

This is a post-peer-review, pre-copyedit version of an article published in *Vegetation history and archaeobotany*.
The final authenticated version is available online at: <http://dx.doi.org/10.1007/s00334-019-00751-4>

1 Relative pollen productivity estimates for 2 alpine meadow vegetation, northeastern 3 Tibetan Plateau

4
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17 Abstract

18 A promising method of reconstructing palaeovegetation from pollen records uses
19 mathematical models of the relationship between pollen and vegetation, which can be
20 calibrated using the Extended R-Value (ERV) approach on datasets of modern pollen
21 assemblages and related vegetation survey data. This study presents the results of
22 calibrating the models for non-arboreal pollen types in alpine meadow habitats on the
23 Tibetan Plateau.

24 Pollen assemblages from surface soil samples and surrounding vegetation data
25 were collected for 30 randomly located sites in the Zoige Basin, northeastern Tibetan
26 Plateau. ERV analysis found that the most reliable results were obtained when using
27 ERV sub-models 1 and 2 and distance-weighting the vegetation data by applying the
28 taxon-specific Prentice-Sutton method.

29 The relevant source area of pollen (RSAP) for soil samples in alpine meadows of
30 the northeastern Tibetan Plateau is ca. 200 m. Relative pollen productivities (RPPs) of
31 15 non-arboreal taxa were estimated relative to Cyperaceae (RPP_{Cyp}). The taxa can be
32 divided into 3 groups according to their RPPs, those with high RPP_{Cyp} (> 1.68:
33 *Thalictrum*, *Artemisia*, Caryophyllaceae, Chenopodiaceae and *Plantago*), those with
34 moderate RPP_{Cyp} (0.42 - 0.62: *Taraxacum*-type, Apiaceae, *Polygonum* and *Aster*-type),
35 and those with low RPP_{Cyp} (≤ 0.4 ; Gentianaceae, *Potentilla*, Brassicaceae, *Saussurea*-
36 type and Poaceae). RPP values obtained differ from previous studies in other parts of
37 China, and form the basis for future reconstruction of palaeovegetation in the Tibetan
38 Plateau through model-based methods (e.g. Landscape Reconstruction Algorithm,
39 Multiple Scenario Approach).

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1 **Key words:**

2 Relative pollen productivity; relevant source area of pollen; alpine meadow; ERV
3 approach; Tibetan Plateau

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1. Introduction

1.1 Pollen-vegetation model

Pollen analysis is one of the key tools available for understanding past vegetation, climate and ecosystems (e.g. Birks et al. 2016). Fluctuations in pollen percentages through time were first used to reconstruct the dynamics of vegetation over time by von Post (1916), and this remains an important tool today. The basic assumption of the method is that there is a consistent, comprehensible relationship between the type and amount of pollen preserved in a sedimentary record and the type and amount of plants producing that type of pollen in the landscape around the sediment record. However, the relationship between pollen and plant percentages is non-linear, and percentages of different taxa are interdependent (the “Fagerlind effect”; Fagerlind 1952), which makes it complicated to convert pollen percentages into quantitative reconstructions of vegetation.

One approach to reconstructing vegetation cover from pollen percentages uses mathematical models of the relationship between pollen and vegetation. This approach began when Davis (1963) proposed the “R-value model”, which calculates a constant correction value for each taxon (the R value), then applies it to past pollen values to reconstruct past vegetation. An R-value is calculated as the ratio between pollen percentage and vegetation percentage, and whilst the R-value for individual taxa can vary, the approach assumes that the ratio between the R-values of two taxa is a constant. This initial model assumed that all pollen came from within the range of the vegetation survey. Anderson (1970) modified the approach to include a background term, developing a model suitable for situations where independent data were available (e.g. pollen influx rather than pollen percentage). The model was then adapted to accommodate percentage data by Parsons and Prentice (1981), who added a correction term to what was now termed the “Extended R-Value model” (ERV model, Parsons and Prentice 1981; Prentice and Parsons 1983). A second challenge was that pollen assemblages tend to recruit more pollen from plants close by than from plants growing further away, therefore vegetation data needed to be modified by some form of distance weighting. Prentice (1985) proposed the use of an empirically derived Gaussian plume particle transport model, usually referred to as Sutton’s equation (Sutton 1953), assuming that the majority of pollen was transported by wind above the vegetation canopy, and presented equations to model the formation of a pollen assemblage in a mire. Sugita (1993) then modified this model to simulate pollen deposition in a lake basin, where mixing in the water column can also occur. The form of the ERV model using one of these forms of the Sutton weighting term is often referred to as the Prentice-Sugita model, and is widely used in quantitative reconstruction of land cover from pollen records (e.g. Sugita 2007a; Sugita 2007b; Trondman et al. 2015; Bunting et al. 2018). It can be written in a simplified linear form as:

where P_{ik} is pollen loading of taxon i at site k ; P_i is the pollen productivity of taxon i ; A_{ik} is plant abundance of taxon i around site k distance-weighted using the Sutton

1 term or another model; p_i is background pollen of taxon i .

2 The background pollen term is included to reflect that component of the pollen
3 assemblage which is uniform within the study region, and this has been defined in
4 various ways. Three different assumptions, which theoretically should all produce the
5 same output, have been suggested, in the form of three sub-models. ERV sub-model 1
6 assumes a constant background pollen percentage for each taxon (Parsons and Prentice
7 1981); while sub-model 2 assumes the background pollen for each taxon is a constant
8 proportion of total plant abundance (Prentice and Parsons 1983); and sub-model 3
9 assumes the background pollen to be the pollen loading coming from beyond the
10 relevant source area of pollen (RSAP). RSAP was a concept proposed by Sugita (1994),
11 defining as “the area beyond which correlations between pollen loading for all taxa and
12 vegetation abundance do not continue to improve” (Sugita 2007b: page 245). The
13 pollen transported from beyond RSAP could be considered to be background pollen, a
14 regional constant, and variations between pollen assemblages in a region reflect the
15 variations in vegetation within the RSAP of the sample points.

17 **1.2 Taxon-specific parameters for pollen based vegetation** 18 **reconstruction**

19 In order to apply ERV model to reconstruction of past vegetation abundance, the
20 two taxon-specific parameters of the Prentice-Sugita model, pollen productivity (P_i)
21 and background pollen (p_i), need to be calculated. Where absolute data on both pollen
22 (e.g., long-term monitoring record of pollen trap) and vegetation are available, an
23 absolute pollen productivity (APP) can be estimated using a linear regression method
24 (e.g. Sjögren et al. 2008; Sjögren et al. 2015; Sugita et al. 2010). However, in most
25 cases only percentage pollen data are available. In order to estimate these parameters
26 from percentage data, Prentice and Parsons (1981) proposed an iterative approach
27 (maximum likelihood estimation) using the ERV model (usually referred to as the ERV-
28 approach or ERV method). In this case, pollen productivity is estimated in a relative
29 term (relative pollen productivity, RPP hereafter) by assigning a reference taxa (whose
30 RPP is 1) preliminarily. RSAP can be estimated by analyzing the Likelihood Function
31 Scores produced as part of the ERV-approach.

32 Using modern pollen and plant data for a region, values of pollen productivity and
33 background pollen can be estimated. This allows the pollen-vegetation model to be
34 applied to reconstruct the palaeovegetation quantitatively from fossil pollen spectra.
35 Two reconstruction approaches are generally in use at present, the Landscape
36 Reconstruction Algorithm (LRA, Sugita 2007a; Sugita 2007b) and the Multiple
37 Scenario Approach (MSA, Bunting and Middleton 2009).

38 Relative pollen productivity (RPP) is usually assumed to be a constant over time
39 within a given geographic region, but can vary between regions due to variations in the
40 species making up a given pollen taxon. Comparative studies show wide variation in
41 published estimates (e.g. Broström et al. 2008; Mazier et al. 2012; Li et al. 2018), which
42 may relate to methodological differences, but may also show that the assumption of

1 constant RPP is not valid, with variations between regions due to factors such as climate,
2 soil, vegetation structure and land-use/landscape management (Broström et al. 2008).
3 Bunting et al. (2013) proposed a compromise vegetation survey method for estimation
4 of RPP in order to minimize differences caused by methodological variation in input
5 data.

6 Most published studies of RPP in China (reviewed by Li et al. 2018) concern the
7 vegetation biomes of northern China, e.g. steppe (Li et al. 2011; Xu et al. 2014; Ge et
8 al. 2015; He et al. 2016; Ge et al. 2017; Han et al. 2017; Li et al. 2017b), steppe-forest
9 (Wu et al. 2013), forest (Li et al. 2015; Zhang et al. 2017) and cultural landscape (Li et
10 al. 2017a). Other biomes are less well represented, with one study of alpine meadow
11 and alpine steppe on Tibetan Plateau (Wang and Herzschuh 2011), and two of
12 subtropical forest in eastern (Chen et al. 2019) and southeastern (Fang et al. unpublished)
13 China.

14 There are at least 220 late Quaternary pollen records with relatively good age
15 constraints and sampling resolution published across China (summarised by Cao et al.
16 2013, with more sites added since), but only two studies so far have used the estimated
17 RPP values to carry out quantitative reconstruction of Holocene plant cover (on the
18 eastern Tibetan Plateau: Wang and Herzschuh 2011; and for northern China: Xu et al.
19 2014). The contrast of number between fossil pollen spectra and quantitative
20 reconstruction can, to a large extent, be attributed to the lack of RPP values for the
21 subtropical and temperate forests of southern/central/eastern China, the deserts of
22 northwestern China, and the alpine/sub-alpine vegetation of the Tibetan Plateau. In this
23 paper, we present a study of pollen-vegetation relationships from the northeastern
24 Tibetan Plateau.

25 The Tibetan Plateau is the highest and largest plateau on earth, and influences both
26 global climate and the intensity of the Asian monsoon (e.g. Kutzbach et al. 1989; An et
27 al. 2001; Molnar et al. 2010; Wu et al. 2015). Wang & Herzschuh (2011) reported RPP
28 estimates for four major taxa on the Tibetan Plateau, i.e. *Artemisia*, *Chenopodiaceae*,
29 *Cyperaceae*, and *Poaceae*, and used these values to reconstruct the Holocene vegetation
30 changes around four lakes in central and eastern parts of the plateau using the
31 REVEALS (Sugita 2007a) method. Their results suggested that alpine meadow was far
32 more widespread in central and northeastern Tibetan Plateau during the Holocene than
33 previous studies had concluded. This paper presents results of an investigation into
34 pollen-vegetation relationships in alpine meadow communities of the northeastern
35 Tibetan Plateau, in order to better understand the pollen signal of these communities
36 and to obtain RPP estimates for more taxa for future reconstructions of the Holocene
37 vegetation.

38

2. Materials and methods

2.1 Study area

The alpine vegetation of the Tibetan Plateau can generally be divided into three vegetational subregions from southeast to northwest, a subalpine scrub and alpine meadow subregion, an alpine steppe subregion and an alpine desert subregion (Zhang 2007). The Zoige Basin in the eastern part of the subalpine scrub and alpine meadow subregion (Fig. 1) was selected for this study. The climate of this area is primarily controlled by the Asian Monsoon. Mean annual precipitation (MAP) recorded at nearby meteorological stations (<http://data.cma.cn/site/index.html>) was ca. 615 - 750 mm (1951-1980), with most precipitation falling during the period from June to September. Mean annual temperature (MAT) ranged from 0.7 to 1.1 °C, with mean July temperature around 10.8 °C and mean January temperature -10 °C. Mean annual wind speed ranged from 2.1 to 2.7 m/s.

Vegetation in the Zoige Basin (Wang et al. 2002; Zhang 2007; field survey) is primarily alpine meadow and mire. The dominant taxa recorded were Cyperaceae (e.g., *Carex*, *Kobresia*), with significant Poaceae presence (e.g., *Deschampsia*, *Elymus*, *Leymus*, *Poa*, *Roegneria*, *Stipa*). The families Asteraceae (*Ajania*, *Anaphalis*, *Artemisia*, *Cirsium*, *Cremanthodium*, *Leontopodium*, *Ligularia*, *Saussurea*, *Tamaxacum*), Gentianaceae (*Comastoma*, *Halenia*, *Lomatogonium*, *Gentiana*, *Gentianopsis*, *Swertia*), Polygonaceae (mainly *Polygonum*), Ranunculaceae (*Aconitum*, *Anemone*, *Caltha*, *Delphinium*, *Halerpestes*, *Ranunculus*, *Thalictrum*, *Trollius*), Scrophulariaceae (mainly *Pedicularis*), and Rosaceae (mainly *Potentilla*) are widely found, and can be dominant taxa in some communities. In addition, Apiaceae (*Bupleurum*, *Chamaesium*, *Heracleum*, *Tongoloo*), Brassicaceae (*Descurainia*, *Draba*), Dipsacaceae (*Morina*), Caryophyllaceae (*Cerastium*, *Dianthus*), Euphorbiaceae (*Euphorbia*), Fabaceae (*Astragalus*, *Oxytropis*, *Medicago*, *Tibetia*), Geraniaceae (*Geranium*), Lamiaceae (*Ajuga*, *Dracocephalum*, *Elsholtzia*, *Salvia*, *Scutellaria*), Liliaceae (*Allium*), Plantaginaceae (*Plantago*), Saxifragaceae (*Parnassia*, *Saxifraga*), Thymelaeaceae (*Stellera*) and Valerianaceae (*Nardostachys*) are common elements. *Equisetum*, *Juncus*, *Triglochin* are prevalent in the mire. Shrublands occur in the surrounding mountain areas, mainly consisting of *Caragana*, *Hippophaea*, *Potentilla*, *Rhododendron*, *Salix*, and *Sibiraea*. To the east and south of Zoige Basin, needle-leaved forest occurs primarily on north-facing slopes of mountains, dominated by *Picea* and *Abies*. Patches of *Sabina* and *Larix* forest occasionally occur on south-facing slopes, and occasional patches of broad-leaved deciduous forest dominated by *Betula* or *Quercus* are also found.

[Fig. 1 Maps showing (a) the locations of this study and previous studies in China, (b) location of sampling sites within then Zoige Basin and (c) the landcover of the study area extracted from a satellite image (see text for details). Locations in map (a) refer to: a. this study; b. Li et al. 2011; c. Wang and Herzsuh 2011; d. Wu et al. 2013; e. Xu et al. 2014; f. Ge et al. 2015; g. Li et al. 2015; h, i, j. He et al. 2016; k, l. Han et al. 2017;

1 m. Li et al. 2017a; n. Li et al. 2017b; o, p. Zhang et al. 2017; q. Chen et al. 2019]

2.2 Site selection and sample collection

4 A random sampling strategy was adopted (e.g. Broström et al. 2005), placing
5 sampling sites randomly within a ca. 100 km × 100 km area (33°10' - 34°20' N, 102 -
6 103° 15' E) in the Zoige Basin (Fig. 1). Thirty sampling sites were selected, meeting
7 the requirement that the distance between sites was at least 5 km in order to avoid spatial
8 autocorrelation (Bunting et al. 2013). The 30 sites are located across an elevation range
9 from 3283 to 3608 m a.s.l. (Table 1). Sample collection and vegetation survey were
10 carried out in July - August 2017. Moss polsters were rarely found in the study area
11 during the field survey, so surface soil samples were used for pollen analysis. At each
12 sampling site, several subsamples of topsoil were collected within a 1 m × 1 m square
13 area, then amalgamated into one sample for pollen analysis.

15 [Table 1 Location of the sampling sites in the Zoige Basin, northeastern Tibetan
16 Plateau]

2.3 Pollen analysis

19 Pollen samples were treated following the procedures of Faegri & Iversen (1989)
20 and Moore et al. (1991) including chemical treatments of 10% HCl, 10% NaOH, 40%
21 HF, followed by acetolysis treatment, sieving (10 µm) in an ultrasonic bath, and finally
22 mounting in glycerol. Prior to chemical treatment, a known number of exotic
23 *Lycopodium* spores (19332 grains) was added to each sample to enable estimation of
24 pollen concentrations. Pollen were observed and counted under an optical microscope
25 at 400× magnification. Pollen identifications were based on published palynological
26 literature (e.g. Xi and Ning 1994; Wang et al. 1995; Tang et al. 2016) and reference
27 collections from study area. A minimum of 1000 terrestrial pollen grains were counted
28 for each sample. Relative abundance (expressed as percentage) of each pollen taxon in
29 a sample was calculated against the sum of terrestrial pollen. Tilia 1.7.16 (Grimm 2011)
30 was used to construct a pollen diagram.

2.4 Vegetation data collection

33 Since the influence of vegetation survey strategy on the estimates of RPP and
34 RSAP has been discussed (Broström et al. 2008; Bunting and Hjelle 2010), vegetation
35 survey around the sampling point was carried out following the standard procedure of
36 the field protocol of Crackles Bequest Project (Fig. 2, Bunting et al. 2013):

37 **Zone A** (radius 0 - 10 m): A total of 21 quadrats (1 m × 1 m) were surveyed in this
38 zone, including: a central one around the sampling point, and 20 quadrats centered at
39 the distances 1, 2.25, 4.5, and 8 m in four directions N, E, S, W, and 8 m in the NE, SE,
40 SW, and NW directions. The cover of each plant taxon was visually estimated and

1 recorded for each quadrat.

2 **Zone B** (radius 10 - 100 m): Firstly, a community distribution map was drawn in
3 this zone. Boundaries between communities were established by walking along 12
4 radial transects from sampling point to 100 m, and visually defining the boundary lines
5 with the help of hand-held GPS. Secondly, 4 randomly-located quadrats were surveyed
6 in each community. 1 m × 1 m quadrat was used throughout the whole field survey,
7 since all involved communities are open ones.

8 **Zone C** (radius > 100 m): Vegetation data in this zone was extracted from a
9 landcover map. This was created using satellite images from Sentinel-2 (resolution =
10 10 m, <https://scihub.copernicus.eu/>). Classification was performed using the maximum
11 likelihood classification procedures in ArcMap 10.5.1. Plant cover data was collected
12 from these maps within 3000 m radius of each sampling site, since none of the
13 published studies suggested RSAP wider than 3000 m for herb-dominated vegetation
14 in China (Li et al. 2018). Plant taxa composition in each landcover type was estimated
15 from the field vegetation survey data collected within zones A & B.

16
17 [Fig. 2 Illustration of vegetation survey strategy]
18

19 2.5 ERV analysis

20 The standard “rule of thumb” is that for a dataset of 2n samples, analysis should
21 include no more than n target taxa in order to reduce the standard deviations of pollen
22 productivity (Soepboer et al. 2007; Sugita 2007b). Therefore, fifteen pollen taxa were
23 selected for ERV analysis to estimate the relative pollen productivities (RPP) and
24 relevant source area of pollen (RSAP). Taxa were chosen on the basis that they were
25 found in multiple samples with a range of values in both pollen assemblage and
26 vegetation data, and on the basis of observed relationships between pollen proportion
27 and distance weighted plant abundance (Fig. 3). Therefore, Ranunculaceae (showed a
28 negative relationship between pollen and vegetation) and Fabaceae (showed almost no
29 relationship) were not selected, although they had significant proportions in pollen
30 assemblages and/or vegetation. We also explored the effects of including different
31 numbers of taxa in ERV analysis, repeating analysis with 7, 10, 13, 15 and 17 taxa
32 (details presented in the Electronic Supplementary Material, hereafter ESM), and
33 concluded that the results from the analysis of 15 taxa presented here were reliable.

34 Vegetation survey data were input into Survey v 2.0.1 (Middleton, unpublished)
35 to calculate the distance-weighted plant abundance (DWPA) for the concentric rings
36 around sampling points within 100 m radius (zone A & B). Concentric-ring vegetation
37 data of zone C (from 100 to 3000 m radius) were collected using PolFlow v 4.0 and
38 PolLog v 4.2 (Bunting and Middleton 2005) from the landcover map, in 10 m wide
39 rings, and distance weighted using the Prentice form of the Sutton weighting term
40 (Sutton 1953; Prentice 1985). When using the Prentice-Sutton distance weighting
41 method, wind speed and pollen fall speed parameters are also required. A constant wind
42 speed of 2.5 m/s, which approximates the mean annual wind speed in the Zoige Basin,
43 was employed. Pollen fall speeds of selected taxa were estimated following Stoke's law

1 (Gregory 1973) based on their pollen sizes. To estimate pollen sizes, the diameter of
2 spherical pollen types, and both the polar and equatorial axes of elliptical types were
3 measured on 30 grains of each pollen taxa on pollen slides from the Zoige Basin to
4 obtain a mean for calculation of fall speed (Table 2). Vegetation data were also weighted
5 using the non-taxon-specific inverse distance (1/d) and inverse squared distance (1/d²)
6 methods for comparison with the Prentice-Sutton weighting results.
7

8 [Table 2 Size and pollen fall speed of selected taxa in alpine meadows of the
9 Tibetan Plateau]

10
11 ERV analysis was carried out using PolERV v 4.0 (Middleton, unpublished).
12 Cyperaceae was chosen as the reference taxon, since it was present in both pollen
13 assemblage and vegetation of all sites with the widest variations of abundance between
14 sites (Fig. 3). All three sub-models of the ERV model were tried in the analysis. RSAP
15 was defined visually from the plots of likelihood function score by identifying the
16 distance beyond which the score approaches an asymptote. The RPP of each taxon was
17 estimated as the average of values obtained for all distances greater than the RSAP,
18 since the estimates beyond RSAP should all be equally good (Sugita 1994). Its error
19 was calculated following the principle of error propagation (Taylor 1997), i.e. where Z
20 = $k(A + B + C)$ and k is a constant, the error on Z can be calculated as $\Delta Z = |k| \sqrt{(\Delta A)^2$
21 + $(\Delta B)^2 + (\Delta C)^2$.
22

23 [Fig. 3 Scatter plots showing the relationships between pollen proportion and
24 distance weighted plant abundance to 3000 m for main pollen taxa in the Zoige Basin,
25 northeastern Tibetan Plateau]
26

3. Results

3.1 Pollen assemblages

The surface pollen assemblages from the Zoige Basin (Fig. 4) yielded 63 palynomorphs, consisting of 47 non-arboreal and 16 arboreal elements. The relative abundance of non-arboreal pollen ranges from 73.2% to 96.2%, among which Cyperaceae was the dominant element (relative abundance 18.0 - 91.0 %), along with *Artemisia* (0.2 - 30.5 %), Poaceae (1.2 - 21.9 %), *Potentilla* (0.2 - 14.6 %), and Ranunculaceae (2.0 - 24.8 %). Palynomorphs from the Asteraceae family, i.e. *Aster*-type (0.1 - 10.8 %), *Saussurea*-type (0 - 1.9 %) and *Taraxacum*-type (0 - 4.3 %), as well as Gentianaceae (1.1 - 4.4 %), *Hippophaea* (0.2 - 2.9 %), *Polygonum* (0 - 5.6 %) and *Thalictrum* (0.2 - 10.8 %) were commonly seen. Small amounts of Chenopodiaceae (0 - 1.9 %) and Fabaceae (0 - 0.8 %) were frequently found. Caryophyllaceae (0 - 9.4 %), Crassulaceae (0 - 9.4 %) and *Plantago* (0 - 13.2 %) only occasionally occurred at high proportions. Arboreal pollen made up 3.8 - 26.7 % of the samples, among which *Betula* (0.9 - 15.3%), *Abies* (0 - 5.5 %), *Picea* (0.2 - 7.3 %), *Pinus* (0.3 - 4.0 %) and *Quercus* (0 - 1.9 %) were the most important.

[Fig. 4 Pollen spectra of the 30 surface soil samples from alpine meadows of the Zoige Basin, northeastern Tibetan Plateau]

3.2 Results of ERV analysis

The results of ERV analysis showed that likelihood function scores declined sharply within the first 200 m when vegetation data were weighted using Prentice-Sutton method (Fig. 5), and the score approached an asymptote at distances beyond 200 m regardless of the choice of sub-model. Likelihood function scores derived from using ERV sub-model 1 were lower than those from sub-model 2 at the same distances. When inverse distance ($1/d$) weighted vegetation data were used, the likelihood function scores of all three sub-models decreased until 100 m, thereafter exhibited continuous increases. The likelihood function scores based on inverse square distance ($1/d^2$) weighted vegetation data did not show an obvious decreasing trend toward an asymptote. Therefore, the Prentice-Sutton method was considered the most appropriate vegetation-weighting method for ERV analysis in the study area. The combination of this weighting and ERV sub-model 3 yielded a fluctuating curve of likelihood function score, implying that the sub-model 3 assumption may not be reasonable for the dataset. Accordingly, the results from the Prentice-Sutton distance-weighted vegetation data obtained using sub-models 1 and 2 are focused on for further discussion, and the RSAP is identified as 200 m.

[Fig. 5 Plots of the likelihood function scores calculated using three ERV sub-models and three distance weighting methods for plant abundance. a) Prentice-Sutton method; b) $1/d$ weighting; c) $1/d^2$ weighting]

1
2 The RPPs of the 15 selected taxa estimated using ERV sub-models 1 and 2 with
3 Prentice-Sutton distance weighting method are shown in Fig. 6 and Table 3. Results of
4 the two sub-models are not substantially different, although the rank order of mean RPP
5 values is not exactly the same. RPP relative to Cyperaceae (hereafter RPP_{Cyp}) values
6 for *Thalictrum* are the highest using both sub-models, followed by *Artemisia*.
7 Caryophyllaceae, Chenopodiaceae, and *Plantago* also have high RPP_{Cyp} values using
8 both sub-models, but their rank order differs. RPP_{Cyp} for Caryophyllaceae is higher than
9 that for Chenopodiaceae and *Plantago* using sub-model 1, whilst Chenopodiaceae and
10 *Plantago* have higher RPP_{Cyp} than Caryophyllaceae using sub-model 2. RPP_{Cyp} values
11 for *Taraxacum*-type, Apiaceae, *Polygonum* and *Aster*-type are around 0.5 using both
12 sub-models, and sub-model 2 always yield higher values. Gentianaceae also has higher
13 RPP_{Cyp} value using sub-model 2 than sub-model 1, but its RPP_{Cyp} value never exceed
14 0.38 in both cases. The remaining 4 taxa have RPP_{Cyp} values less than 0.21, which
15 suggests that they are under-represented in the pollen record. RPP_{Cyp} values for
16 Brassicaceae are the highest in this group. Results from sub-model 1 produce higher
17 RPP_{Cyp} value for *Potentilla* than that from sub-model 2. Sub-models 1 and 2 produce
18 similar RPP_{Cyp} values for *Saussurea*-type. RPP_{Cyp} values for Poaceae using both sub-
19 models are very low, while that using sub-model 2 is higher.

20
21 [Fig. 6 Relative pollen productivity estimates and errors for 15 selected taxa in
22 alpine meadows of the northeastern Tibetan Plateau using plant cover data weighted by
23 Prentice-Sutton method and ERV sub-model 1 & 2]

24
25 [Table 3 Relative pollen productivity (RPP) estimates for 15 selected taxa in alpine
26 meadows of the northeastern Tibetan Plateau]

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28 ERV analyses including different numbers of taxa indicated that Prentice-Sutton
29 method of distance-weighting vegetation produced the most coherent likelihood
30 function score plots. The “best” ERV sub-model changed depending on how many taxa
31 were included in the calculations, but there was little difference in overall trends (ESM
32 Fig. 1). The rank order of RPP_{Cyp} values generally remained the same no matter how
33 many taxa were included, although the actual RPP_{Cyp} values changed (ESM Fig. 2),
34 appearing to decrease when fewer taxa were included.

4. Discussion

4.1 Relevant source area of pollen in alpine meadow

The plots of likelihood function scores against distance indicates that the RSAP for soil samples from pseudobasins ca. 0.5 m in radius in alpine meadows of the northeastern Tibetan Plateau is ca. 200 m using plant cover data weighted by the Prentice-Sutton method (Fig. 5a). Previous RSAP estimates for alpine meadow - alpine steppe region in the eastern and central Tibetan Plateau (Wang and Herzschuh 2011) were around 2200 m, but were calculated for lake basin surface samples with radii of ca. 100 m. This difference is expected given the difference in site types (Sugita 1994).

Other comparisons of surface vegetation samples versus lakes include studies in the forest-steppe ecotone of northern China where moss polster RSAP was 600 m (Li et al. 2017b), while that from lake sediments (average radius ca. 400 m) was 1600 m (Han et al. 2017). In sub-arctic vegetation in northern Siberia (Niemeyer et al. 2015), moss polsters had an RSAP around 10 m and lakes had an RSAP in excess of 25000 m.

[Table 4 Comparison of the relevant source area of pollen (RSAP) estimated in this study and previous research studies]

Another important factor influencing the RSAP estimate is vegetation structure in the study area. Sugita et al. (1999) modelled RSAP in two hypothetical patchy landscapes of southern Sweden with different openness, and suggested that differences between the RSAP in the two landscapes were mainly caused by the distribution of vegetation patches in the landscapes. The simulation experiments of Bunting et al. (2004) on simplified forest landscapes indicated that the size of patches within the landscape is the principal control on estimate of RSAP when basin size is constant, and grid size (resolution of vegetation map) also has a significant effect. Enlarging the size of patches and grids will lead to an increase of RSAP. Broström et al. (2005) carried out simulation experiments on landscapes containing both arboreal and herbaceous communities, and also found that the size of vegetation patches affects the size of RSAP.

In this study, vegetation within 100 m radius from each sampling sites was surveyed by using a detailed scheme (see section 2.4), and the vegetation map beyond 100 m radius derived from the high-resolution (10 m grid) satellite images. In contrast, previous research (Wang and Herzschuh 2011) on eastern and central Tibetan Plateau extracted vegetation data from the 1:1000000 vegetation map of China, therefore the size of patches and resolution of vegetation data is also smaller in this study than in Wang & Herzschuh's (2011), which could also lead to a smaller RSAP.

Other factors can also influence the estimated RSAP, such as the taxa included in the calculation and the method used to select sample locations. Comparison of RSAP estimates using 11 versus 4 taxa from the same dataset in Denmark (Nielsen and Sugita 2005) found that RSAP estimated using 4 taxa was larger even though vegetation structure was constant. This study used 15 taxa whilst Wang & Herzschuh (2011) considered 4, which may also contribute to their larger RSAP estimate. Broström et al.

12 and Ge et al. (2015) tested that in steppe of northeastern China. Both studies indicated that
13 wind speed caused negligible variation of RSAP estimates.
14

15 4.2 Relative pollen productivities in alpine meadow

16 The results (section 3.2) indicate that the taxon-specific distance-weighting
17 method (Prentice-Sutton method) was most effective when using the ERV approach to
18 estimate RPP. Analysis using sub-model 1 yielded lower likelihood function scores at
19 given distance than sub-model 2 (Fig. 5), but there is no reason to consider that RPP
20 estimates from sub-model 2 are problematic.

21 RPP_{Cyp} values for the 15 taxa in alpine meadow vegetation of the northeastern
22 Tibetan Plateau generally show comparable rank order for the two sub-models (Fig. 6).
23 The taxa can be divided into 3 groups, those with high RPP_{Cyp} (RPP_{Cyp} > 1.68; including
24 *Thalictrum*, *Artemisia*, Caryophyllaceae, Chenopodiaceae and *Plantago*), those with
25 moderate RPP_{Cyp} (0.42 - 0.62; *Taraxacum*-type, Apiaceae, *Polygonum* and *Aster*-type),
26 and those with low RPP_{Cyp} (≤ 0.4 ; Gentianaceae, *Potentilla*, Brassicaceae, *Saussurea*-
27 type and Poaceae). Most taxa in the moderate and low RPP_{Cyp} groups are
28 entomophilous, while most taxa in the high RPP_{Cyp} group are anemophilous. Plants of
29 *Thalictrum*, *Artemisia*, Caryophyllaceae, Chenopodiaceae and *Plantago* are only minor
30 components of the vegetation in alpine meadows of the northeastern Tibetan Plateau,
31 but their pollen commonly occurs in surface soils (Fig. 4), especially that of *Thalictrum*
32 and *Artemisia*. Most of the common plants of the alpine meadows are in the moderate
33 and low RPP_{Cyp} groups, such as Apiaceae, different types of Asteraceae, Gentianaceae,
34 *Polygonum*, *Potentilla*, etc.
35

36 [Table 5 Comparison of the relative pollen productivities estimated relative to
37 Poaceae (RPP_{Poa}) in China for the taxa represented in this study]
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39 In order to compare these findings with previous studies, RPPs for the studied taxa
40 are re-calculated to values relative to Poaceae (RPP_{Poa}; Table 5). RPP_{Poa} estimated using
41 ERV sub-model 2 is adopted for further comparison (see ESM for further discussion).

42 Previous research on the Tibetan Plateau (Wang and Herzschuh 2011) produced
43 RPP_{Poa} estimates which are quite different from our findings (Table 5). Nevertheless,
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1 Chenopodiaceae and *Artemisia* showed high productivities in both this study and others.
2 The RPP_{Poa} estimate for Cyperaceae from Wang & Herzsuh (2011) was close to 1,
3 but in this study Cyperaceae was estimated to have a pollen productivity at least 40
4 times that of Poaceae. This may reflect differences in sample type between the studies.
5 The pollen assemblages from surface soil receive more pollen from local plants and
6 have a better ability to reflect fine-scale vegetation pattern than those from lake
7 sediment (Sugita 1994; Zhao and Herzsuh 2009). Another possible reason is that the
8 vegetation data from the previous study were extracted from a vegetation map, which
9 may have lacked details of variation in vegetation close to the lake shore, which in turn
10 may lead to error in estimating RPP. In addition, the area chosen for this study was quite
11 homogenous, but the sampling sites of Wang & Herzsuh (2011) were distributed
12 across a much larger area which included alpine meadow and alpine steppe. Therefore,
13 the same pollen taxon could have derived from different species in different locations
14 in that study, which could also affect RPP estimates.

15 RPP_{Poa} presented here for alpine meadow on the Tibetan Plateau are not
16 comparable to values from any of the previous studies in other regions (Table 5).
17 Nevertheless, some common characteristics can be seen. Chenopodiaceae and
18 *Artemisia* normally had high RPPs, with few exceptions, e.g., Chenopodiaceae in
19 cultural landscape of Shandong (0.18, Li et al. 2017a), *Artemisia* in the desert-steppe
20 of Sunitezuoqi (0.47, He et al. 2016) and warm temperate forest of Taiyue Mountain
21 (0.01, Zhang et al. 2017). Previous studies mostly estimated a moderate or low RPP_{Poa}
22 for Cyperaceae, with values ranging from 0.01 (forest-steppe ecotone of Inner
23 Mongolia, Han et al. 2017) to 0.66 (alpine steppe and alpine meadow on the Tibetan
24 Plateau, Wang and Herzsuh 2011), apart from the forest-steppe of Hulunbeier (2.66,
25 He et al. 2016) and steppe of Bashang (8.9, Ge et al. 2015).

26 *Thalictrum*, Caryophyllaceae, and *Taraxacum*-type have much higher RPP_{Poa} in
27 the alpine meadows of the Tibetan Plateau than in other parts of China. In this study,
28 RPP_{Poa} of *Aster*-type, Brassicaceae and *Potentilla* have different values when using
29 different sub-models (ESM Fig. 4), which is also seen in other studies. RPP_{Poa} of *Aster*-
30 type ranges from 1.26 (cultural landscape of Shandong, Li et al. 2017a) to 7.53
31 (subtropical forest of Ta-pieh Mountain, Chen et al. 2019). Published RPP_{Poa} of
32 Brassicaceae ranges from 0.89 (cultural landscape of Shandong, Li et al. 2017a) to 7.56
33 (typical-steppe of Xilinguole, Xu et al. 2014); RPP_{Poa} of *Potentilla* ranges from 0.22
34 (steppe of Bashang, Ge et al. 2015) to 1.12 (typical-steppe of Xilinguole, Xu et al. 2014).

35 Many factors may explain the differences in RPP_{Poa} estimates seen. Previous
36 reviews on RPP estimates in Europe (Broström et al. 2008) and China (Li et al. 2018)
37 have discussed these factors and divided them into two groups: i.e. methodological
38 issues and environmental issues. Methodological issues include site selection strategy
39 (random, systematical), methods of vegetation survey (quadrat survey, concentric
40 survey, vegetation atlas, satellite image), reference taxon selection, pollen sample types
41 (moss polster, surface soil, lake sediment), selection of ERV sub-model, methods of
42 distance weighting (Prentice-Sutton, 1/d, 1/d²), etc. Environmental issues include
43 climate factors influencing pollen productivity (temperature) and pollen dispersal (wind
44 speed), landscape management (farmland, grazing land), vegetation structure, species

1 composition, etc. All of these factors could contribute to the discrepancy of RPP
2 estimates for the same taxa, and some of them have been discussed above (see section
3 4.1), such as pollen sample types, methods of vegetation survey, vegetation structure.

4 Our study also shows the effect of the selection of the reference taxon, another
5 methodological issue affecting inter-study comparisons. The RPPs relative to Poaceae
6 were lower than RPPs relative to Cyperaceae for the same taxa (See ESM Fig 4 for
7 more details), while the rank order of the 15 taxa was quite similar. Poaceae has become
8 a standard reference taxon in RPP studies because of its extensive occurrence in the
9 pollen-vegetation datasets (Broström et al. 2008). However, in this study Cyperaceae
10 seemed to be a better reference taxon, since 1) Cyperaceae had a wider range of values in
11 both pollen and vegetation data (Fig. 3); 2) Cyperaceae had an intermediate pollen
12 productivity (inferred from scatter plots and confirmed by Fig. 6); and 3) Cyperaceae
13 showed a better linear correlation between pollen and vegetation before correction than
14 Poaceae (see Fig. 3). Therefore, RPPs relative to Cyperaceae should be applied in
15 reconstruction of palaeovegetation in the alpine meadow region of the northeastern
16 Tibet Plateau.

18 4.3 Implications

19 The estimated RSAP indicates that non-arboreal pollen assemblages from surface
20 soil are sensitive to changes in plant cover patterning within 200 m radius around the
21 sampling point in alpine meadows of the northeastern Tibetan Plateau. Pollen records
22 in this area typically come from peat cores taken from small basins, therefore the RSAP
23 of non-arboreal fossil pollen assemblages from these records in the study region should
24 also be on the order of a few hundred meters. Therefore these records are suitable for
25 reconstruction of local-scale vegetation dynamics such as community change in
26 response to changing distributions of mire, or changes in forcing factors such as
27 moisture availability, fire regime or grazing pressure.

28 Tree pollen makes up 3.8 - 26.7 % of the pollen assemblages, mainly from *Betula*,
29 *Picea*, *Pinus*, and *Quercus*. Tree dominated plant communities occur only in the
30 northeastern corner of the landscape (Fig. 1c), and including trees in the ERV analysis
31 will therefore increase the RSAP substantially. This study was designed to obtain RPPs
32 for the meadow community taxa. All of the studied sites are herb-dominated
33 communities (meadow and mire), and the distance between studied sites and the nearest
34 forest is greater than 1 km.

35 Of the 15 studied pollen taxa, RPPs for Apiaceae, Gentianaceae, *Plantago* and
36 *Saussurea*-type are reported for the first time from China. In addition, values for *Aster*-
37 type, Brassicaceae, Caryophyllaceae, *Polygonum*, *Potentilla*, *Taraxacum*-type, and
38 *Thalictrum* are reported for the first time from the Tibetan Plateau. These values can be
39 used in two ways: in model-based quantitative reconstruction of palaeovegetation at the
40 local scale in the alpine meadows of the Tibetan plateau (e.g. LRA and MSA), and in
41 simulation experiments (e.g. Broström et al. 2005; Bunting 2008; Gaillard et al. 2008;
42 Sugita 1994) to explore the pollen representation of vegetation in a given landscape or
43 to test the reliability of palynological hypotheses.

1 A key future step will be to obtain RPPs for both arboreal and non-arboreal taxa
2 of the shrub and forest communities found in the region to the east and south of the
3 Zoige Basin following the same methods of RPP estimate (Bunting et al. 2013). This
4 would enable regional-scale reconstruction of past land cover, which could be applied
5 to studies of the movement of tree line in the eastern Tibetan Plateau during the
6 Holocene and landscape change in the alpine meadow-conifer forest ecotone.

7 In addition, our work highlights gaps in understanding of the replicability of ERV
8 analysis on different subsets of a given dataset, e.g. the influence of reference taxon
9 selection and number of target taxa on estimates of RSAP and RPP. Better
10 understanding of these questions would also increase confidence in inter-study
11 comparisons.
12

5. Conclusion

This study presents estimates of relative pollen productivity for 15 non-arboreal pollen taxa characteristic of the alpine meadow region of the northeastern Tibetan Plateau based on analysis of pollen data from surface soil samples and vegetation data collected using a standard field method. The RSAP for soil samples in alpine meadows of the northeastern Tibetan Plateau is ca. 200 m, which is much smaller than a previous estimate (2200 m) for the alpine meadow - alpine steppe region in the eastern and central Tibetan Plateau (Wang and Herzschuh 2011) for lake basins. This difference can be attributed to differences in site type, vegetation structure, vegetation survey methods, and taxa included in calculation.

The taxa can be divided into 3 groups, those with high RPP_{Cyp} (> 1.68 ; *Thalictrum*, *Artemisia*, Caryophyllaceae, Chenopodiaceae and *Plantago*), moderate RPP_{Cyp} (0.42 - 0.62; *Taraxacum*-type, Apiaceae, *Polygonum* and *Aster*-type), and low RPP_{Cyp} (< 0.4 ; Gentianaceae, *Potentilla*, Brassicaceae, *Saussurea*-type and Poaceae). RPP estimates for *Artemisia*, Chenopodiaceae, Cyperaceae, Poaceae are different from those reported by Wang & Herzschuh (2011) for the Tibetan Plateau, and RPPs for the other 11 taxa are presented for the first time in the Tibetan Plateau. The RPP estimates of this study are different from those reported from other studies in China, although some common characteristics can be seen. This shows the necessity of conducting RPP estimation in different vegetation biomes, rather than assuming values are constant between biomes. The RPP estimates produced by this study form the basis for future work using model-based land cover reconstruction methods (e.g. Landscape Reconstruction Algorithm, Multiple Scenario Approach) in the Tibetan Plateau.

Acknowledgements

The authors wish to thank Graham Ferrier and Rodney M. Forster (University of Hull, UK) for their help with constructing the zone C landcover map, Yiman Fang (University of Hull, UK) for her helpful discussions, Furong Li (Linnaeus University, Sweden) for her helpful suggestions on fieldwork, Hanfei Yang and Rongwei Geng (Institute of Geographic Sciences and Natural Resources Research, China) for their assistance with fieldwork. This research was supported by the National Natural Science Foundation of China (Grant Nos. 41671202, 41690113, 41471169, 41630753, 41401227), the National Key Research and Development Program of China (Grant No. 2016YFA0600501), and the Strategic Priority Research Program of Chinese Academy of Sciences (Grant No. XDA20070101).

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1 **Figure legends**

2 **Fig. 1** Maps showing (a) the locations of this study and previous studies in China, (b)
3 location of sampling sites within then Zoige Basin and (c) the landcover of the study
4 area extracted from a satellite image (see text for details). Locations in map (a) refer to:
5 a. this study; b. Li et al. 2011; c. Wang and Herzsuh 2011; d. Wu et al. 2013; e. Xu et
6 al. 2014; f. Ge et al. 2015; g. Li et al. 2015; h, i, j. He et al. 2016; k, l. Han et al. 2017;
7 m. Li et al. 2017a; n. Li et al. 2017b; o, p. Zhang et al. 2017; q. Chen et al. 2019

8 **Fig. 2** Illustration of vegetation survey strategy

9 **Fig. 3** Scatter plots showing the relationships between pollen proportion and distance
10 weighted plant abundance to 3000 m for main pollen taxa in the Zoige Basin,
11 northeastern Tibetan Plateau

12 **Fig. 4** Pollen spectra of the 30 surface soil samples from alpine meadows of the Zoige
13 Basin, northeastern Tibetan Plateau

14 **Fig. 5** Plots of the likelihood function scores calculated using three ERV sub-models
15 and three distance weighting methods for plant abundance. a) Prentice-Sutton method;
16 b) $1/d$ weighting; c) $1/d^2$ weighting

17 **Fig. 6** Relative pollen productivity estimates and errors for 15 selected taxa in alpine
18 meadows of the northeastern Tibetan Plateau using plant cover data weighted by
19 Prentice-Sutton method and ERV sub-model 1 & 2

Figure 1

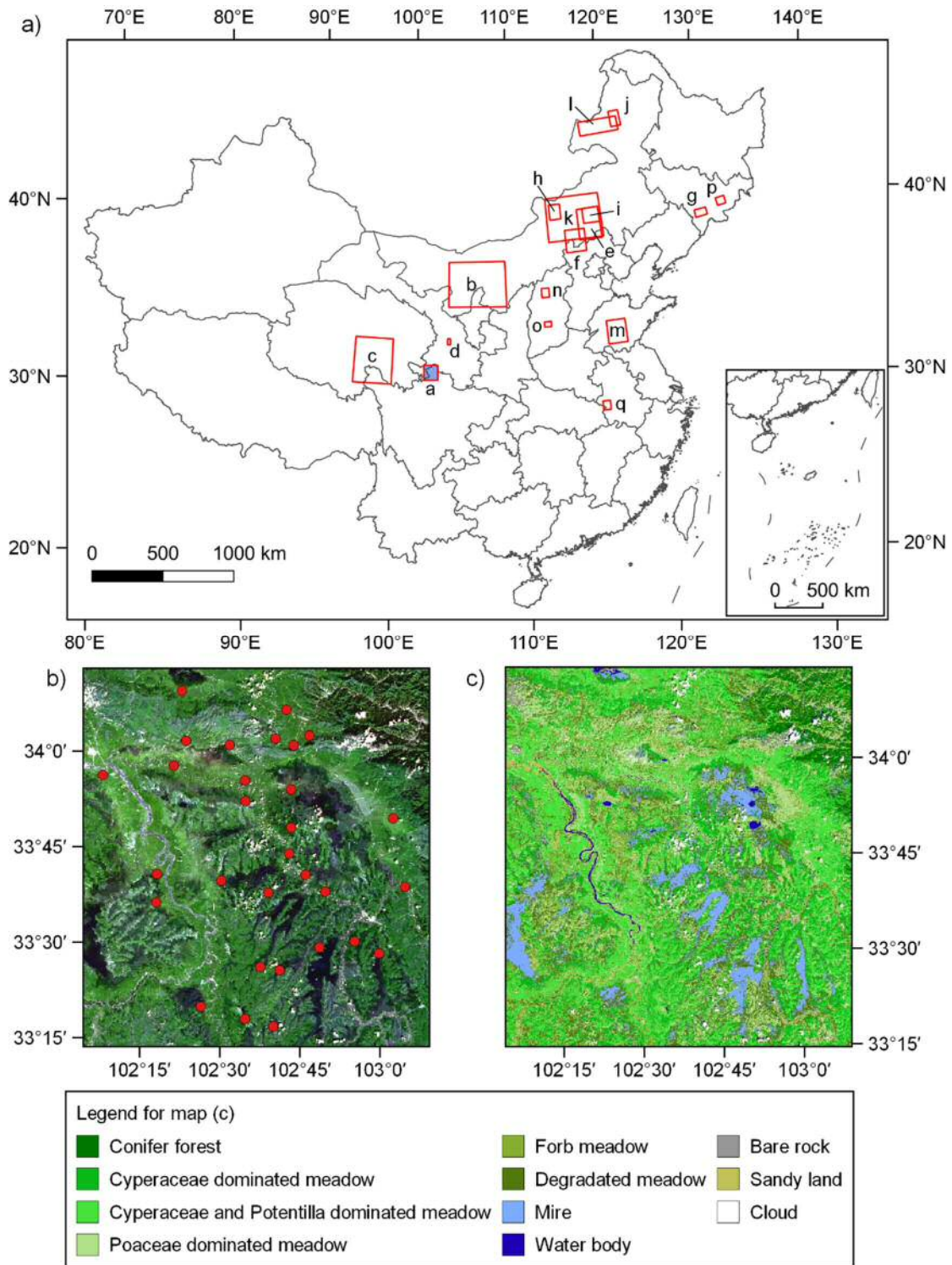


Figure 2

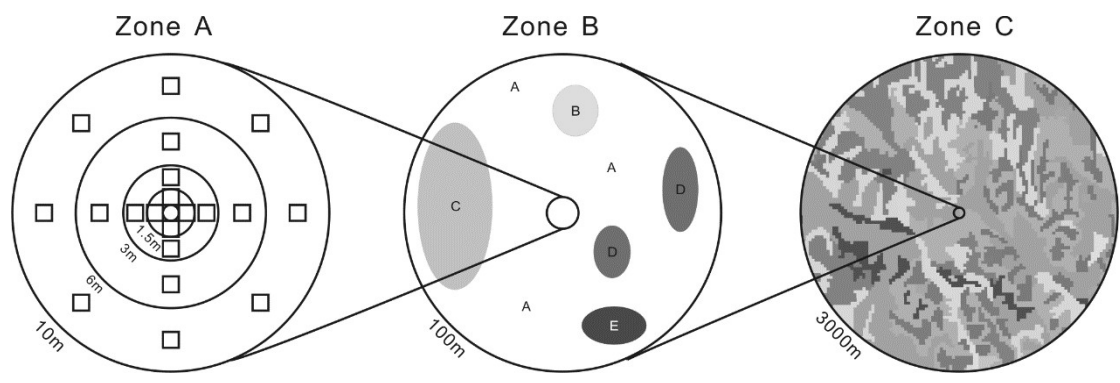


Figure 3

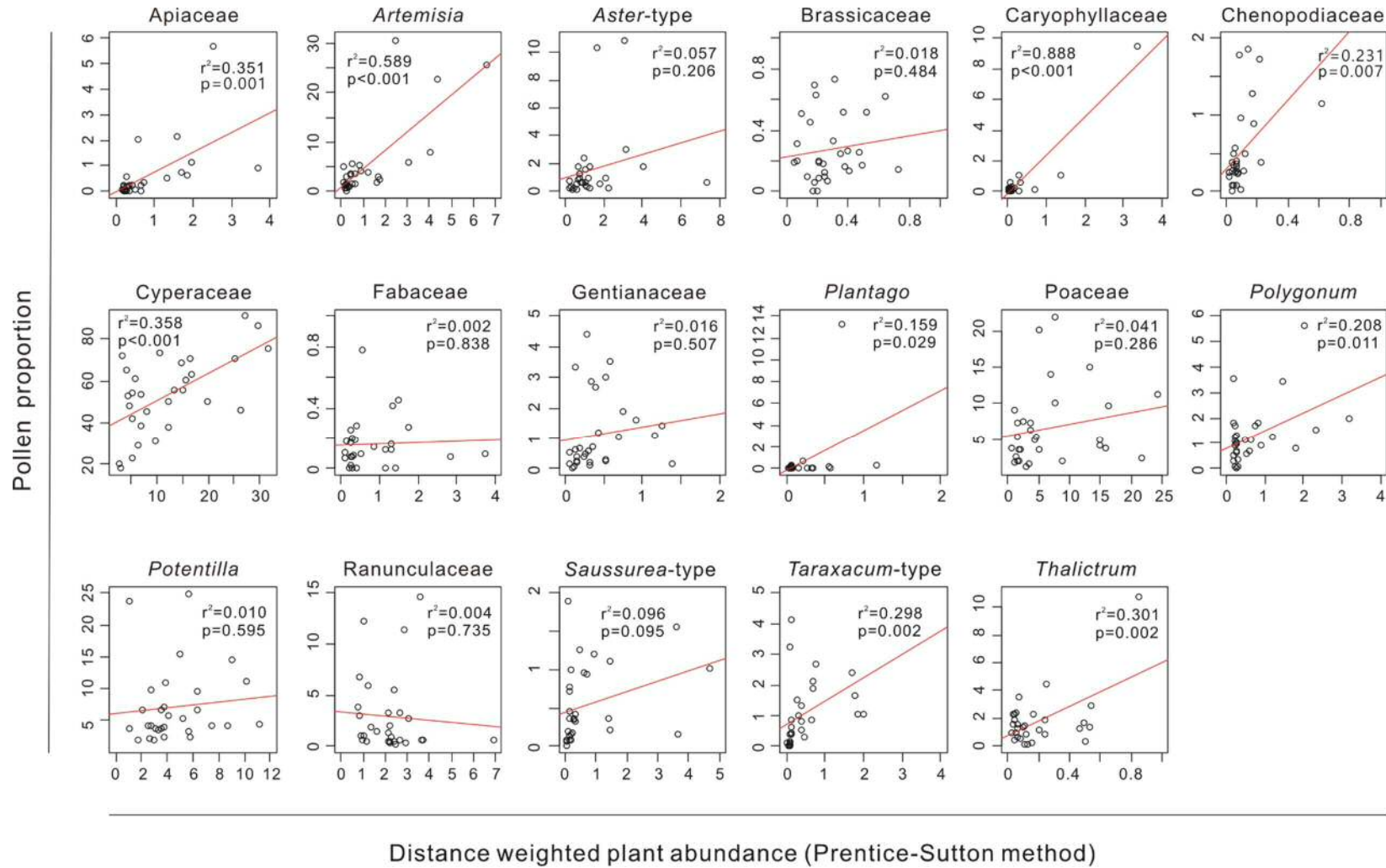


Figure 4

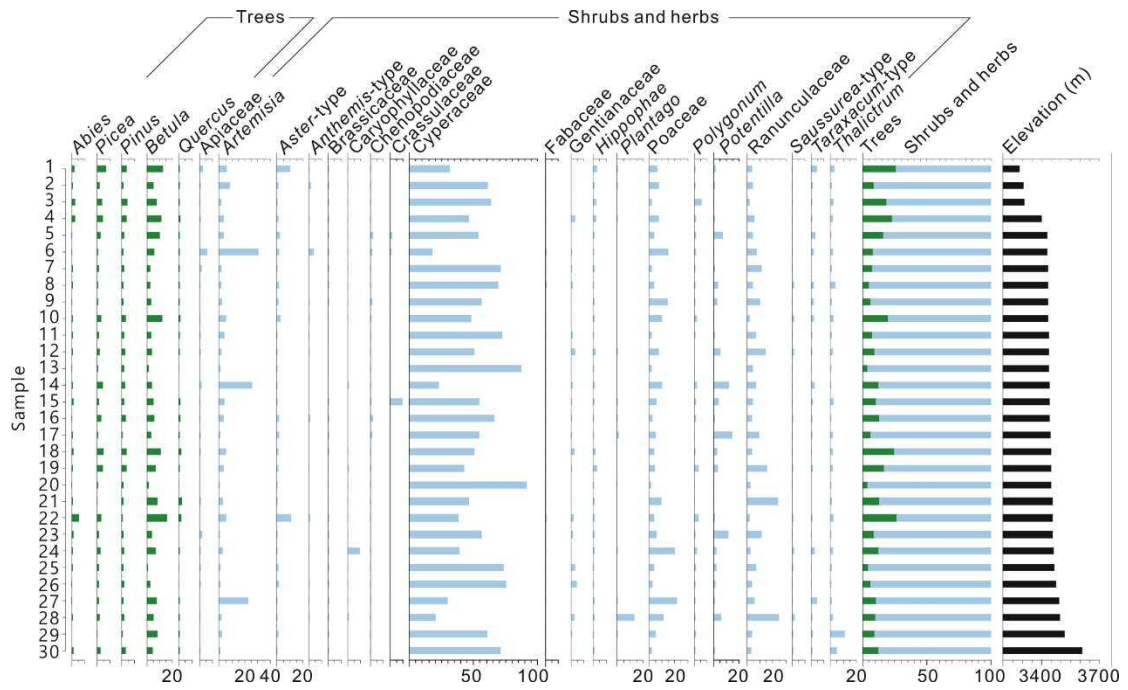


Figure 5

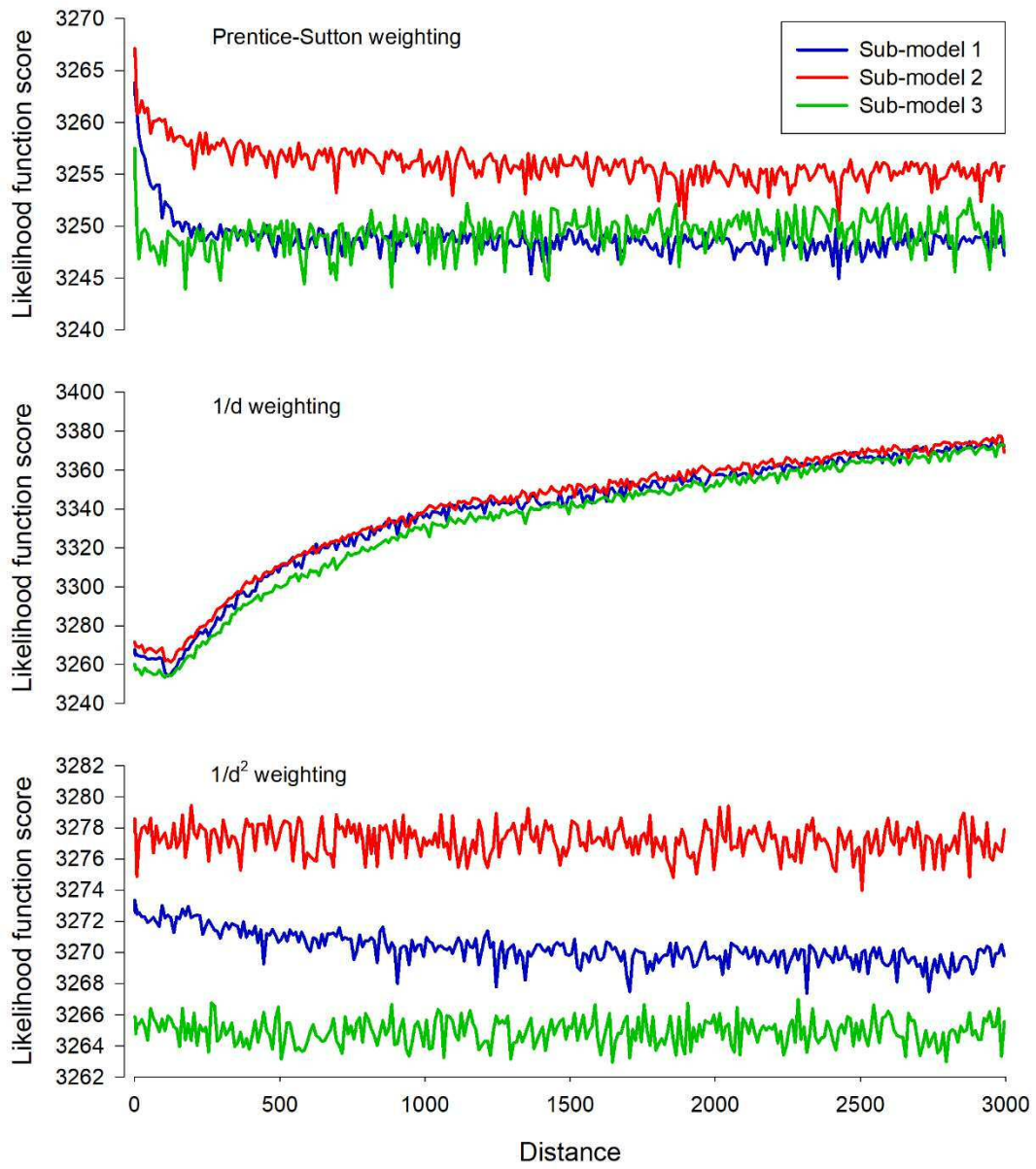
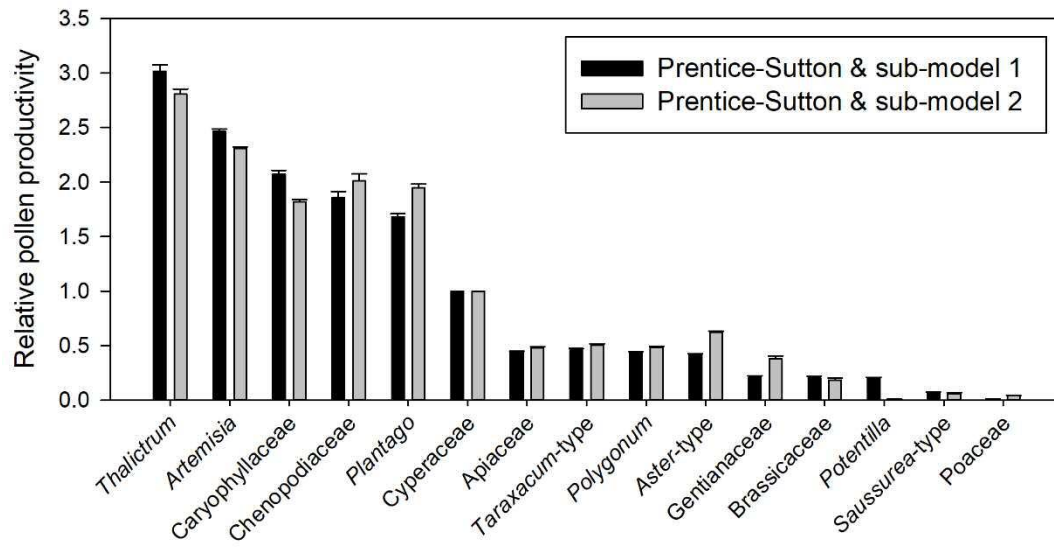
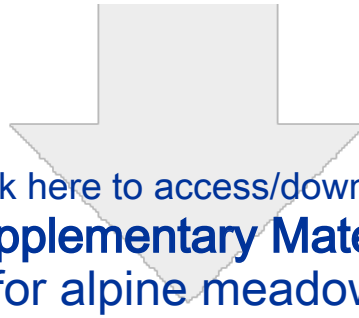


Figure 6





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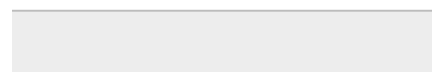


Table 1 Location of the sampling sites in the Zoige Basin, northeastern Tibetan Plateau

Sample No.	Latitude (N)	Longitude (E)	Elevation(m)
ZB1	34°03'21.29"	102°45'31.42"	3283
ZB2	34°01'45.40"	102°42'34.93"	3305
ZB3	34°07'19.49"	102°41'5.62"	3310
ZB4	34°02'46.57"	102°39'8.82"	3401
ZB5	33°54'49.40"	102°42'17.03"	3428
ZB6	33°58'07.60"	102°20'03.59"	3430
ZB7	33°48'47.66"	102°42'27.48"	3433
ZB8	33°56'20.01"	102°06'41.30"	3434
ZB9	33°20'21.28"	102°26'16.74"	3434
ZB10	33°56'03.99"	102°33'33.60"	3434
ZB11	33°38'51.81"	102°49'09.70"	3436
ZB12	33°44'42.94"	102°42'11.89"	3436
ZB13	33°38'29.97"	102°38'26.03"	3438
ZB14	33°41'26.82"	102°45'22.84"	3439
ZB15	33°40'13.99"	102°29'32.22"	3441
ZB16	33°36'33.99"	102°17'24.26"	3442
ZB17	33°41'01.00"	102°17'24.06"	3444
ZB18	33°29'18.78"	102°59'32.08"	3447
ZB19	33°52'48.90"	102°33'44.41"	3448
ZB20	33°30'3.87"	102°48'16.34"	3449
ZB21	33°26'21.80"	102°40'54.37"	3458
ZB22	34°01'35.00"	102°30'30.10"	3458
ZB23	33°31'08.09"	102°54'51.93"	3458
ZB24	33°39'52.08"	103°04'07.89"	3460
ZB25	33°18'35.34"	102°34'36.16"	3467
ZB26	33°26'48.21"	102°37'15.77"	3472
ZB27	34°09'55.33"	102°21'13.08"	3492
ZB28	33°17'29.54"	102°39'57.09"	3496
ZB29	34°02'03.36"	102°22'14.82"	3520
ZB30	33°50'36.24"	103°01'39.75"	3608

Table 2 Size and pollen fall speed of selected taxa in alpine meadows of the Tibetan Plateau

	Diameter / short, long axis of pollen (um)	Pollen fall speed (m/s)	Published pollen fall speed (m/s)*
Apiaceae	13.30, 27.51	0.011	
<i>Artemisia</i>	20.17, 20.87	0.013	0.007 - 0.021
<i>Aster</i> -type	21.86, 24.04	0.016	
Brassicaceae	18.17, 25.31	0.014	0.003 - 0.02
Caryophyllaceae	13.41	0.022	0.022 - 0.039
Chenopodiaceae	11.93	0.017	0.009 - 0.027
Cyperaceae	28.31, 33.19	0.028	0.014 - 0.037
Fabaceae	17.82, 23.39	0.013	0.012 - 0.022
Gentianaceae	25.92, 26.10	0.020	
<i>Plantago</i>	10.50	0.013	
Poaceae	15.25	0.028	0.016 - 0.035
<i>Polygonum</i>	25.43, 36.49	0.028	0.019 - 0.019
<i>Potentilla</i>	19.77, 22.61	0.014	0.007 - 0.012
Ranunculaceae	21.18, 23.86	0.015	0.007 - 0.007
<i>Saussurea</i> -type	38.81, 39.41	0.046	
<i>Taraxacum</i> -type	32.18, 35.91	0.035	
<i>Thalictrum</i>	10.24	0.013	0.007 - 0.013

* Refer to the synthesis of Li et al. (2018) with an update from Chen et al. (2019)

Table 3 Relative pollen productivity (RPP) estimates for 15 selected taxa in alpine meadows of the northeastern Tibetan Plateau

	Prentice-Sutton & sub-model 1		Prentice-Sutton & sub-model 2	
	RPP	sd	RPP	sd
<i>Thalictrum</i>	3.02	0.06	2.81	0.05
<i>Artemisia</i>	2.47	0.02	2.31	0.01
Caryophyllaceae	2.07	0.04	1.82	0.02
Chenopodiaceae	1.86	0.05	2.01	0.06
<i>Plantago</i>	1.68	0.03	1.95	0.04
Cyperaceae	1	0	1	0
<i>Taraxacum</i> -type	0.46	0.01	0.51	0.01
Apiaceae	0.44	0.01	0.48	0.01
<i>Polygonum</i>	0.43	0.01	0.48	0.01
<i>Aster</i> -type	0.42	0.01	0.62	0.01
Gentianaceae	0.21	0.02	0.38	0.02
<i>Potentilla</i>	0.21	0.003	0.004	0.007
Brassicaceae	0.20	0.02	0.18	0.02
<i>Saussurea</i> -type	0.07	0.00	0.06	0.01
Poaceae	0.01	0.001	0.04	0.003

Table 4 Comparison of the relevant source area of pollen (RSAP) estimated in this study and previous research studies

	vegetation	Location	sample	RSAP
This study	alpine meadow	northeastern Tibet Plateau	soil	200
China				
Wang and Herzs Schuh 2011	alpine steppe and alpine meadow	central and northeastern Tibet Plateau	lake	2200
Wu et al. 2013	warm temperate deciduous broad-leaved forest, mixed conifer and deciduous broad-leaved forest, steppe	northwestern China	moss	1000
Xu et al. 2014	typical steppe and woodland	northern China	moss	1000
Ge et al. 2015	steppe	northern China	soil or moss	2000-2700
Li et al. 2015	temperate mixed conifer and deciduous broad-leaved forest, deciduous broad-leaved forest	northeastern China	moss	2000-2500
He et al. 2016 (Hulunbeier)	forest-steppe	northern China	pollen trap	20
He et al. 2016 (Xilinhaote)	typical-steppe	northern China	pollen trap	9
He et al. 2016 (Sunitezuoqi)	desert-steppe	northern China	pollen trap	8
Han et al. 2017	forest steppe ecotone	northern China	lake	1600
Li et al. 2017a	cultural landscape	eastern China	moss	92-173
Li et al. 2017b	forest steppe ecotone	northern China	soil or moss	600
Zhang et al. 2017 (Changbai)	temperate mixed conifer and deciduous broad-leaved forest	northeastern China	moss	1000
Zhang et al. 2017 (Taiyue)	warm temperate deciduous broad-leaved forest	northern China	moss	2000
Chen et al. 2019	subtropical evergreen and deciduous broad-leaved mixed forest	eastern China	moss	340
Other parts of the world				
Calcote 1995 (Sylvania)	forest	northern America	moss and soil	50
Calcote 1995 (Wisconsin)	forest	northern America	moss and soil	70-80
Bunting 2003	heath, woodland, grass	northwestern	moss	2

	land	Scotland		
Broström et al. 2004	cultivated land (open and semi-open)	southern Sweden	moss	400
Nielson & Sugita 2005	various vegetation	Denmark	lake	1700-2360
Bunting et al. 2005	woodland and wetland	southeastern UK	moss	50-150
Räsänen et al. 2007	boreal forest	Finland	moss	1000
Soepboer et al. 2007	agricultural land and woodland	Swiss Plateau	lake	800
Mazier et al. 2008	pasture woodland	Jura Mountain of Switzerland	moss	250-300
von Stedingk et al. 2008	forest-tundra ecotone	western-central Sweden	moss	500
Duffin & Bunting 2008	savanna	southern Africa	pond, lake	600
Poska et al. 2011	woodland and agricultural land	southern Estonia	lake	1500-2000
Abraham & Kozáková 2012	agricultural land and woodland	central Bohemia of Czech Republic	moss	1050
Matthias et al. 2012	forest	northeastern German	lake	7000
Twiddle et al. 2012	pine forest	eastern Scotland	moss	537
Commerford et al. 2013	prairie	eastern Kansas, central America	pond, lake	900-1060
Niemeyer et al. 2015	sub-arctic vegetation	northern Siberia of Russia	moss	10
			lake	25000
Baker et al. 2016	forest	Poland	moss	400
Chaput & Gajewski 2018	forest	southeastern Canada	lake	1600

Table 5 Comparison of the relative pollen productivities estimated relative to Poaceae (RPP_{Poa}) in China for the taxa represented in this study

	This study	Wang and Herzschuh, 2011	Li et al., 2011	Wu et al., 2013	Xu et al., 2014	Ge et al., 2015	He et al., 2016	He et al., 2016	He et al., 2016	Li et al., 2017a	Li et al., 2017b	Zhang et al., 2017	Zhang et al., 2017	Han et al., 2017	Chen et al., 2019
	Zoige, sub-model 2	eastern-central Tibet Plateau	Alashan*	Xinglong Mountain*	Xilinguol	Bashang	Hulunbeier*	Xilinguol	Sunitezuoqi*	Shangdong	Guancen Mountain	Changbai #	Taiyue#	Xilinguol	Ta-pieh Mountain
<i>Thalictrum</i>	67.37				2.83										
<i>Artemisia</i>	51.01	3.27	226.43	908	11.05	19.33	2.44	100	0.47	24.7	2.3	24.7	0.01	1.29	16.74
<i>Plantago</i>	43.59														
Cyperaceae	40.75	0.66		0.4	0.86	8.9	2.66	0.13	0.19	0.21		0.05	0.03	0.01	
Chenopodiaceae	37.93	5.38	71.43		5.95	21.01	10.88	205	16.85	0.18				50.49	
Caryophyllaceae	24.82									0.87					
<i>Aster</i> -type	14.77									1.26					7.53
Apiaceae	11.50														
<i>Taraxacum</i> -type	8.88									0.86					
<i>Polygonum</i>	9.92														
Gentianaceae	6.46														
Brassicaceae	2.94				7.56					0.89					
<i>Saussurea</i> -type	1.45														
Poaceae	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>Potentilla</i>	0.02				1.12	0.22									
Asteraceae					0.18	7.73	0.73	472	3.13		1			0.19	

Notes: * RPPs have been converted to values relative to Poaceae; # RPPs have been recalculated using Poaceae as reference taxon by Li et al. (2018)