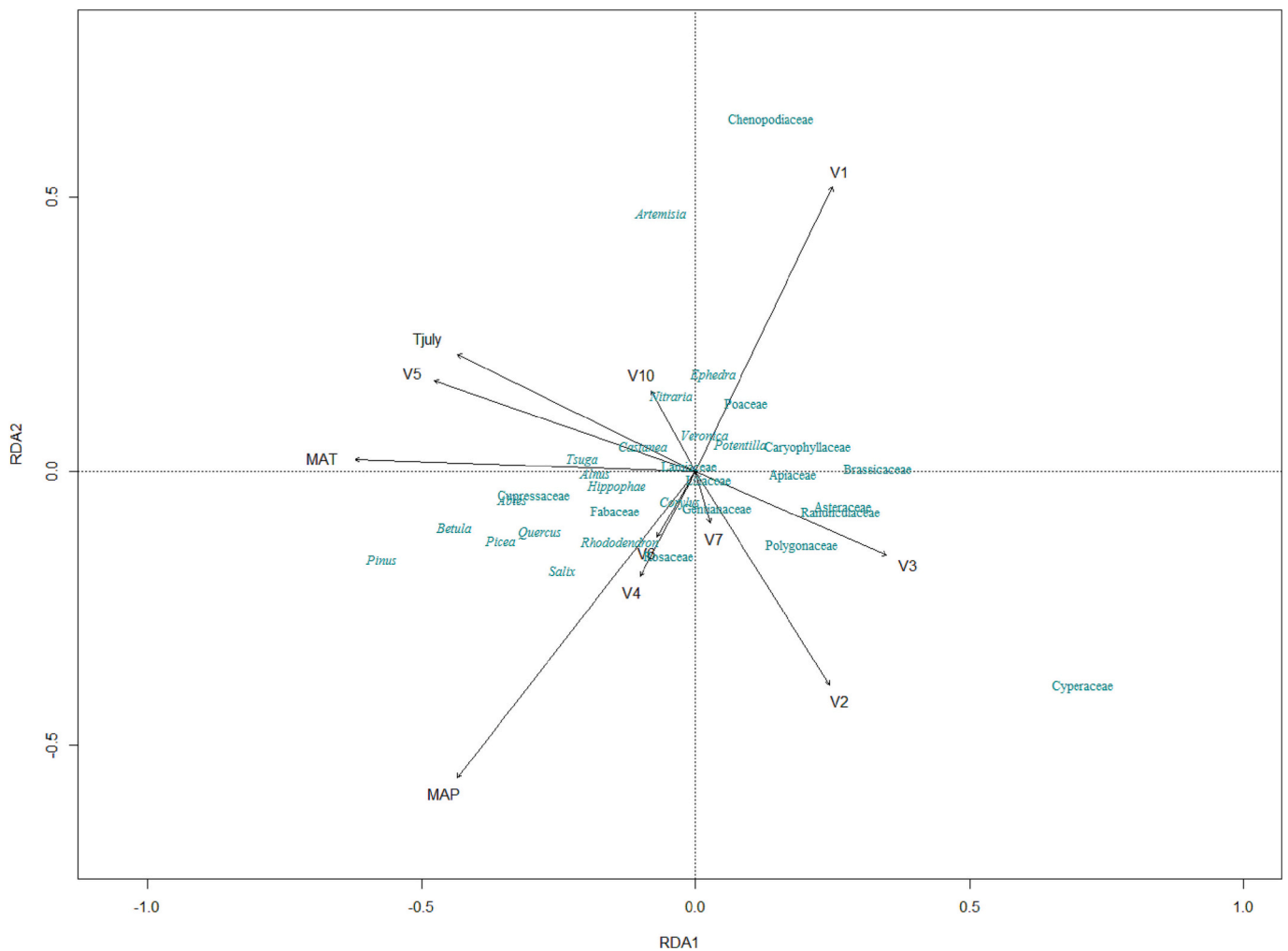


Fig. 2. Biplot of the RDA model for all pollen taxa.

It is difficult to discuss the ecological interpretation of latent spatial variables produced by AEM. These variables are derived from the site by edge matrix via SVD, like principal components in ordination methods. The latent variables do not have a clear ecological meaning; however, they can represent the directional spatial process shaping the observed pattern of response variables (Blanchet et al., 2010). In our case, the underlying directional process is driven by the ASM. In Fig. 3, we can see three AEM variables kept by model selection all showed clear spatial distribution changing from south to north of the TP. The variation of AEM variables across space probably indicates intensity change of the ASM on its path to the interior part of the plateau.

#### 4.2. AP vs. NAP

AP and NAP pollen compositions are best explained by models assuming different wind directions. AP is best explained by the southeast model with an 8% unique contribution by ASM, while NAP is best explained by the south model with 9% unique contribution. In the case of the southeast model, the pure spatial component of the ASM explains 8% and 4% of the total variance in AP and NAP taxa respectively; supporting that AP is more heavily affected by the ASM, while the model with a southern source represents a contrary trend (3% vs. 9%, Fig. S1). We believe that this pattern can be attributed to the coupling of forest distribution and monsoon pathway. Distribution of forest is concentrated on the south-southeastern margin of the TP, which is also the deposition center of the AP (Yu et al., 2001; Li et al., 2020). The

monsoon transports arboreal pollen from these regions toward the northwest, reaching the interior part of the plateau. The contrast between the south and southeast models in explanatory power of AP and NAP implies that at least for our sampling sites, the southeastern monsoon is the most important driver of long-distance dispersal of AP. The roles of different wind directions in shaping different pollen assemblages also supports the idea that pollen records can be proxy of monsoon directions. However, we assumed a single wind source in current study, which is clearly an oversimplification of the complex monsoon circulation. A more realistic approach to model monsoon induced dispersal may produce more insights into pollen-monsoon direction relationship. The AP taxa also have higher portion of variation explained commonly by the ASM and local climate variables than the NAP (18% vs. 6%, by the southeastern model and 16% vs. 11%, by the southern model, Fig. S1), which probably reflects that local climate is more closely coupled with the ASM in the forested area in the southern and eastern margins of the TP. In these parts, the monsoon brings large volume of moist air, causing high annual rainfall and nourished forest vegetation (Jarvis and Clay-Poole, 1992; Xiao et al., 2011; Yu et al., 2001). In general, our study supports that tree pollen can be a good indicator of past monsoon path. Recent studies showed that this is a promising research direction. For example, Zhao et al. (2019) used backward trajectory analysis to reveal fossil *Tsuga* pollen in the western TP were transported by paleo-monsoon from the southern TP in the late Holocene; Li et al. (2021) found the abundance of fossil AP closely corresponds to intensity of paleo-monsoon.

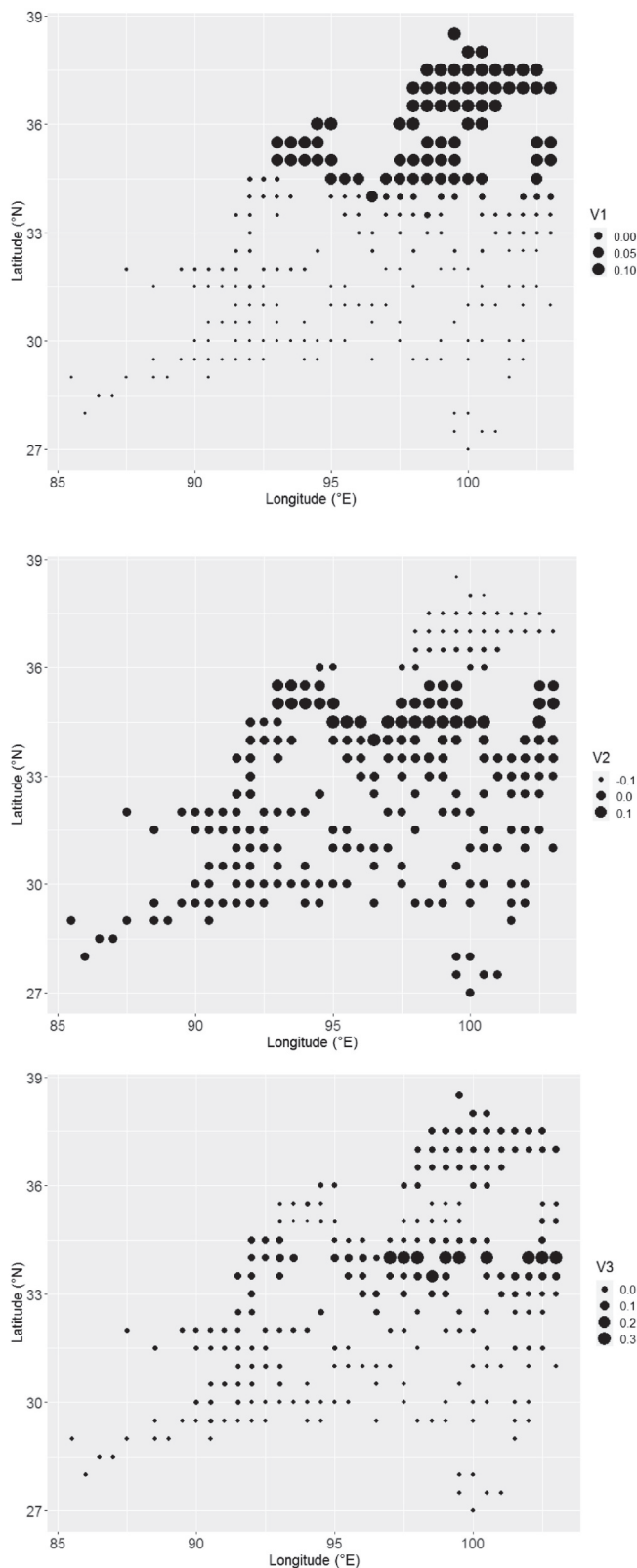


Fig. 3. Spatial distributions of three AEM variables V1~V3.

Though long-distance dispersal of AP on the TP is frequently observed, the ASM is also found to significantly affect NAP assemblages. This is partially mirrored by the latest study on the significant correlations between non-arboreal pollen (*Artemisia*, *Cyperaceae* and *Poaceae*) and the Asian summer monsoon on the southeastern Tibetan Plateau

(Zhang et al., 2023). We used wind data at a coarse scale of  $\sim 50$  km. Our results imply that long-distance transport of NAP may still operate at this scale. However, NAP is found to be a good representation of vegetation zone in the TP (Yu et al., 2001). Thus, long-distance transport of NAP may happen at much shorter distance than AP, mostly within the same vegetation zone. Still, exotic NAP has the potential to bias vegetation reconstruction work like AP in the unforested area. Pollen-based vegetation reconstruction model with state-of-the-art mechanistic pollen dispersal model should be used to further investigate the probability of long-distance of NAP transportation (Kuparinen, 2006; Theuerkauf et al., 2012; Theuerkauf and Couwenberg, 2021). This result indicates that fossil NAP could also be useful in reconstructing ancient monsoon, though its relationship with monsoon needs further investigation.

#### 4.3. Anemophilous vs. non-anemophilous pollen

Anemophilous pollen is best explained by the model with the south source (8% unique contribution by the ASM, Fig. 4). Non-anemophilous pollen is best explained by the south and southeast models, both of which have a unique contribution of 5% by the ASM. This result shows that spatial effect of the ASM does have a larger effect on anemophilous pollen. The significant influence of the ASM on non-anemophilous pollen may imply that, though not generally considered as wind-dispersed, non-anemophilous pollen can still be dispersed at a great distance by monsoon winds. Culley et al. (2002) proposed that joint pollination of both wind and insect (ambophily) could be more common than presumed in plants. As a matter of fact, ambophily has been found in species on the TP and worldwide, in taxa like Brassicaceae, Caryophyllaceae, Ranunculaceae and *Salix* (Culley et al., 2002; Duan et al., 2009), which are present in our pollen dataset. For species with ambophily, wind and animal pollinators may act at different spatial scales in pollen dispersal process (Robledo-Arnuncio et al., 2014).

#### 4.4. Potential implications for interpretation of fossil pollen

Our research investigated the relationship between modern pollen assemblage and Asian Summer Monsoon with the AEM method and supports the idea that pollen data can act as a proxy of ancient monsoon. The AEM approach cannot be applied directly to reconstruct paleo-monsoon intensity and trajectory. However, it can still be a useful tool for studying paleo-climate and paleo-vegetation based on fossil pollen data. Paleoclimate models can make simulations of Quaternary wind fields (Jiang and Lang, 2010). Therefore, similar approach used here can be applied to ancient monsoon simulations and fossil pollen data, to explore how the role of directional dispersal caused by monsoon, or other prevailing winds, in shaping pollen assemblages changes over time. Herzschuh et al. (2019) discovered that position and direction of westerly is crucial for determining Holocene rainfall patterns in China, therefore correct simulation of prevailing winds is important for studying paleoclimate and predicting future climate. The explanatory power of AEM variables based on simulations of different paleoclimate models and scenarios on observed variations of fossil pollen assemblages can be compared for the same period, and potentially be used to evaluate different paleowind simulations.

Studying effect of directional pollen dispersal by wind also has implications for past vegetation reconstruction via fossil pollen. Pollen-based plant cover reconstruction is important for studying past land-use and how it affects climate during the Holocene (Harrison et al., 2020). Many pollen-vegetation models, like REVEALS and STEPPS use pollen sediment record from lakes, bogs and ponds to reconstruct vegetation, and assume pollen dispersal by wind is anisotropic (Dawson et al., 2016; Sugita, 2007). Implications of directional dispersal of pollen on vegetation reconstruction still need more investigations (Dawson et al., 2016). Our result implies a significant role of long-distance directional dispersal caused by monsoon in shaping pollen compositions. Thus, models modified to incorporate wind direction might be

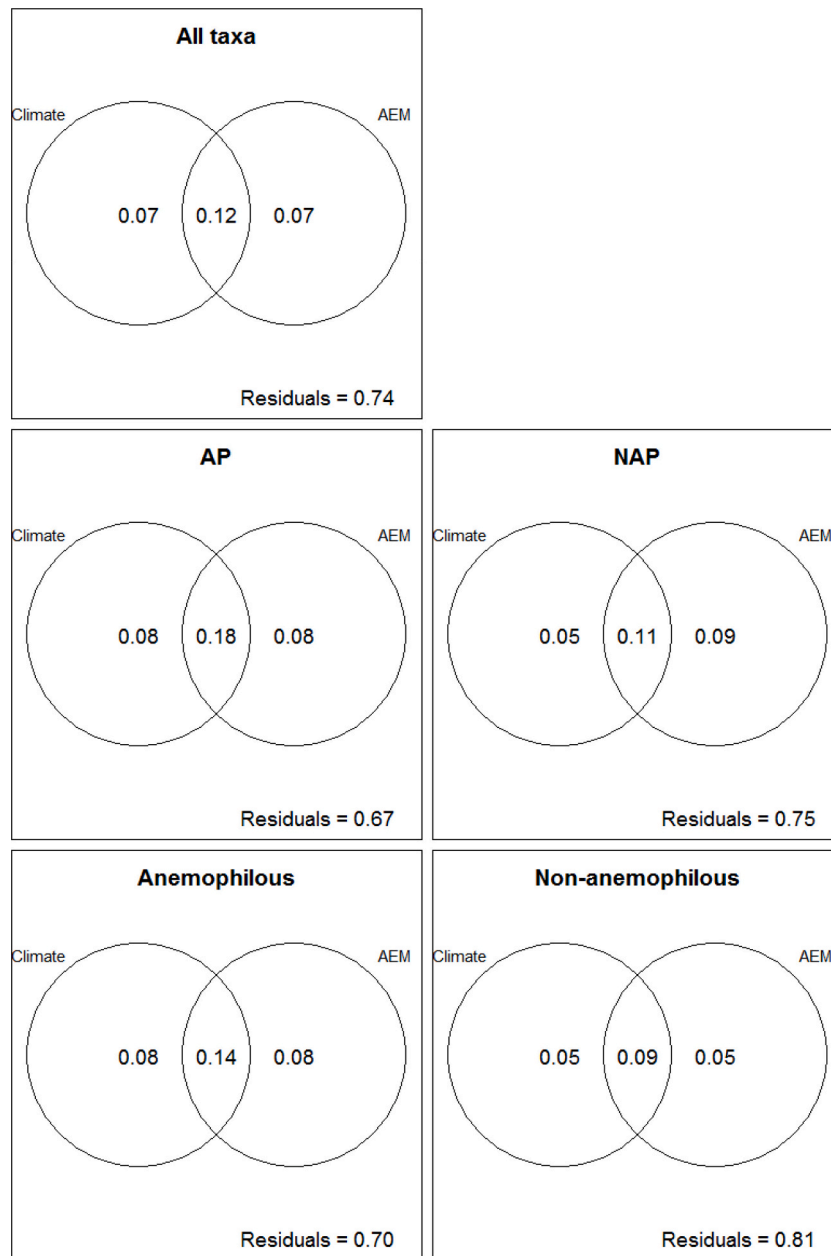


Fig. 4. Variation partitioning results performed on corresponding best AEM+climate models for five taxa groups. All unique fractions are significant at  $P < 0.001$  level.

more realistic under many circumstances (Azuara et al., 2019; Bunting and Middleton, 2005). REVEALS also assumes pollen transportation by river is negligible (Sugita, 2007). The relative importance of river transportation versus wind transportation of pollen is rarely compared. Dispersal by river and dominating wind are both highly directional and can be modeled by the AEM approach (Legendre and Gauthier, 2014). Given available data (like a series of pollen samples collected from multiple lakes along a river), a novel study could be conducted to compare the importance of these two directional dispersal processes (riverborne and windborne) in determining the spatial patterns of pollen assemblages.

## 5. Conclusion

In this study we quantified contribution of the ASM on TP pollen assemblages and provided evidence that directional dispersal caused by monsoon can significantly affect large-scale pollen composition. The

relative importance of local climate and directional spatial effect of ASM varies among different pollen groups. This result agrees with the idea that AP is suitable for reconstruction of monsoon pathway (Li et al., 2020). Furthermore, monsoon not only affects tree pollen or anemophilous pollen but the whole pollen assemblages, as well as NAP and non-anemophilous pollen considered separately. In further studies constructing pollen deposition model in TP and reconstructing monsoon pathway, abundance of NAP may also provide valuable information. The probability that NAP is carried long distance by monsoon should also be taken into consideration when reconstructing vegetation based on fossil pollen assemblages. We believe that this study increased our understanding of how dominant wind shapes pollen assemblages together with local climate and provided reference for studies reconstructing the evolution of the ASM via pollen data.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.palaeo.2023.111690>.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

## Data availability

Data of pollen assemblages can be accessed as supplemental material of Chen et al. (2021) (<https://www.plant-ecology.com/CN/Y2021/V45/I7/799>, in Chinese). Wind data can be downloaded from The Global Forecasting System via *rwind* package (Fernández-López and Schliep (2019)). Climate data can be downloaded from the WorldClim database (Fick and Hijmans, 2017) (<https://www.worldclim.org/>).

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