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

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Abstract
A promising method of reconstructing past vegetation from pollen records uses mathematical models of the relationship between pollen and vegetation. These can be calibrated using the extended R-value (ERV) approach on datasets of modern pollen assemblages and related vegetation surveys. This study presents the results of calibrating the pollen-vegetation models for non-arboreal pollen types in alpine meadow habitats on the Tibetan Plateau. Surface soil samples were analysed for pollen and the surrounding vegetation was recorded at 30 randomly located sites in the Zoige basin, northeastern Tibetan Plateau. ERV analysis found that the most reliable results were obtained when using ERV sub-models 1 and 2, and distance-weighting the vegetation data by applying the taxon-specific Prentice–Sutton method. The relevant source area of pollen for these soil samples was found to be ca. 200 m. Relative pollen productivities (RPP) of 15 non-arboreal taxa were estimated relative to Cyperaceae (RPPCyp). The taxa can be divided into three groups according to their RPPCyp values, those with high RPPCyp values > 1.68 (Thalictrum, Artemisia, Caryophyllaceae, Chenopodiaceae and Plantago), those with moderate values (0.42–0.62) (Taraxacum-type, Apiaceae, Polygonum and Aster-type), and those with low values < 0.4 (Gentianaceae, Potentilla, Brassicaceae, Saussurea-type and Poaceae). The RPP values obtained from our study differ from those of previous studies in other parts of China, and form the basis for future reconstruction of palaeovegetation on the Tibetan Plateau through model-based methods, such as the Landscape Reconstruction Algorithm, or Multiple Scenario Approach.

Keywords Relative pollen productivity · Relevant source area of pollen · Alpine meadow · ERV approach · Tibetan Plateau

Introduction

Pollen-vegetation model

Pollen analysis is one of the key tools available for understanding past vegetation, climate and ecosystems (for example, 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 and understandable relationship between the amounts of particular pollen types preserved in a sedimentary record and the amounts of plants corresponding to those pollen types in the landscape around the sediment site. However, the relationship between the percentages of pollen and the plants producing it 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 cover.
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), and then applies it to past pollen values to reconstruct past vegetation. An R-value is calculated as the ratio between pollen percentage and vegetation cover 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. Andersen (1970) modified the approach to include a background pollen term, developing a model suitable for situations where independent data were available, for instance pollen influx in pollen grains per unit area, rather than pollen percentages. 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 receive more pollen from plants growing close by than from further away, therefore vegetation cover 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 is transported by wind above the vegetation canopy, and he 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 type of 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 (Sugita 2007a, b; Trondman et al. 2015; Bunting et al. 2018). It can be written in a simplified linear form as:

\[ y_{i,k} = \alpha_i x_{i,k} + \omega_i \]

where \( y_{i,k} \) is pollen loading of taxon \( i \) at site \( k \); \( \alpha_i \) is the pollen productivity of taxon \( i \); \( x_{i,k} \) is plant abundance of taxon \( i \) around site \( k \) distance-weighted using the Sutton term or another model; \( \omega_i \) is background pollen of taxon \( i \).

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

**Taxon-specific parameters for pollen-based vegetation reconstruction**

In order to apply the ERV model to reconstruction of past vegetation abundance, the two taxon-specific parameters of the Prentice–Sugita model, pollen productivity \( (\alpha_i) \) and background pollen \( (\omega_i) \), need to be calculated. Where absolute data on both pollen, such as from the long-term monitoring record of a pollen trap, and the surrounding vegetation are available, the absolute pollen productivity \( (\text{APP}) \) can be estimated using a linear regression method (Sjögren et al. 2008, 2015; Sugita et al. 2010). However, in most cases only percentage pollen data are available. In order to estimate these parameters from percentage data, Parsons and Prentice (1981) proposed an iterative approach, maximum likelihood estimation, using the ERV model (usually referred to as the ERV approach or method). In this case, pollen productivity is estimated in a relative term (relative pollen productivity, RPP) by first deciding upon a reference taxon whose RPP is defined as 1. The RSAP (source area) can be estimated by analyzing the Likelihood Function Scores produced as part of the ERV approach.

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

Relative pollen productivity (RPP) is usually assumed to be a constant over time within a given geographical region, but it can vary between regions due to variations in the particular plants making up a given pollen taxon or pollen type. Comparative studies show wide variation in published estimates of pollen productivity and background (Broström et al. 2008; Mazier et al. 2012; Li et al. 2018), which may relate to methodological differences, but may also show that the assumption of a constant RPP is not valid, with variations between regions due to factors such as climate, soil,
vegetation structure and land use/landscape management (Broström et al. 2008). Bunting et al. (2013) proposed a compromise vegetation survey method for estimation of RPP in order to minimize differences caused by methodological variation in input data.

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

There are at least 220 late Quaternary pollen records with relatively good dating and sampling resolution published from across China (summarised by Cao et al. 2013, with more sites added since), but only two studies so far have used estimated RPP values to carry out quantitative reconstructions of Holocene plant cover, on the eastern Tibetan Plateau (Wang and Herzschuh 2011) and in northern China (Xu et al. 2014). The contrast between the numbers of fossil pollen spectra and those of quantitative reconstructions can, to a large extent, be attributed to the lack of RPP values for the subtropical and temperate forests of southern, central and eastern China, the deserts of northwestern China, and the alpine/sub-alpine vegetation of the Tibetan Plateau. In this paper, we present a study of pollen-vegetation relationships from the latter.

The Tibetan Plateau is the highest and largest plateau on earth, and it influences both global climate and the intensity of the Asian monsoon (Kutzbach et al. 1989; An et al. 2001; Molnar et al. 2010; Wu et al. 2015). Wang and Herzschuh (2011) calculated RPP estimates for four major taxa there. Artemisia, Chenopodiaceae, Cyperaceae and Poaceae, and used these values to reconstruct the Holocene vegetation changes around four lakes in central and eastern parts of the plateau using REVEALS (Sugita 2007a). Their results suggested that alpine meadow was far more widespread on the central and northeastern Tibetan Plateau during the Holocene than previous studies had shown. This paper presents results of an investigation into pollen-vegetation relationships in alpine meadow plant communities of the northeastern Tibetan Plateau, in order to better understand the pollen signals of these vegetation types and to obtain RPP estimates for more taxa for future reconstructions of the Holocene vegetation.

Materials and methods

Study area

The alpine vegetation of the Tibetan Plateau can generally be divided into three sub-regions from southeast to northwest, a sub-alpine scrub and alpine meadow sub-region, an alpine steppe sub-region and an alpine desert sub-region (Zhang 2007). The Zoige basin in the eastern part of the sub-alpine scrub and alpine meadow sub-region was selected for this study (Fig. 1). The climate of this area is primarily controlled by the Asian monsoon. Mean annual precipitation (MAP) recorded at nearby meteorological stations was ca. 615–750 mm (1951–1980), with most precipitation falling during the period from June to September (http://data.cma.cn/site/index.html). 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 area is primarily alpine meadow and mire (Wang et al. 2002; Zhang 2007; field survey). The dominant taxa recorded are Cyperaceae (Carex, Kobresia), with significant numbers of Poaceae (Deschampsia, Elymus, Leymus, Poa, Roegneria, Stipa). The families Asteraceae (Ajania, Anaphalis, Artemisia, Cirsium, Cremanthodium, Leontopodium, Ligularia, Saussurea, Taraxacum), 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, common plants include Apiaceae (Bupleurum, Chamaeium, Heracleum, Tongoloa), Brassicaceae (Descurainia, Draba), Dipsacaceae (Morina), Caryophyllaceae (Cerastium, Dianthus), Euphorbiaceae (Euphorbia), Fabaceae (Astragalus, Oxtropis, Medicago, Tibetia), Geraniaceae (Geranium), Lamiaceae (Ajuga, Dracocephalum, Elsholtzia, Salvia, Scutellaria), Liliaceae (Allium), Plantaginaceae (Plantago), Saxifragaceae (Parnassia, Saxifraga). Thymelaeaceae (Stellera) and Valerianaceae (Nardostachys, Equisetum, Juncus and Triglochin are common on the mire. Shrublands occur in the surrounding mountain areas, mainly consisting of Caragana, Hippophae, Potentilla, Rhododendron, Salix, Sibiraea and Spiraea. To the east and south of the Zoige basin, coniferous woodland occurs primarily on north-facing slopes of mountains, dominated by Picea and Abies. Patches of Sabina and Larix woodlands occasionally occur on south-facing slopes, and occasional patches of broad-leaved deciduous woods dominated by Betula or Quercus are also found.
Site selection and sample collection

A random sampling strategy was adopted (Broström et al. 2005), placing sampling sites randomly within a ca. 100×100 km area (33°10′–34°20′ N, 102–103°15′ E) in the Zoige basin (Fig. 1). Thirty sampling sites were selected, meeting the requirement that the distance between sites should be at least 5 km in order to avoid spatial autocorrelation (Bunting et al. 2013). The 30 sites are located across an elevation range from 3,283 to 3,608 m a.s.l. (Table 1). Sample collection and vegetation surveys were carried out in July–August 2017. Moss polsters were rarely found in the study area during the field survey, so surface soil samples were used for pollen analysis. At each sampling site, several subsamples of topsoil were collected within a 1×1 m square area and then amalgamated into one sample for pollen analysis.

Pollen analysis

Pollen samples were treated following the procedures of Fægri and Iversen (1989) and Moore et al. (1991) including chemical treatments with 10% HCl, 10% NaOH, 40% HF, followed by acetolysis, sieving with a 10 μm mesh in an ultrasonic bath, and finally mounting in glycerol. Before chemical treatment, a known number of exotic Lycopodium

Fig. 1  Maps showing a, the locations of this study and previous studies in China with the inset at bottom right showing the extent of the South China Sea; b location of sampling sites within the Zoige basin, shown as red dots; c, the land cover of the study area, 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 Herzschuh (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); m, Li et al. (2017a); n, Li et al. (2017b); o, p, Zhang et al. (2017); q, Chen et al. (2019)
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″ | 3,283         |
| ZB2        | 34°01′45.40″  | 102°42′34.93″ | 3,305         |
| ZB3        | 34°07′19.49″  | 102°41′5.62″  | 3,310         |
| ZB4        | 34°02′46.57″  | 102°39′8.82″  | 3,401         |
| ZB5        | 33°54′49.40″  | 102°42′17.03″ | 3,428         |
| ZB6        | 33°58′07.60″  | 102°20′03.59″ | 3,430         |
| ZB7        | 33°48′47.66″  | 102°42′27.48″ | 3,433         |
| ZB8        | 33°56′20.01″  | 102°06′41.30″ | 3,434         |
| ZB9        | 33°20′21.28″  | 102°26′16.74″ | 3,434         |
| ZB10       | 33°56′03.99″  | 102°33′33.60″ | 3,434         |
| ZB11       | 33°38′51.81″  | 102°49′09.70″ | 3,436         |
| ZB12       | 33°44′42.94″  | 102°42′11.89″ | 3,436         |
| ZB13       | 33°38′29.97″  | 102°38′26.03″ | 3,438         |
| ZB14       | 33°41′26.82″  | 102°45′22.84″ | 3,439         |
| ZB15       | 33°40′13.99″  | 102°29′32.22″ | 3,441         |
| ZB16       | 33°36′33.99″  | 102°17′24.26″ | 3,442         |
| ZB17       | 33°41′01.00″  | 102°17′24.06″ | 3,444         |
| ZB18       | 33°29′18.78″  | 102°59′32.08″ | 3,447         |
| ZB19       | 33°52′48.90″  | 102°33′44.41″ | 3,448         |
| ZB20       | 33°30′3.87″   | 102°48′16.34″ | 3,449         |
| ZB21       | 33°26′21.80″  | 102°40′54.37″ | 3,458         |
| ZB22       | 34°01′35.00″  | 102°30′30.10″ | 3,458         |
| ZB23       | 33°31′08.09″  | 102°54′5.19″  | 3,458         |
| ZB24       | 33°39′52.08″  | 103°04′07.89″ | 3,460         |
| ZB25       | 33°18′35.34″  | 102°34′36.16″ | 3,467         |
| ZB26       | 33°26′48.21″  | 102°37′15.77″ | 3,472         |
| ZB27       | 34°09′55.33″  | 102°21′13.08″ | 3,492         |
| ZB28       | 33°17′29.54″  | 102°39′57.09″ | 3,496         |
| ZB29       | 34°02′03.36″  | 102°22′14.82″ | 3,520         |
| ZB30       | 33°50′36.24″  | 103°01′39.75″ | 3,608         |

Vegetation data collection

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

Zone A (radius 0–10 m). A total of 21 1 × 1 m quadrats were surveyed in this zone, including a central one around the sampling point and 20 quadrats radiating outwards at 1, 2.25, 4.5 and 8 m from the centre in four directions, north, south, east and west. Quadrats were also placed 8 m from the centre to the northeast, southeast, southwest and northwest (Fig. 2). The percentage cover of each plant taxon was visually estimated and recorded for each quadrat.

Zone B (radius 10–100 m). The distribution of plant communities in this zone was mapped in the field (Fig. 2, Zone B, A–E). Boundaries between the communities were established by walking along 12 radial transects from the sampling point to 100 m, and visually defining the vegetation boundary lines with the help of a hand-held GPS. Four randomly located quadrats were surveyed in each community. A 1 × 1 m quadrat was used throughout the whole field survey, since all involved communities are open ones.

Fig. 2 Illustration of vegetation survey strategy, left to right. Zone A shows the arrangement of the 1 × 1 m quadrats within a 10 m radius; Zone B shows the distribution of main plant communities within a 100 m radius in which A, B, C, D, and E represent different kinds of communities; Zone C shows the land cover within a radius up to 3,000 m, and grey areas indicate various plant communities in the same shades as in Zone B and within a radius of > 100 m, from the satellite map of land cover.
Zone C (radius > 100 m). The vegetation data in this zone are from a land cover map, which was created at a 10 m resolution with satellite images from Sentinel-2 (https://scihub.copernicus.eu/). The vegetation areas were decided with the maximum likelihood classification procedures in ArcMap v. 10.5.1. Plant cover data was collected from these maps within a 3,000 m radius of each sampling site, since none of the published studies suggested a source area (RSAP) more than 3,000 m away for herb-dominated vegetation in China (Li et al. 2018). Plant taxa composition in each land cover type was estimated from the field vegetation survey data collected from zones A and B.

ERV analysis

The standard working practice is that for a dataset of 2n samples, analysis should include no more than n target taxa in order to reduce the standard deviations of pollen productivity (Soepboer et al. 2007; Sugita 2007b). Therefore, 15 pollen taxa were selected for ERV (extended R-value) analysis to estimate the relative pollen productivities (RPP) and relevant source areas of pollen (RSAP). These taxa were chosen on the basis that they were found in many samples with a range of values in both the soil pollen assemblages and vegetation data, and because of observed relationships between pollen proportion and distance-weighted plant abundance (Fig. 3). Therefore Ranunculaceae which showed a negative relationship between pollen and vegetation and Fabaceae (almost no relationship) were not selected, although they represented significant proportions of the pollen assemblages and/or vegetation. We also explored the effects of including different numbers of taxa in the ERV analysis, repeating calculations with 7, 10, 13, 15 and 17 taxa (details presented in ESM), and we concluded that the results from the analysis of the 15 taxa presented here are reliable.

Vegetation survey data were input into Survey v. 2.0.1 (Middleton, unpublished) to calculate the distance-weighted plant abundance (DWPA) for the concentric rings around the sampling points within a radius of 100 m (zones A and B). Concentric ring vegetation data of zone C (100–3,000 m radius) were collected using PolFlow v. 4.0 and PolLog v. 4.2 (Bunting and Middleton 2005) from the land cover map, in 10 m wide rings, and distance-weighted using the Prentice form of the Sutton weighting term (Sutton 1953; Prentice 1985). When using the Prentice–Sutton distance-weighting method, wind speed and pollen fall speed parameters are also required. A constant wind speed of 2.5 m/s, which approximates the mean annual wind speed in the region, was used. Pollen fall speeds of selected taxa were estimated following Stoke’s law based on their pollen sizes (Gregory 1973). To estimate pollen sizes, the diameters of spherical pollen types, and both the polar and equatorial axes of

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![Fig. 3](https://example.com/figure3.png) Scatter plots showing the relationships between pollen percentage and distance-weighted plant abundance up to 3 km for the main pollen taxa in the Zoige basin
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1 elliptical types were measured on 30 grains of each pollen taxon on pollen slides from the Zoige basin to obtain a mean value for calculation of the fall speed (Table 2). Vegetation data were also weighted using the non-taxon-specific inverse distance (1/d) and inverse squared distance (1/d²) methods for comparison with the Prentice–Sutton weighting results.

ERV analysis was carried out using PolERV v. 4.0 (Middleton unpublished). Cyperaceae was chosen as the reference taxon, since it was present in both the pollen assemblage and vegetation of all sites with the widest variations of abundance between sites (Fig. 3). All three sub-models of the ERV model were tried in the analysis. Source area (RSAP) was defined visually from the plots of likelihood function score (LFS) by identifying the distance beyond which the score approaches an asymptote, a line that the LFS curve continually approaches but never meets. The productivity (RPP) of each taxon was estimated as the average of values obtained for all distances greater than the RSAP, since the estimates beyond the RSAP should all be equally good (Sugita 1994). Its error was calculated following the principle of error propagation (Taylor 1997), so where Z = k(A + B + C) and k is a constant, the error on Z can be calculated as

\[
\Delta Z = k \sqrt{(\Delta A)^2 + (\Delta B)^2 + (\Delta C)^2}
\]

Results

Pollen assemblages

The surface pollen assemblages from the Zoige basin yielded 63 pollen taxa, consisting of 47 non-arboreal and 16 arboreal types (Fig. 4). The relative abundance of non-arboreal pollen ranged from 73.2 to 96.2%, among which Cyperaceae was the dominant element (relative abundance 18–91%), along with Artemisia (0.2–30.5%), Poaceae (1.2–21.9%), Potentilla (0.2–14.6%) and Ranunculaceae (2–24.8%). Pollen from the Asteraceae family, Aster-type (0.1–10.8%), Saussurea-type (0–1.9%)

| Species            | Diameter/short, long axis of pollen (µm) | Pollen fall speed (m/s) | Published pollen fall speed (m/s)a |
|--------------------|------------------------------------------|-------------------------|-----------------------------------|
| Apiaceae           | 13.30, 27.51                             | 0.011                   |                                   |
| Artemisia          | 20.17, 20.87                             | 0.013                   | 0.007–0.021                       |
| Aster-type         | 21.86, 24.04                             | 0.016                   |                                   |
| Brassicaceae       | 18.17, 25.31                             | 0.014                   | 0.003–0.02                       |
| Caryophyllaceae    | 26.82                                    | 0.022                   | 0.022–0.039                      |
| Chenopodiaceae     | 23.85                                    | 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                   |                                   |
| Plantago           | 21.01                                    | 0.013                   |                                   |
| Poaceae            | 30.50                                    | 0.028                   | 0.016–0.035                      |
| Polygonum          | 25.43, 36.49                             | 0.028                   | 0.019–0.019                      |
| Potentilla         | 19.77, 22.61                             | 0.014                   | 0.007–0.012                      |
| Ranunculaceae      | 21.18, 23.86                             | 0.015                   | 0.007–0.007                      |
| Saussurea-type     | 38.81, 39.41                             | 0.046                   |                                   |
| Taraxacum-type     | 32.18, 35.91                             | 0.035                   |                                   |
| Thalictrum         | 20.49                                    | 0.013                   | 0.007–0.013                      |

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

![Fig. 4 Pollen spectra of the 30 surface soil samples from alpine meadows of the Zoige basin](image-url)
and *Taraxacum*-type (0–4.3%), as well as Gentianaceae (1.1–4.4%), *Hippophae* (0.2–2.9%), *Polygonum* (0–5.6%) and *Thalictrum* (0.2–10.8%) were commonly found. Small amounts of Chenopodiaceae (0–1.9%) and Fabaceae (0–0.8%) were frequent. Caryophyllaceae (0–9.4%), Crassulaceae (0–9.4%) and *Plantago* (0–13.2%) only occasionally occurred in large amounts. Tree 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%) and *Quercus* (0–1.9%) were the most important.

**Results of ERV analysis**

The results of extended R-value (ERV) analysis showed that likelihood function scores declined sharply within the first 200 m when vegetation data were weighted using the 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, and then showed 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 used for further discussion, and the RSAP (source area) is identified as 200 m.

The RPPs (pollen productivities) of the 15 selected taxa were estimated using ERV sub-models 1 and 2 with the Prentice–Sutton distance-weighting method (Fig. 6, Table 3). Results using the two sub-models are not substantially different, although the rank order of the mean RPP values is not exactly the same. RPP relative to Cyperaceae, called RPP_Cyp values, for *Thalictrum* are the highest with both sub-models, followed by *Artemisia*. Caryophyllaceae, Chenopodiaceae and *Plantago*, which also have high RPP_Cyp values using both sub-models, but their rank order differs. The value for Caryophyllaceae is higher than those for Chenopodiaceae and *Plantago* using sub-model 1, whilst Chenopodiaceae and *Plantago* have higher RPP_Cyp than Caryophyllaceae using sub-model 2. Values for *Taraxacum*-type, Apiaceae, *Polygonum* and *Aster*-type are around 0.5 using both sub-models, and sub-model 2 always yield higher values. Gentianaceae also has a higher RPP_Cyp value from sub-model 2 than sub-model 1, but it never exceeds 0.38 in either case. The remaining four taxa have RPP_Cyp values less than 0.21, which suggests that they are under-represented in the pollen record. Values for Brassicaceae are the highest in this group. Results from sub-model 1 produce higher values for *Potentilla* than that from sub-model 2. Sub-models 1 and 2 produce similar RPP_Cyp values for *Saussurea*-type. Values

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**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. Distances are from the sampling site.

**Fig. 6** Relative pollen productivity estimates and errors for 15 selected taxa, using plant cover data weighted by the Prentice–Sutton method and ERV sub-models 1 and 2.
for Poaceae using both sub-models are very low, while that using sub-model 2 is higher.

ERV analyses with different numbers of taxa indicated that the Prentice–Sutton method of distance-weighting vegetation produced the most coherent likelihood function score plots for pollen productivity. The “best” ERV sub-model changed, depending on how many taxa were included in the calculations, but there was little difference in overall trends (ESM Fig. 1). The rank order of RPP values generally remained the same no matter how many taxa were included, although the actual values changed, appearing to decrease when fewer taxa were included (ESM Fig. 2).

**Discussion**

**Relevant source area of pollen in alpine meadow**

The plots of likelihood function scores against distance indicate that the RSAP for soil samples from pseudobasins ca. 0.5 m in radius in alpine meadows on the northeastern Tibetan Plateau is ca. 200 m when using plant cover data weighted by the Prentice–Sutton method (Fig. 5a). Previous RSAP estimates for the alpine meadow and alpine steppe region on the eastern and central Tibetan Plateau were around 2,200 m, but these were calculated for surface samples from lake basins with radii of ca. 100 m (Wang and Herzschuh 2011). This difference is expected, given the difference in site types (Sugita 1994).

Other comparisons of surface vegetation samples versus those from lakes include studies on the transition (ecotone) between forest and steppe biomes in northern China where the moss polster RSAP was 600 m (Li et al. 2017b), while that from lake sediments with an average radius ca. 400 m was 1,600 m (Han et al. 2017). In sub-arctic vegetation in northern Siberia, moss polsters had an RSAP around 10 m and lakes in excess of 25 km (Niemeyer et al. 2015).

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

In this study, vegetation within 100 m radius of each sampling site was surveyed by using a detailed scheme (see section on “Vegetation data collection”), and the vegetation map beyond 100 m radius is derived from high resolution satellite images with a 10 m grid. In contrast, previous research on the eastern and central Tibetan Plateau used vegetation data from the 1:1,000,000 vegetation map of China, so the size of the patches and resolution of vegetation data is also smaller in this study (Wang and Herzschuh 2011). This could also lead to a smaller RSAP.

Other factors can also influence the estimated RSAP, such as the particular 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 found that the RSAP estimated using four taxa was larger, even though the vegetation structure was constant (Nielsen and Sugita 2005). This study used 15 taxa whilst Wang and Herzschuh (2011) considered four, which may also contribute to their larger RSAP estimate. Broström et al. (2005) showed that systematic selection of sampling sites can also increase RSAP values. Published moss and soil sample studies on a cultural landscape in eastern China (Li et al. 2017a) and a steppe in northern China (He et al. 2016), which adopted random selection of sites, also yielded small RSAPs, < 200 m, while other similar studies using semi-systematic sampling methods estimated RSAP values ranging from 600 m to 2,700 m (details in Table 4).

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

| Taxon       | Prentice–Sutton sub-model 1 | Prentice–Sutton sub-model 2 |
|-------------|-----------------------------|-----------------------------|
|             | RPP  | SD   | RPP  | SD   |
| Thalictrum  | 3.02 | 0.06 | 2.81 | 0.05 |
| Artemisia   | 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 |
| Plantago    | 1.68 | 0.03 | 1.95 | 0.04 |
| Cyperaceae  | 1.0  | 0.0  | 1.0  | 0.0  |
| Taraxacum-type | 0.46 | 0.01 | 0.51 | 0.01 |
| Apiaceae    | 0.44 | 0.01 | 0.48 | 0.01 |
| Polygonum   | 0.43 | 0.01 | 0.48 | 0.01 |
| Aster-type  | 0.42 | 0.01 | 0.62 | 0.01 |
| Gentianaceae | 0.21 | 0.02 | 0.38 | 0.02 |
| Potentilla  | 0.21 | 0.003 | 0.004 | 0.007 |
| Brassicaceae | 0.20 | 0.02 | 0.18 | 0.02 |
| Saussurea-type | 0.07 | 0.005 | 0.06 | 0.01 |
| Poaceae     | 0.01 | 0.001 | 0.04 | 0.003 |
A slightly lower wind speed of 2.5 m/s was adopted in this study than was commonly used in previous researches (usually 3 m/s), but this should not influence the estimate of RSAP markedly. For instance, Nielsen and Sugita (2005) found that the estimated RSAP remained broadly the same with wind speeds from 1 to 25 m/s. Wang and Herzschuh (2011) tested the influence of wind speed on RSAP estimates.

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

| Vegetation | Location | Sample | RSAP (m) |
|------------|----------|--------|----------|
| Alpine meadow | Northeastern Tibetan Plateau | Soil | 200 |
| Alpine steppe and alpine meadow | Central and northeastern Tibetan Plateau | Lake | 2,200 |
| Warm temperate deciduous broad-leaved forest, mixed coniferous and deciduous broad-leaved forest, steppe | Northwestern China | Moss | 1,000 |
| Typical steppe and woodland | Northern China | Moss | 1,000 |
| Steppe | Northern China | Soil or moss | 2,000–2,700 |
| Temperate mixed coniferous and deciduous broad-leaved forest, deciduous broad-leaved forest | Northwestern China | Moss | 2,000–2,500 |
| Forest steppe | Northern China | Pollen trap | 20 |
| Typical steppe | Northern China | Pollen trap | 9 |
| Desert steppe | Northern China | Pollen trap | 8 |
| Forest-steppe ecotone | Northern China | Lake | 1,600 |
| Cultural landscape | Eastern China | Moss | 92–173 |
| Forest-steppe ecotone | Northern China | Soil or moss | 600 |
| Temperate mixed coniferous and deciduous broad-leaved forest | Northeastern China | Moss | 1,000 |
| Warm temperate deciduous broad-leaved forest | Northern China | Moss | 2,000 |
| Subtropical evergreen and deciduous broad-leaved mixed forest | Eastern China | Moss | 340 |
| Forest | Northern America | Moss and soil | 50 |
| Forest | Northern America | Moss and soil | 70–80 |
| Heath, woodland, grassland | Northwestern Scotland | Moss | 2 |
| Cultivated land (open and semi-open) | Southern Sweden | Moss | 400 |
| Various vegetation | Denmark | Lake | 1,700–2,360 |
| Woodland and wetland | Southeastern UK | Moss | 50–150 |
| Boreal forest | Finland | Moss | 1,000 |
| Agricultural land and woodland | Swiss Plateau | Lake | 800 |
| Pasture woodland | Jura mountains, Switzerland | Moss | 250–300 |
| Forest-tundra ecotone | Western-central Sweden | Moss | 500 |
| Savanna | Southern Africa | Pond, lake | 600 |
| Woodland and agricultural land | Southern Estonia | Lake | 1,500–2,000 |
| Agricultural land and woodland | Central Bohemia, Czech Republic | Moss | 1,050 |
| Forest | Northeastern Germany | Lake | 7,000 |
| Pine woodland | Eastern Scotland | Moss | 537 |
| Prairie | Eastern Kansas, central US | Pond, lake | 900–1,060 |
| Sub-arctic vegetation | Northern Siberia, Russia | Moss | 10 |
| | | Lake | 25,000 |
| Forest | Poland | Moss | 400 |
| Forest | Southeastern Canada | Lake | 1,600 |
in the eastern and central Tibetan Plateau, and Ge et al. (2015) in the steppe of northern China. Both studies indicated that wind speed caused negligible variation of RSAP estimates.

Relative pollen productivities in alpine meadows

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

RPP\textsubscript{Cyp} values for the 15 taxa in alpine meadow vegetation on the northeastern Tibetan Plateau generally show comparable rank order for the two sub-models (Fig. 6). The taxa can be divided into three groups, those with high RPP\textsubscript{Cyp} values > 1.68, including Thalictrum, Artemisia, Caryophyllaceae, Chenopodiaceae and Plantago, those with moderate values (0.42–0.62), Taraxacum-type, Apiaceae, Polygonon and Aster-type, and those with low values < 0.4, including Gentianaceae, Potentilla, Brassicaceae, Saussurea-type and Poaceae. Most taxa in the moderate and low RPP\textsubscript{Cyp} groups are insect pollinated, while most taxa with high values are wind pollinated. Thalictrum, Artemisia, Caryophyllaceae, Chenopodiaceae and Plantago are only minor components of the vegetation cover in alpine meadows in our study area, but their pollen commonly occurs in surface soils, especially that of Thalictrum and Artemisia (Fig. 4). Most of the common plants in the alpine meadows are in the moderate and low RPP\textsubscript{Cyp} groups, such as Apiaceae, various Asteraceae, Gentianaceae, Polygonon, Potentilla, etc.

In order to compare these findings with previous studies, RPPs for the studied taxa have been recalculated to values relative to Poaceae (RPP\textsubscript{Poa}) (Table 5). Values estimated using ERV sub-model 2 are used for further comparison (see ESM for further discussion).

Previous research on the Tibetan Plateau produced RPP\textsubscript{Poa} estimates which are quite different from our findings (Table 5; Wang and Herzschuh 2011). Nevertheless, Chenopodiaceae and Artemisia showed high productivity values in both this study and others. The RPP\textsubscript{Poa} estimate for Cyperaceae from Wang and Herzschuh (2011) was close to 1, but in our study Cyperaceae was estimated to have a pollen productivity of at least 40 times that of Poaceae. This may reflect differences in sample type between the studies. The pollen assemblages from surface soil receive more pollen from local plants and have a better ability to reflect fine-scale vegetation patterns than those from lake sediments (Sugita 1994; Zhao and Herzschuh 2009). Another possible reason is that the vegetation data from the previous study came from a map, which may have lacked details of variation in vegetation close to the lake shore, which in turn may have led to errors in estimating RPP. In addition, the area chosen for our own study was quite homogenous, but the sampling sites of Wang and Herzschuh (2011) were distributed across a much larger area, which included both alpine meadow and alpine steppe. Therefore, the same pollen taxon could have come from different plant species growing in different locations in that study, which could also have affected the RPP estimates.

The RPP\textsubscript{Poa} values presented here for alpine meadow on the Tibetan Plateau are not comparable to those from any of the previous studies in other regions (Table 5). Nevertheless, some common characteristics can be seen. Chenopodiaceae and Artemisia normally have high RPPs, with few exceptions, such as Chenopodiaceae in a cultural landscape in Shandong (0.18) (Li et al. 2017a), Artemisia in the desert-steppe of Sunitezuoqi (0.47) (He et al. 2016) and in warm temperate forest on Taiyue mountain (0.01) (Zhang et al. 2017). Previous studies mostly estimated a moderate or low RPP\textsubscript{Poa} for Cyperaceae, with values ranging from 0.01 for the forest-steppe ecotone of Inner Mongolia (Han et al. 2017) to 0.66 for alpine steppe and alpine meadow on the Tibetan Plateau (Wang and Herzschuh 2011), except the forest-steppe of Hulunbeier (2.66) (He et al. 2016) and steppe at Bashang (8.9) (Ge et al. 2015).

Thalictrum, Caryophyllaceae and Taraxacum-type have much higher RPP\textsubscript{Poa} values in the alpine meadows on the Tibetan Plateau than in other parts of China. In this study, Aster-type, Brassicaceae and Potentilla have different values when using different sub-models (ESM Fig. 4), and this is also seen in other studies. RPP\textsubscript{Poa} values of Aster-type range from 1.26 in the cultural landscape of Shandong (Li et al. 2017a) to 7.53 in subtropical forest on Ta-pieh mountain (Chen et al. 2019). Published RPP\textsubscript{Poa} values of Brassicaceae range from 0.89 for the cultural landscape of Shandong (Li et al. 2017a) to 7.56 in typical steppe at Xilinguole (Xu et al. 2014). Values of Potentilla range from 0.22 on the steppe of Bashang (Ge et al. 2015) to 1.12 on typical steppe at Xilinguole (Xu et al. 2014).

Many factors may explain these differences in RPP\textsubscript{Poa} estimates. Reviews of RPP estimates from Europe (Broström et al. 2008) and China (Li et al. 2018) have discussed these factors and divided them into two groups, methodological and environmental issues. Methodological issues include site selection strategy (random or systematic), methods of vegetation survey (quadrat survey, concentric survey, vegetation atlas, or satellite image), reference taxon selection, pollen sample types (moss polster, surface soil or lake sediment), selection of ERV sub-model, methods of distance weighting (Prentice–Sutton, 1/d, 1/d\(^2\)), etc. Environmental issues include climatic factors influencing pollen productivity (temperature) and dispersal (wind speed), landscape management (farmland, grazing land), vegetation structure,
Table 5  Comparison of the relative pollen productivities estimated relative to Poaceae (RPPPpoa) in China for the taxa represented in this study

| Table 5 | Comparison of the relative pollen productivities estimated relative to Poaceae (RPPPpoa) 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 a  | Xilinguole  | Bashang Hulunbeier a  | Xilinguole b  | Sunitezuqi b  | Shangdong  | Guancen Mountain  | Changbai b  | Taiyue b  | Xilinguole-Hulunbeier  | Ta-pieh Mountain  |
| Thalictrum  | 67.37  | 2.83  | 51.01  | 0.66  | 10.05  | 2.44  | 0.47  | 24.7  | 2.3  | 21.53  | 0.01  | 1.29  | 16.74  |
| Artemisia  | 43.59  | 0.4  | 226.43  | 0.4  | 908  | 19.33  | 21.5  | 8.9  | 0.13  | 0.19  | 0.21  | 0.05  | 0.03  | 0.01  |
| Cyperaceae  | 37.93  | 5.38  | 71.43  | 5.95  | 21.01  | 10.88  | 205  | 16.85  | 0.18  | 50.49  |
| Chenopodiaceae  | 24.82  | 0.87  | 9.92  | 8.88  | 7.53  | 1.26  | 0.86  |
| Caryophyllaceae  | 14.77  | 11.50  | 2.94  | 7.56  | 0.39  |
| Aster-type  | 6.46  | 2.94  | 7.56  | 0.39  |
| Apiaceae  | 9.92  | 6.46  | 2.94  | 7.56  | 0.39  |
| Taraxacum-type  | 2.94  | 0.02  | 1.12  | 0.22  |
| Polygnum  | 2.94  | 0.02  | 1.12  | 0.22  |
| Gentianaceae  | 2.94  | 0.02  | 1.12  | 0.22  |
| Brassicaceae  | 2.94  | 0.02  | 1.12  | 0.22  |
| Saussurea-type  | 1.45  | 0.02  | 1.12  | 0.22  |
| Poaceae  | 1  | 0.18  | 7.73  | 0.73  | 0.02  | 0.19  |
| Potentilla  | 0.02  | 1.12  | 0.22  | 0.02  | 1.12  | 0.22  |
| Asteraceae  | 0.02  | 1.12  | 0.22  | 0.02  | 1.12  | 0.22  |

aRPPs have been converted to values relative to Poaceae; bRPPs have been recalculated using Poaceae as reference taxon by Li et al. (2018)
taxon composition, etc. All of these factors could contribute to the differences of RPP estimates found for the productivities of the same taxa, and some of them have been discussed above (see section ‘Relevant source area of pollen in alpine meadow’), such as pollen sample types, methods of vegetation survey and vegetation structure.

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

Implications

The estimated RSAP (source area) values indicate that non-arboreal pollen assemblages from surface soil are sensitive to changes in plant cover patterning within 200 m radius around the sampling point in our study area. Pollen records in this area typically come from peat cores taken from small basins, therefore the RSAPs of non-arboreal fossil pollen assemblages from these records should also be within about a few hundred metres. Therefore these fossil pollen data are suitable for reconstruction of local-scale vegetation dynamics such as community change in response to changing distributions of mires, or changes in forcing factors such as moisture availability, fire regime or grazing pressure.

Tree pollen makes up 3.8–26.7% of the pollen assemblages, mainly from *Betula, Picea, Pinus* and *Quercus*. Tree dominated plant communities occur only in the northeastern corner of our study area (Fig. 1c), and including trees in the ERV analysis would therefore increase the RSAP substantially. This study was designed to obtain RPPs for the meadow plant community. All of the studied sites are herb-dominated communities such as meadows and mires, and the distance between studied sites and the nearest woodland is greater than 1 km.

Of the 15 studied pollen taxa, RPPs for *Apiaceae, Gentianaceae, Plantago* and *Saussurea*-type are reported for the first time from China. In addition, values for *Aster*-type, *Brassicaceae, Caryophyllaceae, Polygonum, Potentilla, Taraxacum*-type and *Thalictrum* are reported for the first time from the Tibetan Plateau. These values can be used in two ways: in model-based quantitative reconstruction of past vegetation at the local scale in the alpine meadows of this area such as Landscape Reconstruction Algorithm (LRA) and Multiple Scenario Approach (MSA), and in simulation experiments (Sugita 1994; Broström et al. 2005; Bunting 2008; Gaillard et al. 2008) to explore the pollen representation of vegetation in a given landscape or to test the reliability of palynological hypotheses.

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

In addition, our work highlights gaps in understanding how ERV analysis can be replicated when using different subsets of a given dataset, and thus the influence of reference taxon selection and the number of target taxa on estimates of RSAP and RPP. Better understanding of these questions would also increase confidence in inter-study comparisons.

Conclusions

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 our study area indicates a source area within ca. 200 m, which is much smaller than a previous estimate of 2,200 m for lake basins in the alpine meadow and alpine steppe region on the eastern and central Tibetan Plateau (Wang and Herzschuh 2011). This difference can attributed to differences in site type, vegetation structure, vegetation survey methods and the particular taxa included in calculation.

The taxa in our study can be divided into three productivity groups, those with high $RPP_{Cyp} > 1.68$ for *Thalictrum, Artemisia*, Caryophyllaceae, Chenopodiaceae and *Plantago*, moderate values (0.42–0.62) for *Taraxacum*-type, *Apiaceae, Polygonum* and *Aster*-type, and low values <0.4 for *Gentianaceae, Potentilla, Brassicaceae, Saussurea*-type and *Poaceae*. RPP estimates for *Artemisia*, Chenopodiaceae, *Cyperaceae* and *Poaceae* are different from those reported by Wang and Herzschuh (2011) for the Tibetan Plateau, and the values for the other 11 taxa are presented for the first time for this area. The RPP estimates calculated in this study are different
from those already published 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 that values are constant between them. The RPP estimates produced by this study form the basis for future work on the Tibetan Plateau using model-based land cover reconstruction methods, for example the Landscape Reconstruction Algorithm and the Multiple Scenario Approach.

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