https://doi.org/10.5194/egusphere-2026-7103
Preprint. Discussion started: 24 November 2026
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Quantitative land-cover reconstruction in Asian temperate deserts: relative pollen productivity estimates and an RPP-based correction framework

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Abstract: Relative pollen productivity (RPP) is a key parameter in pollen-based quantitative reconstructions of past vegetation and land cover, yet dominant taxa in temperate deserts remain poorly calibrated, constraining our ability to quantify long-term land-cover dynamics in arid regions. We estimated taxon-specific RPP values for major desert plants using the Extended R-value (ERV) model, based on pollen assemblages from 60 topsoil samples and vegetation data from 1,362 quadrats in Akesai County and Ejina Banner, inland Northwest China. In Akesai, with Chenopodioideae as the reference taxon (RPP = 1), RPP values are: Nitraria (1.305 ± 0.171), Calligonum (0.913 ± 0.069), Asteraceae (0.577 ± 0.041), Ephedra (0.543 ± 0.020), Poaceae (0.337 ± 0.039), Gymnocarpos (0.197 ± 0.026), and Tamaricaceae (<0.001 ± 0.005). In Ejina, with Ephedra as the reference (RPP = 1), the corresponding values are: Calligonum (3.508 ± 0.073), Nitraria (1.125 ± 0.038), and Tamaricaceae (0.006 ± 0.025). The

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extremely low RPP of Tamaricaceae in both regions indicates strong under-representation in pollen assemblages, implying that modest increases in Tamaricaceae pollen percentages may record substantial expansion of Tamaricaceae-dominated vegetation and thus intensified desertification. Comparisons with published RPP datasets from other arid and semi-arid regions suggest that regional RPP variation is driven by plant community composition, landscape structure, and extra-local pollen input to the regional pollen background. Building on these results, we develop an RPP-based reconstruction–correction framework tailored to drylands, which adjusts conventional pollen-percentage land-cover reconstructions for differential taxon representation. In both study areas, corrected reconstructions closely approximate observed land-surface vegetation composition, providing a methodological basis for more robust quantitative reconstructions of Holocene vegetation and land-cover change in arid regions and for integrating desert biomes into large-scale pollen-based land-cover datasets used in climate and Earth system modelling.

Keywords: Temperate deserts; Extended R-value model; Relative pollen productivity; Quantitative land-cover reconstruction; Arid regions

1. Introduction

Drylands cover approximately 41% of the global land surface and support more than one-third of the world's population (Chen et al., 2024; Bernardino et al., 2025). In these water-limited ecosystems, changes in vegetation composition and cover influence evapotranspiration, carbon uptake, and surface energy partitioning (Poulter et al., 2014; Kannenberg et al., 2024; Koppa et al., 2024). Long-term reconstructions of vegetation and land cover are therefore needed to assess ecosystem responses to environmental change and their implications for land–atmosphere feedbacks (Claussen et al., 1999; Gaillard et al., 2010; Strandberg et al., 2022). However, reliable quantitative reconstructions remain scarce in dryland regions, limiting the empirical basis for evaluating climate and Earth system models.

https://doi.org/10.5194/egusphere-2026-7103
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Pollen provides an important basis for reconstructing past vegetation and land-cover change, as pollen assemblages preserve information on regional vegetation composition (Gaillard et al., 2010; Fastovich et al., 2025). However, pollen percentages do not directly represent vegetation cover because plant taxa differ in pollen production, dispersal, deposition, and preservation (Davis, 1963; Xu et al., 2016). To quantify pollen–vegetation relationships, Andersen (1970) proposed relative pollen productivity (RPP), defined as the ratio of the absolute pollen productivity of a given taxon to that of a reference taxon. Numerous studies of modern pollen–vegetation relationships and RPP estimation have since been conducted in forest, grassland, and alpine ecosystems across Europe, North America, and East Asia (Mazier et al., 2012; Xu et al., 2014; Ma et al., 2025; Sun et al., 2026). RPP estimates, combined with pollen dispersal–deposition models (Sugite, 2007), have enabled quantitative reconstructions of past vegetation and land cover at regional and continental scales (Trondman et al., 2015; Li et al., 2020; Githumbi et al., 2022; Shi et al., 2022; Dawson et al., 2025; Xiao et al., 2025).

However, reliable RPP estimates remain scarce for temperate deserts, despite their broad distribution and ecological importance across arid regions (Wieczorek and Herzschuh, 2020). Existing studies have mainly focused on mountainous and transitional ecosystems within arid regions, such as desert steppes, montane steppes, and montane forests (Li et al., 2011; Wang et al., 2021; Fang et al., 2025). Moreover, previous studies have shown that RPP values for the same plant taxon may vary markedly among vegetation types, with such variation likely driven by differences in vegetation openness, climatic conditions, and land-use intensity (Broström et al., 2008; Li et al., 2018; Sun et al., 2026). This variability challenges the transferability of estimates across ecological settings and introduces uncertainty into desert vegetation reconstructions based on parameters derived from other ecosystems. Therefore, it is necessary to establish RPP estimates for dominant taxa in temperate deserts and assess their variability among vegetation types in arid regions, as well as the potential drivers of this variation.

A further limitation is that RPP-based vegetation estimates generally represent the

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Preprint. Discussion started: 24 November 2026
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relative cover of the plant taxa rather than actual land-cover composition (Davis, 1963; Xu et al., 2016; Cheng et al., 2022; Sun et al., 2022a; Dallmeyer et al., 2023). In sparsely vegetated drylands with extensive bare ground, interpreting these relative estimates as actual vegetation cover may systematically overestimate the proportion of the landscape occupied by vegetation. Using these estimates as land-cover inputs without accounting for bare ground may consequently introduce biases into palaeoclimate and Earth system simulations (Sun et al., 2022b; Strandberg et al., 2022; Hopcroft et al., 2026). Addressing this limitation is therefore essential for reconstructing past dryland landscapes and providing reliable land-cover inputs for assessing land–atmosphere feedbacks in these simulations.

Here, we selected Akesai County and Ejina Banner in the temperate desert region of arid inland Asia as the study areas. Based on detailed field vegetation surveys and surface soil pollen analyses, we systematically evaluated modern pollen-vegetation relationships and taxon-specific pollen representation in temperate deserts, estimated the relative pollen productivity (RPP) of dominant plant taxa in temperate deserts, and compared these estimates with RPP values for major taxa from other vegetation types in arid regions to evaluate RPP variability and its potential drivers. Finally, we assessed the applicability of RPP estimates for quantitative land-cover reconstruction, providing a methodological basis for interpreting fossil pollen records and reconstructing past vegetation and land-cover change in arid regions.

2. Regional setting

Akesai County (Akesai) is located in a desert basin along the northern foothills of the Altun Mountains in northwestern China (Fig. 1a). This area has a warm-temperate continental desert climate (Ding, 2013), with mean annual temperature of 9.7 °C and average annual precipitation of only 5.1 mm (http://data.cma.cn/en). The vegetation belongs to the warm-temperate shrub and semi-shrub desert zone (Chen, 2014; Fig. 1b), with extremely sparse vegetation cover, generally below 10%. Field surveys show that the vegetation is dominated by *Gymnocarpos przewalskii* and *Sympegma regelii*,

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accompanied by xerophytic shrub and subshrub species such as *Ephedra* spp., *Nitraria tangutorum*, *Calligonum* spp., *Asterothamnus alyssoides*, and *Salsola* spp., with herbaceous taxa such as *Taraxacum* spp. and *Allium mongolicum*.

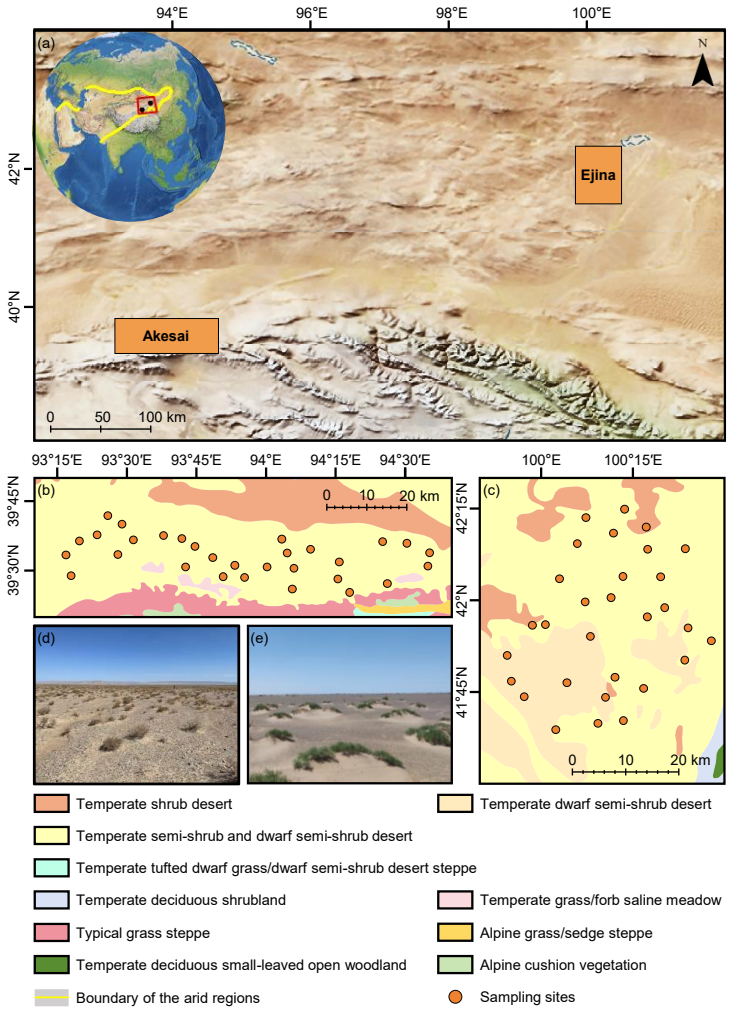


Fig. 1 Location of the study areas and distribution of the sampling sites. (a) Location of the study areas. Distribution of sampling sites and major vegetation types in (b) Akesai and (c) Ejina. (d) Communities dominated by *Gymnocarpos* and *Reaumuria soongorica* in Akesai. (e) *Calligonum* community in Ejina (taken in July 2024).

https://doi.org/10.5194/egusphere-2026-7103
Preprint. Discussion started: 24 November 2026
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Ejina Banner (Ejina) is located in the lower reaches of the Heihe River Basin, on the western Alashan Plateau of Inner Mongolia, northern China (Fig. 1a). This area has a mid-temperate continental desert climate (Ding, 2013), with mean annual temperature of 9.4 °C and average annual precipitation of only 4.1 mm (http://data.cma.cn/en). The vegetation belongs to the temperate shrub and semi-shrub desert zone (Chen, 2014; Fig. 1c), with extremely sparse vegetation cover, generally below, generally below 10%. Field surveys show that the vegetation is dominated by *Reaumuria songarica* and *Nitraria tangutorum*, accompanied by xerophytic shrub and subshrub species such as Calligonum spp., *Haloxylon ammodendron*, and *Ephedra* spp., with only scattered individuals of *Populus euphratica* occurring locally.

3. Materials and methods

3.1. Field work

To avoid the influence of collinearity on RPP estimates, we followed the field strategy proposed by Bunting et al. (2013) for sampling site selection and the vegetation surveys. Prior to fieldwork, 50 candidate sampling sites were randomly generated in each study area using ArcMap 10.8, with a minimum inter-site distance of 3 km. Based on satellite imagery, sites with substantial anthropogenic disturbance (e.g., roads, urban areas, and farmland), and 30 sampling sites were ultimately retained in each study area (Fig. 1b, c).

During July to August of 2024, sample collection and vegetation surveys were conducted in the study area. The procedures used were as follows. (i) Sample collection. Sampling locations were identified using a handheld GPS. Surface soil samples were collected at each sampling site, and the geographic coordinates and elevation were recorded. (ii) Vegetation survey. Within a 0–10 m radius, vegetation was surveyed using 1 m × 1 m quadrats. A total of 21 quadrats were established in different directions, and the projected cover of each plant species within the quadrats was recorded (Bunting et al., 2013). For the 10–100 m radius vegetation survey, the boundaries of different plant communities were first determined using a handheld GPS, and then the plant covers

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within each community was surveyed and recorded. For the vegetation beyond 100 m radius, the survey focused on community types not present within the 100 m radius (e.g., other vegetation types, roads, rivers, etc.). In total, 689 vegetation quadrats were surveyed in Akesai and 673 in Ejina.

3.2. Pollen analysis and vegetation data processing

Pollen grains were extracted using the standard HCl–NaOH–HF procedure, with 50 g of dry soil per sample in Akesai and 150 g per sample in Ejina (Fægri et al., 2001). Pollen identification was conducted under an Olympus DP74 microscope with reference to *Pollen Flora of China* (Wang, 1995), *Atlas of Quaternary Pollen and Spores in China* (Tang et al., 2020), and modern pollen extracted from plants collected in the field. More than 500 terrestrial pollen grains were identified in each sample, and pollen diagrams were plotted using *Tilia 3.0.1* (Grimm, 2019). To calculate the fall speeds of pollen (FSP), at least 100 grains were measured for each major pollen taxon (the diameter for spherical pollen, and the long- and short-axes for elliptica). The FSP of the major taxa were calculated using the Stokes and Falck methods (Gregory, 1973).

Vegetation data within the 0–10 m and 10–100 m were processed using *Vegetation Survey Manager 2.0* (Middleton, 2011). Vegetation data for the 100–3000 m range were digitized from satellite images in ArcGIS 10.8 using the maximum likelihood classification method (Li et al., 2017; Sun et al., 2019). Vegetation compositions were then assigned based on the mean species composition of each community type, calculated from three to four nearby sampling sites with similar habitat conditions (Sun et al., 2019). Vegetation diagrams were plotted using *Tilia 3.0.1* (Grimm, 2019).

3.3. ERV model

The Extended R-Value (ERV) model was applied to estimate the relative pollen productivity (RPP) and relevant source area of pollen (RSAP). This model is based on pollen dispersal models and corrects for the non-linearity between pollen percentages and vegetation percentages. As the distance from the sampling point increases, the

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correlation between pollen percentages and vegetation cover increases and eventually stabilizes. The distance is defined as the RSAP, within which the RPP values are estimated (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994; Gaillard et al., 2008). The ERV model includes three sub-models that differ in their assumptions about background pollen input and vegetation data requirements. Sub-models 1 and 3 assume that background pollen input is constant across sampling sites, whereas sub-model 2 treats background pollen loading as a function of distance-weighted surrounding vegetation. Sub-models 1 and 2 use relative vegetation cover as input data, whereas sub-model 3 requires absolute vegetation cover (Parsons and Prentice, 1981; Prentice and Parsons, 1983; Sugita, 1994).

In this study, surface soil samples were collected for pollen analysis, with the radius of the sedimentary basins being relatively small (~0.5 m). Hence, we selected the taxon-specific vegetation distance-weighting method (Prentice's model) (Prentice, 1985) and the inverse distance method (1/d model) (Prentice and Webb, 1986), both of which are suitable for small sedimentary basins. Wind speed was set to 3 m s^{-1}, broadly consistent with the modern mean annual wind speed across mainland China (Li et al., 2017). Other input parameters included FSP and vegetation data at 5 m intervals within a 1,500 m radius of each sampling site. Based on their high occurrence frequencies in both vegetation and pollen datasets, as well as the good fit between pollen and vegetation data, Chenopodioideae was selected as the reference taxon in Akesai (RPP = 1), whereas *Ephedra* was selected as the reference taxon in Ejina (RPP = 1). The ERV model was performed using *ERV. Analysis 2.5.3* (Sugita, 2017).

3.4. Statistical analysis

Davis indices were used to evaluate the representativeness of pollen taxa for the corresponding vegetation (Davis, 1984; Hjelle, 1997; Bunting, 2003; Dugerdil et al., 2025). This method uses presence–absence data from paired pollen and vegetation records to quantify pollen–vegetation correspondence within a binary analytical framework. For each pollen taxon *i*, the association index (*A*), under-representation

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index (U), and over-representation index (O) were calculated. An A value approaching 1 indicates a strong correspondence between pollen and vegetation taxon. A U value approaching 1 indicates a higher degree of underestimation of vegetation presence by that pollen taxon, whereas an O value approaching 1 indicates a higher degree of overestimation of vegetation presence. The indices were calculated as follows.

$$A = B_0 \times (P_0 + P_1 + B_0)^{-1} \quad (1)$$

$$U = P_1 \times (P_1 + B_0)^{-1} \quad (2)$$

$$O = P_0 \times (P_0 + B_0)^{-1} \quad (3)$$

where B_0 denotes the number of sites where taxon i occurs in both pollen and vegetation samples, P_0 denotes the number of sites where taxon i occurs only in pollen samples, and P_1 denotes the number of sites where taxon i occurs only in vegetation samples.

Pollen taxa were further classified according to the threshold criteria proposed by Davis (1984). Taxa with $A > 0.65$ were classified as strongly associated taxa, whereas those with $0.50 \leq A \leq 0.65$ were classified as associated taxa. Taxa with $A < 0.50$ and high values of both U and O were classified as weakly associated, and taxa with $A = 0$ were classified as unassociated taxa. Taxa with $A < 0.50$ and $U = 0$ were defined as over-represented taxa, indicating that their pollen occurs readily but does not necessarily correspond to the local presence of the corresponding vegetation taxon.

4. Results

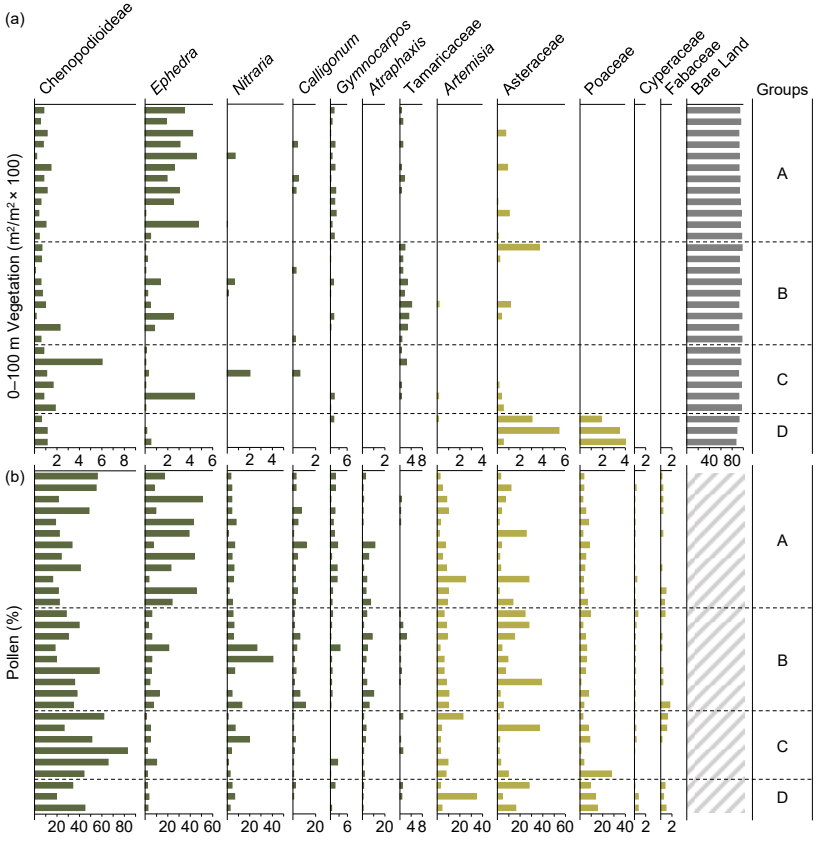
4.1. Vegetation composition

4.1.1. Akesai

In the Akesai region, vegetation cover was extremely low, with 19 plant taxa recorded and a mean total vegetation cover of less than 6%. The vegetation consisted only of shrubs and herbs, with absolute covers of 4.25% and 0.96%, respectively. Based on vegetation surveys within 0–100 m radius, the study area was classified into four community types, namely the *Ephedra–Gymnocarpos* (n = 12), Tamaricaceae (n = 9), Chenopodioideae (n = 6), and Poaceae community (n = 3) (Fig. 2a). The *Ephedra–Gymnocarpos* community was dominated by *Ephedra* (2.69%), *Gymnocarpos* (0.90%),

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241 Chenopodioideae (0.69%) and Tamaricaceae (0.44%). The Tamaricaceae community
242 was dominated by Tamaricaceae (2.03%), Chenopodioideae (0.64%), Asteraceae
243 (0.61%) and *Ephedra* (0.60%). The Chenopodioideae community was dominated by
244 Chenopodioideae (1.83%), *Ephedra* (0.79%) and Tamaricaceae (0.61%). The Poaceae
245 community was dominated by Poaceae (3.12%) and Asteraceae (3.06%), while sample
246 site 12 supported abundant *Caragana*, with a cover reaching 6%.



247

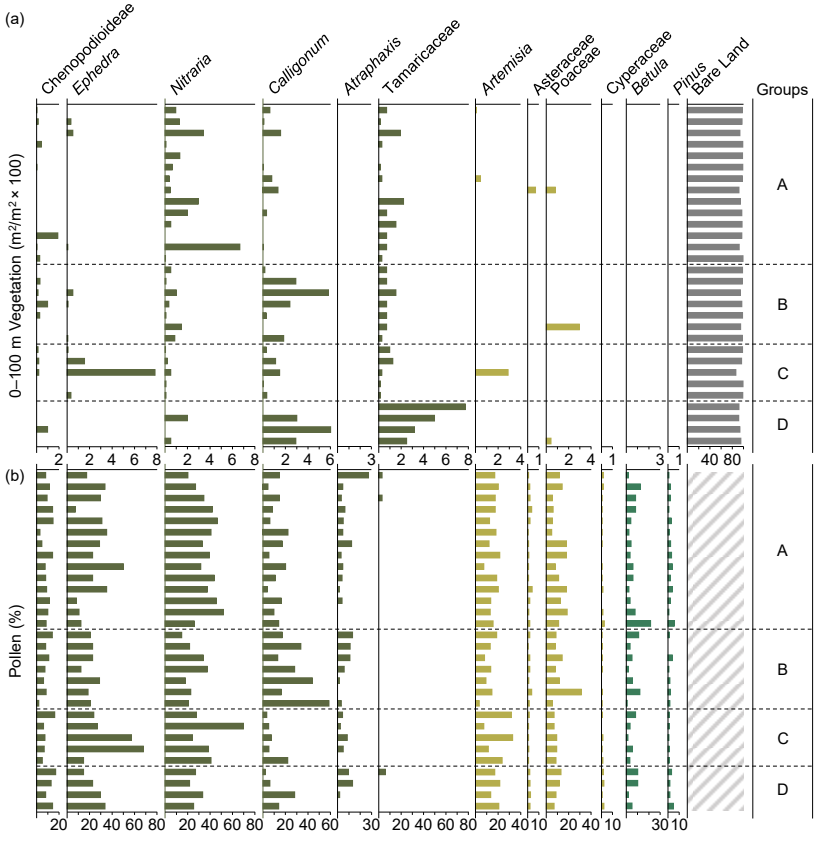
248 **Fig. 2** Vegetation composition (a) and pollen assemblages (b) in Akesai. Community types: (A)
249 Ephedra–Gymnocarpos community; (B) Tamaricaceae community; (C) Chenopodioideae
250 community; (D) Poaceae community.

251 4.1.2. Ejina

252 In the Ejina region, vegetation cover was extremely low, with 11 plant taxa
253 recorded and a mean total vegetation cover of less than 4%. The vegetation consisted

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of shrubs and herbs, with absolute covers of 3.04% and 0.25%, respectively. Arboreal plant was recorded only at site 17, where *Populus euphratica* showed relatively high cover (5.97%). Based on vegetation surveys within 0–100 m radius, the study area was classified into four community types, namely the *Nitraria* ($n = 14$), *Calligonum* ($n = 7$), *Ephedra* ($n = 5$), and Tamaricaceae community ($n = 4$) (Fig. 3a). The *Nitraria* community was dominated by *Nitraria* (1.47%), Tamaricaceae (0.59%) and *Populus* (0.45%). The *Calligonum* community was dominated by *Calligonum* (0.64%), Tamaricaceae (0.61%) and *Nitraria* (0.61%). The *Ephedra* community was dominated by *Ephedra* (1.94%), *Artemisia* (0.59%) and Tamaricaceae (0.53%). The Tamaricaceae community was dominated by Tamaricaceae (4.53%), *Calligonum* (1.00%) and *Nitraria* (0.63%).



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Fig. 3 Vegetation composition (a) and pollen assemblages (b) in Ejina. Community types: (A) *Nitraria* community; (B) *Calligonum* community; (C) *Ephedra* community; (D) Tamaricaceae community.

4.2. Pollen assemblages

4.2.1. Akesai

A total of 15,791 pollen and spore grains were identified from 30 sampling sites (Fig. 2b). These grains represented 43 palynomorph types, comprising 9 shrub taxa, 12 herbaceous taxa, 16 arboreal taxa, and 6 fern spore types. The pollen assemblages from the temperate desert of Akesai were dominated by shrub taxa (65.60%) and herbaceous pollen (30.92%). Among shrub pollen types, Chenopodioideae (36.74%) was the most abundant, followed by *Ephedra* (14.03%), *Nitraria* (6.76%), *Atraphaxis* (3.46%), *Calligonum* (2.54%), and *Gymnocarpos* (1.60%), whereas other shrub taxa had mean percentages below 1%. Among herbaceous pollen types, Asteraceae (11.87%) was dominant, followed by *Artemisia* (8.50%), Poaceae (6.30%), and Cyperaceae (3.26%), with all other types accounting for less than 1%.

4.2.2. Ejina

A total of 15,518 pollen and spore grains were identified from 30 sampling site (Fig. 3b). These comprised 44 palynomorph types, comprising 10 shrub taxa, 16 herbaceous taxa, 12 arboreal taxa, and 6 fern spore types. The pollen assemblages from the temperate desert of Ejina were dominated by shrub pollen (68.76%) and herbaceous pollen (21.21%). Among shrub pollen types, *Nitraria* (28.53%) was the most abundant, followed by *Calligonum* (15.20%), *Ephedra* (10.00%), Chenopodioideae (9.34%), and *Atraphaxis* (5.56%), whereas other shrub types had mean percentages below 1%. Among herbaceous pollen types, Artemisia (12.24%) was dominant, followed by Poaceae (5.27%) and Asteraceae (1.78%), with all other types accounting for less than 1%. Moreover, arboreal pollen accounted for 8.81%, mainly comprising *Betula* (5.90%) and *Pinus* (2.04%), which were likely derived from towns east of the study area or from

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more distant montane regions.

4.3. Fall speed of pollen

Based on objective criteria, eight taxa in Akesai and four taxa in Ejina were selected for FSP estimation. In the Akesai region, seven taxa showed relatively robust pollen–vegetation relationships (Supplementary Fig. S1) and met the thresholds of vegetation cover >0.05% and pollen percentage >1%, including Chenopodioideae, *Ephedra*, *Nitraria*, *Calligonum*, *Gymnocarpos*, Poaceae, and Asteraceae. In the Ejina region, three taxa showed relatively robust pollen–vegetation relationships (Supplementary Fig. S1) and met the thresholds of vegetation cover >0.2% and pollen percentage >1%, including *Ephedra*, *Nitraria*, and *Calligonum*. In addition, Tamaricaceae was included in the estimation because it represents a major plant group in temperate desert vegetation. The FSP of the major plant taxa were broadly consistent between the two study areas (Table 1). *Ephedra* has a relatively fast fall speed (0.038 m s^{-1} ≤ FSP < 0.087 m s^{-1}), and is a relatively heavy pollen. *Nitraria* and *Calligonum* have moderate fall speed (0.025 m s^{-1} ≤ FSP < 0.038 m s^{-1}) and are relatively light pollen. Chenopodioideae, Asteraceae, Poaceae, *Gymnocarpos* and Tamaricaceae have slower fall speeds (FSP < 0.025 m s^{-1}) and are light pollen types (Sugita, 1993).

Table 1 Fall speeds and relative pollen productivity (RPP) estimates with standard deviations (SD) for major pollen taxa in Akesai and Ejina.

Pollen taxon	Akesai					Ejina				
	Pollen morphology (um)		Fall speed	sub-model 3 + Prentice		Pollen morphology (um)		Fall speed	sub-model 1 + 1/d	
	Long axis	Short axis	(m/s)	RPP	SD	Long axis	Short axis	(m/s)	RPP	SD
Chenopodioideae	19.04		0.011	1	0					
Ephedra	36.52	19.28	0.050	0.543	0.020	36.74	18.25	0.052	1	0
Nitraria	31.27	20.61	0.034	1.305	0.171	30.37	19.94	0.032	1.125	0.038
Tamaricaceae	19.24	20.49	0.011	≤ 0.001	0.005	19.24	20.49	0.011	0.006	0.025
Calligonum	30.61	24.69	0.030	0.913	0.069	30.61	24.69	0.030	3.508	0.073
Gymnocarpos	18.26		0.010	0.197	0.026					
Poaceae	26.19		0.021	0.337	0.039					
Asteraceae	23.74	19.81	0.018	0.577	0.041					

*RPP estimates with double underlining indicate values with RPP < SD and thus low reliability.

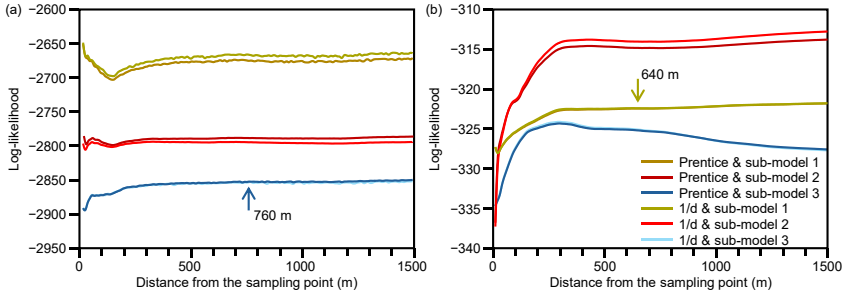
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315

316 4.4. Relevant source area of pollen and relative pollen productivity estimates

317 The ERV model uses a maximum likelihood method to estimate RPPs, assuming
318 that the pollen proportions follow a multinomial distribution (Parsons and Prentice,
319 1981; Sugita, 1994). A higher log-likelihood score indicates a good fit of the observed
320 data (pollen and vegetation) to the model using the estimated parameters (Sugita, 1994;
321 Mazier et al., 2008) and the log-likelihood curve reaches an asymptote that represents
322 the RSAP (Sugita, 1994). We calculated log-likelihood scores for ERV sub-models 1,
323 2, and 3 using vegetation distance-weighting models of 1/d and Prentice's, and the
324 results are presented below.

325 Akesai (Fig. 4a). (1) The log-likelihood scores of sub-models 1 and 2 initially
326 declined and then increased, indicating that these sub-models were not unsuitable for
327 correcting the pollen–vegetation relationship in this study area. By contrast, sub-model
328 3 showed increasing log-likelihood values with vegetation survey radius before
329 reaching a plateau, indicating that the relationship between pollen and vegetation
330 improves and stabilizes with increasing radius. (2) Prentice's model exhibits higher log-
331 likelihood scores than the 1/d model, indicating a better performance. Hence, we used
332 sub-model 3 combined with Prentice's model and obtained an RSAP of 760 m for
333 Akesai.



334

335 **Fig. 4** Log-likelihood curves for (a) Akesai and (b) Ejina derived from ERV sub-models 1, 2, and
336 3 combined with two vegetation distance-weighting methods (1/d and Prentice's). The
337 combination of sub-model 3 and Prentice's model produced the best-fitting log-likelihood curve
338 for Akesai, indicating a relevant source area of pollen (RSAP) of 760 m. The combination of sub-

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model 1 and 1/d model produced the best-fitting log-likelihood curve for Ejina, with the RSAP at 640 m.

Ejina (Fig. 4b). (1) The log-likelihood scores of sub-model 2 increased but did not reach a stable plateau, whereas sub-model 3 showed an initial increase followed by a decline, indicating that neither sub-model was suitable for correcting the pollen–vegetation relationship in this study area. By contrast, the log-likelihood curve of sub-model 1 showed increasing log-likelihood values with vegetation survey radius before reaching a plateau. (2) The 1/d model exhibits higher log-likelihood scores than Prentice's model, indicating a better performance. Hence, we used sub-model 1 combined with the 1/d model and obtained an RSAP of 640 m for Ejina.

In Akesai, the optimal RPP estimates were obtained using vegetation data within the RSAP of 760 m around sampling site, based on the combination of ERV sub-model 3 and Prentice's model. Using Chenopodioideae as the reference taxon (RPP = 1), the RPP values of the other pollen taxa decrease in the following order: *Nitraria* (1.305 ± 0.171), *Calligonum* (0.913 ± 0.069), Asteraceae (0.577 ± 0.041), *Ephedra* (0.543 ± 0.020), Poaceae (0.337 ± 0.039), *Gymnocarpos* (0.197 ± 0.026), and Tamaricaceae (0.001 ± 0.005) (Table 1). In Ejina, the optimal RPP estimates were obtained using vegetation data within the RSAP of 640 m around sampling site, based on the combination of ERV sub-model 1 and the 1/d model. Using *Ephedra* as the reference taxon (RPP = 1), the RPP values of the other pollen taxa decrease in the following order: *Calligonum* (3.508 ± 0.073), *Nitraria* (1.125 ± 0.038), and Tamaricaceae (0.006 ± 0.025) (Table 1).

5. Discussion

5.1. Vegetation-indicative significance of major pollen taxa in temperate deserts

Arid regions are dominated by desert, semi-desert, and steppe ecosystems, where sparse and spatially fragmented vegetation can result in pollen percentages that substantially exceed the cover of the corresponding plant taxa (Xu et al., 2007; Zhao et al., 2009; Wang et al., 2022). In these open landscapes, pollen dispersal is largely wind

https://doi.org/10.5194/egusphere-2026-7103
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368 driven, leading to greater dispersal distances and an enhanced contribution of regional
369 background pollen. This enhanced background input can weaken the correspondence
370 between pollen assemblages and surrounding vegetation, thereby increasing
371 uncertainty in pollen–vegetation relationships (Gaillard et al., 2008; Xu and Zhang,
372 2013). Here, we assessed taxon-specific pollen representation within the RSAP
373 (Supplementary Fig. S2) in Akesai and Ejina using Davis indices and RPP estimates,
374 thereby evaluating the vegetation-indicative significance of major pollen taxa in
375 temperate deserts and their implications for interpreting fossil pollen records.

376 In temperate deserts, several pollen taxa showed a strong ability to indicate the
377 occurrence of their corresponding plant taxa within the RSAP (Fig. 5). In Akesai,
378 Chenopodioideae, *Ephedra*, and *Gymnocarpos* were classified as strongly associated
379 taxa. Chenopodioideae and *Ephedra* both had an *A* value of 1, indicating co-occurrence
380 between pollen and the vegetation across the sampling sites. Chenopodioideae
381 (reference taxon, RPP = 1) accounted for 36.96% of the pollen assemblage but only
382 0.86% of vegetation cover, while *Ephedra* accounted for 14.11% versus 1.19% and had
383 an RPP value of 0.543. *Gymnocarpos* also showed a strong correspondence with the
384 occurrence of its plant taxon (A = 0.793), with 1.62% pollen representation, 0.35%
385 vegetation cover, and an RPP value of 0.197. In Ejina, *Ephedra*, *Nitraria*, *Calligonum*,
386 and Chenopodioideae were all classified as strongly associated taxa (A = 1). Among
387 them, *Ephedra* (reference taxon, RPP = 1) had an absolute vegetation cover of only
388 0.49% but accounted for 9.72% of the pollen assemblage. *Nitraria*, *Calligonum*, and
389 Chenopodioideae showed similar phenomenon, with pollen percentages of 28.89%,
390 15.50%, and 9.47%, respectively, compared with absolute vegetation covers of only
391 0.90%, 0.34%, and 0.26%; the corresponding RPP values were 1.125 for *Nitraria* and
392 3.508 for *Calligonum*. Notably, *Nitraria* and *Calligonum* showed contrasting pollen–
393 vegetation associations between the two study areas. In Ejina, *Nitraria* and *Calligonum*
394 were dominant plants with relatively continuous spatial distributions, resulting in strong
395 pollen–vegetation correspondence. In Akesai, *Nitraria* was classified as an over-
396 represented taxon and *Calligonum* as a weakly associated taxon. Their occurrence
397 mainly as associated taxa with low cover and patchy distributions likely weakened the

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ability of their pollen to indicate local vegetation. Overall, Chenopodioideae and *Ephedra* can be regarded as strongly associated taxa in temperate deserts, and their pollen occurrence can reliably indicates the local presence of the corresponding plant taxa (Zhang et al., 2024). *Gymnocarpos*, *Nitraria*, and *Calligonum* also show relatively strong indicator ability for their corresponding plant taxa (Li et al., 2011).

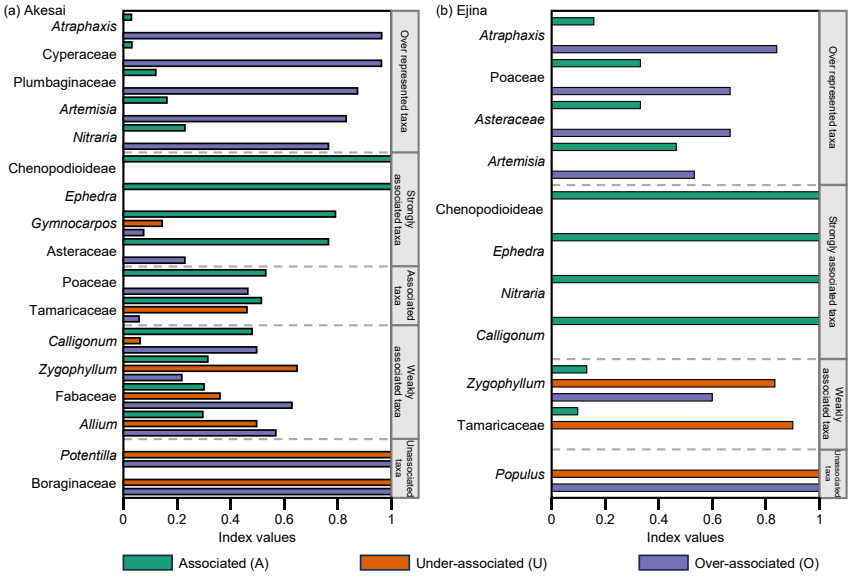


Fig. 5 Davis indices for major pollen taxa in the temperate deserts of (a) Akesai and (b) Ejina.

Over-represented, weakly associated, and unassociated taxa indicate uncertainty in pollen–vegetation relationships. In Akesai, *Artemisia*, *Atraphaxis*, Plumbaginaceae, and Cyperaceae were classified as over-represented taxa, as were *Artemisia*, *Atraphaxis*, Asteraceae, and Poaceae in Ejina (Fig. 5). The frequent occurrence of these pollen taxa in sedimentary assemblages does not necessarily indicate the regional presence of their parent plants, but more likely reflects substantial background pollen input under open landscape conditions (Zhang et al., 2024). By contrast, *Zygophyllum*, Fabaceae, and *Allium* were classified as weakly associated taxa, indicating limited vegetation-indicative ability (Fig. 5). Among them, *Zygophyllum* had a high *U* value, indicating a pronounced underestimation of the plant occurrence, whereas Fabaceae and *Allium* had high values of both *U* and *O*, reflecting bidirectional uncertainty in their pollen–

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vegetation correspondence. *Potentilla*, Boraginaceae, and *Populus* were classified as unassociated taxa ($A = 0$), indicating no stable pollen–vegetation correspondence. The spatial distributions of these plant taxa are largely controlled by local moisture availability and microtopography and are therefore restricted to specific microhabitats. By contrast, pollen assemblages integrate vegetation signals over broader spatial scales (Sugita, 2007; Trondman et al., 2016; Sun et al., 2020), resulting in relatively weak pollen–vegetation correspondence for these taxa at the sampling-site scale.

Notably, Tamaricaceae was classified as associated taxon in Akesai but as weakly associated taxon in Ejina, with low O values and high U values (Fig. 5). This indicates that the occurrence of Tamaricaceae pollen can provide a useful indication of the local presence of Tamaricaceae plants, but that its pollen is often absent or poorly represented at sites where Tamaricaceae plants are present (Li et al., 2005; Wang et al., 2022). In Akesai, Tamaricaceae vegetation cover was 0.92%, whereas its pollen percentage was only 0.30%, with an RPP value of <0.001 relative to Chenopodioideae. Likewise, in Ejina, it had the highest vegetation cover among taxa (1.56%) but contributed only 0.05% of the pollen assemblage, with the lowest RPP value (0.006, relative to *Ephedra*). Across the study areas, Tamaricaceae reached a maximum vegetation cover of 9.61%, whereas its corresponding pollen percentage was only 0.60%, indicating poor pollen representation and confirming Tamaricaceae as a typical under-represented taxon in arid regions (Xu et al., 2007). The strong under-representation of Tamaricaceae suggests that even minor increases in its pollen percentage may reflect a substantial expansion of Tamaricaceae-dominated desert vegetation and intensified regional desertification. Hence, low-percentage pollen types (e.g., Tamaricaceae) may contain important ecological information and should be carefully considered to improve the reliability of regional vegetation reconstructions.

5.2. Comparison of RPP estimates for major plant taxa across arid inland Asia

Arid inland Asia is characterized by diverse landscape patterns and vegetation types, shaped by its broad spatial extent, complex mountain–basin topography, and

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pronounced hydrothermal gradients (Chen et al., 2013; Chen et al., 2025). Previous studies have shown that RPP for the same plant taxon is not constant parameter (Mazier et al., 2012; Li et al., 2018), but instead exhibit pronounced regional variation in response to differences in vegetation type, landscape pattern, and ecological conditions (Xu et al., 2016; Jiang et al., 2020; Sun et al., 2026). Therefore, comparing RPP for the same plant taxa across different vegetation types can improve our understanding of regional variability in pollen–vegetation relationships and enhance the reliability of fossil pollen interpretation and cross-regional quantitative vegetation reconstruction.

Accordingly, we compared the RPP estimates obtained from temperate deserts in this study with those reported for other vegetation types across arid inland Asia (Fig. 6a). To ensure comparability among study areas, the RPP estimates from each region were standardized (Sun et al., 2026). Chenopodioideae was selected as the reference taxon (RPP = 1), owing to its widespread distribution in arid regions and relatively good pollen representation (Fig. 5; Xu et al., 2007; Zhang et al., 2024). For study areas where RPP for Chenopodioideae was not estimated, *Ephedra* was used as an intermediate reference taxon. Specifically, the mean standardized RPP of *Ephedra* was first calculated and then used to convert RPP estimates from studies using *Ephedra* as the reference taxon into values relative to Chenopodioideae, thereby producing comparable standardized RPP data (Ma et al., 2025). The comparison showed that most plant taxa in arid regions had generally low RPP values (RPP < 1; Fig. 6b). *Ephedra*, Tamaricaceae, and Poaceae showed relatively limited regional variation, whereas *Nitraria*, *Calligonum*, and Asteraceae exhibited more pronounced regional variability.

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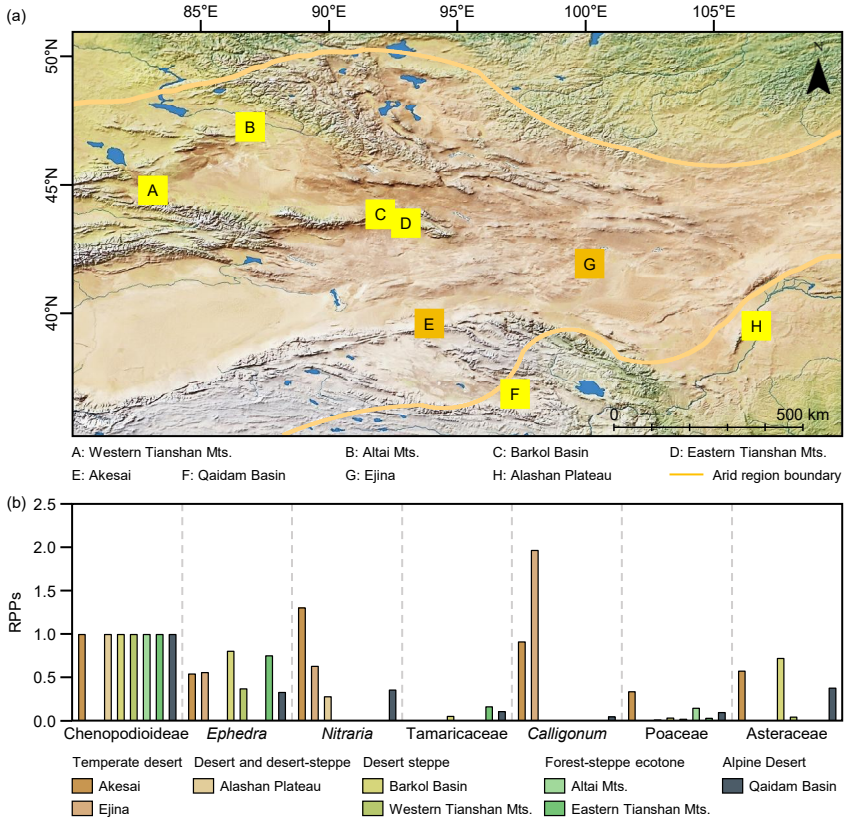


Fig. 6 Distribution of RPP study areas and comparison of RPP estimates for major pollen taxa in arid inland Asia. (a) Locations of the study areas. (b) RPP estimates from Akesai and Ejina (this study), Alashan Plateau (Li et al., 2011), Barkol Basin (Wang et al., 2021), Western Tianshan Mountains (Niu, 2022), Altai Mountains (Xie et al., 2026), Eastern Tianshan Mountains (Fang et al., 2025), and Qaidam Basin (Ma et al., 2026).

We suggest that these differences may be related to regional vegetation composition and the dominance of plant taxa within local communities. The RPP of *Nitraria* in Ejina was slightly higher than in other regions, which may be attributed to its role as a community-forming taxon here. Its relatively high vegetation cover likely enhances local pollen input (Prentice, 1985; Sugita, 1994), resulting in higher RPP values than in Qaidam Basin and Alashan Plateau, where *Nitraria* occurs mainly as an associated species (Li et al., 2011; Ma et al., 2026). Similarly, *Calligonum* shows relatively high RPP values as a dominant taxon in the temperate deserts of Akesai and

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Ejina, whereas its RPP is markedly lower where it occurs as an associated species in the alpine desert of the Qaidam Basin (Ma et al., 2026). These results suggest that dominant and continuously distributed taxa tend to produce stronger local pollen input and higher RPP values, whereas sparsely distributed associated species generally contribute less pollen locally and show lower RPP values (Xu et al., 2014; Li et al., 2018; Wang et al., 2022; Sun et al., 2026).

Beyond these factors, regional background pollen input and variation in pollen source area may further amplify regional variability in RPP (Zhang et al., 2024). The higher RPP of *Nitraria* in Akesai may be attributed to substantial background pollen input from extensive western deserts (Tarim Basin), which increased local *Nitraria* pollen proportions and elevated its RPP estimate (Zhang et al., 2011; Feng et al., 2018). Likewise, Poaceae showed relatively consistent RPP values across most arid regions, but was slightly higher in Akesai. This may be attributed to wind-transported pollen from abundant Poaceae vegetation in the Danghe Nanshan Mountains south of Akesai (Cheng et al., 2004), together with locally favorable gully habitats formed by seasonal snowmelt erosion, where Poaceae occurs widely as azonal vegetation (Du et al., 2024). These sources likely enhanced background pollen input of Poaceae and elevated its RPP estimate. In addition, Asteraceae showed broadly consistent RPP values across regions, except for a lower value in the western Tianshan, likely due to regional differences in its constituent genera (e.g., *Aster*, *Taraxacum*) (Niu, 2022).

Overall, differences in RPP estimates among major plant taxa across vegetation types in arid inland Asia are likely attributable to variations in regional community composition and landscape characteristics. Across regions and vegetation types, dominant taxa with high cover and broad distributions, as well as taxa receiving substantial extra-local pollen input, may both increase their contribution to regional background pollen loading. As a result, these taxa may show higher pollen percentages in sedimentary samples and higher RPP estimates in communities where they are dominant than in communities where they are subordinate or associated taxa. We therefore suggest that regional landscape characteristics, together with the contributions

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of dominant taxa and extra-local pollen to regional background pollen loading, should be carefully considered when interpreting fossil pollen records and reconstructing past vegetation change.

5.3. Towards quantitative land-cover reconstruction in arid regions

Pollen-based reconstructions of past vegetation and land cover are central to paleoecology and global change research, providing key insights into regional vegetation succession, human impacts, and climate responses (Cheng et al., 2022; Raiho et al., 2022; Wang et al., 2023; Hopcroft et al., 2026). However, numerous studies have shown that pollen percentages are not directly equivalent to vegetation composition, and qualitative interpretations based solely on pollen percentages may misrepresent regional vegetation composition and land-cover (Davis, 1963; Xu et al., 2016; Sun et al., 2019). This limitation is particularly pronounced in arid regions, subtle vegetation changes may also be amplified in pollen records, further weakening their reliability for reconstructing long-term vegetation and land-cover dynamics. Thus, pollen data alone may be insufficient to accurately characterize actual vegetation landscapes in arid regions.

The development of the Landscape Reconstruction Algorithm (LRA) marked a major advance in quantitative vegetation reconstruction from pollen data (Sugita, 2007), which uses RPP estimates to convert pollen assemblages into relative vegetation abundance (all plant taxa summing to 100%). Notably, although these reconstructions provide reliable estimates of vegetation abundance (Trondman et al., 2016; Marquer et al., 2020; Ren et al., 2026), they essentially represent the relative proportions of different plant taxa rather than actual land-cover composition (Sun et al., 2022a). This discrepancy may be further amplified in arid regions with extensive bare ground, and the direct use of such reconstructions in paleoclimate or Earth system simulations may therefore introduce systematic biases (Sun et al., 2022a; Dallmeyer et al., 2023; Strandberg et al., 2022; Hopcroft et al., 2026). On this basis, we propose a reconstruction–correction framework for quantitative land-cover reconstruction in arid

https://doi.org/10.5194/egusphere-2026-7103
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regions (Sun et al., 2022a, 2022b). First, using the RPP estimates obtained in this study, we applied the REVEALS model of the LRA (Sugita, 2007) to reconstruct the relative vegetation abundance from surface pollen samples in Akesai and Ejina. We then corrected these reconstructions using modern vegetation-cover data to account for bare ground, thereby producing land-cover estimates that more closely approximate actual landscape conditions. To evaluate the reliability of RPP estimates for quantitative land-cover reconstruction in arid regions and the feasibility of the reconstruction–correction framework, we compared reconstructed and surveyed vegetation composition, and examined the causes of their discrepancies.

We conducted the analysis from two perspectives. First, using surface pollen and vegetation survey data from Akesai and Ejina, we assessed the robustness of the RPP estimates with a leave-one-out (LOO) approach (Chen et al., 2018; Li et al., 2022). Specifically, one sampling site was sequentially excluded from each study area, and RPP estimates were recalculated using the remaining sites, generating 30 sets of estimates. The stability of these estimates and their deviations from the full-sample RPP estimates were used as indicators of RPP reliability (Supplementary Fig. S3). We further used each set of LOO-derived RPP parameters to reconstruct relative vegetation abundance from the pollen assemblage of the corresponding omitted site, and then evaluated the ability of the proposed reconstruction–correction framework to recover land-cover composition in arid regions. Second, to assess the reliability of existing RPP datasets for land-cover reconstruction in Asian arid regions and their potential application to stratigraphic pollen records, we compiled RPP estimates from eight study areas in arid inland Asia and calculated the mean FSP for the corresponding taxa. These study areas include Akesai (this study), Ejina (this study), Alashan Plateau (Li et al., 2011), Barkol Basin (Wang et al., 2021), Western Tianshan Mountains (Niu, 2022), Altai Mountains (Xie et al., 2026), Eastern Tianshan Mountains (Fang et al., 2025) and Qaidam Basin (Ma et al., 2026). Following established criteria for RPP selection and compilation (Mazier et al., 2012; Wieczorek and Herzschuh, 2020), we retained only estimates for which the RPP value exceeded its standard deviations (SD) and removed outliers according to sample-size-based filtering criteria, resulting in reliable RPP data

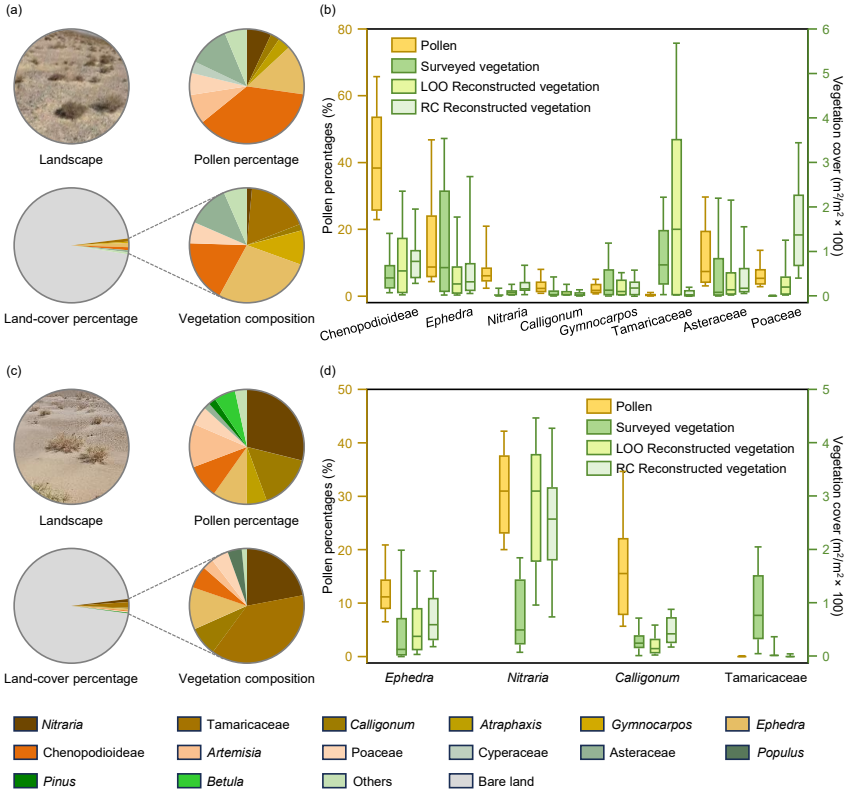
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for 27 plant taxa (Supplementary Table S1). For the REVEALS reconstruction, the model was parameterized with a regional wind speed of 3 m s^{-1}, a deposition basin radius of 0.5 m, and a maximum pollen source area of 1500 m.

Based on the two RPP datasets, vegetation composition was reconstructed separately for Akesai and Ejina, and the reconstructions were subsequently corrected for bare ground using vegetation-cover data (Wang et al., 2021; Sun et al., 2022a). Compared with interpretations based on pollen percentages, vegetation covers reconstructed using either the local LOO-derived RPP estimates or the regional compilation (RC) RPP parameters more closely matched the surveyed vegetation cover (Fig. 7). The reconstructed cover of Chenopodioideae, *Ephedra*, *Calligonum*, *Gymnocarpos*, and Asteraceae was close to the observed values, indicating good reconstruction performance for these taxa. Nevertheless, minor discrepancies were observed for a few taxa, including Tamaricaceae, as well as Poaceae in Akesai and *Nitraria* in Ejina. The underestimation of Tamaricaceae may be attributable to its low pollen representation, whereby extremely low pollen percentages led to relatively low reconstructed cover (Li et al., 2005; Xu et al., 2007; Wang et al., 2022). By contrast, in Akesai, Poaceae cover reconstructed using the RC RPP was slightly overestimated (observed cover is 0.125%, RC-reconstructed cover is 1.692%). This discrepancy may be related to the regional RPP compilation, which includes Poaceae RPP estimates from multiple vegetation types where Poaceae commonly occurs as a major component and therefore exhibits relatively high RPP (Li et al., 2005; Fang et al., 2025; Ma et al., 2026), In contrast, Akesai is characterized by desert vegetation, where Poaceae occurs mainly as a low-cover associated or microhabitat-restricted taxon. Applying the compiled RPP values of Poaceae to the desert may therefore lead to overestimation of Poaceae cover. In Ejina, *Nitraria* cover was also overestimated by both the LOO- and RC-based reconstructions (3.164%, 2.827%), compared with an observed value (0.901%). This overestimation may be related to the role of *Nitraria* as a dominant community-forming taxon with relatively continuous regional distribution (Zhang et al., 2024), which could generate strong local and regional background pollen inputs. Thus, although RPP correction can reduce biases in pollen–vegetation relationships, dominant taxa (e.g.,

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599 *Nitraria*) may still be slightly overestimated when their pollen signals are
600 disproportionately stronger than their actual vegetation cover.



601

602 **Fig. 7** Comparison of pollen percentages, surveyed vegetation cover, and RPP-based vegetation
603 reconstructions in Akesai and Ejina. (a, c) Landscape characteristics and comparison among pollen
604 percentages, land-cover percentages and vegetation composition in Akesai and Ejina, respectively.
605 (b, d) Comparison of pollen percentages, surveyed vegetation cover, and reconstructed vegetation
606 cover for major taxa in Akesai and Ejina, respectively. LOO Reconstructed vegetation refers to
607 vegetation cover reconstructed using RPP derived from the Leave-one-out (LOO) procedure. RC
608 Reconstructed vegetation refers to vegetation cover reconstructed using the regionally compiled
609 (RC) RPP.

610 Overall, the corrected vegetation reconstructions were closer to the surveyed
611 vegetation composition, indicating that the reconstruction–correction framework
612 proposed in this study can effectively improve the accuracy of quantitative land-cover

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reconstruction in arid regions. The LOO-based reconstruction test indicates that the regional RPP parameters obtained in this study are relatively robust. In addition, compiling regional RPP data using standardized criteria can partly reduce biases in RPP estimates arising from differences in community composition, local environmental conditions, and methodological inconsistencies. Such regional RPP datasets provide more regionally representative RPP parameters for future cross-regional quantitative reconstructions of past vegetation and land cover.

These results highlight the importance of distinguishing changes in vegetation composition from changes in total vegetation cover when interpreting dryland pollen records. Such reconstructions would help clarify how dryland vegetation composition and cover responded to past environmental change. Future studies should apply this framework across broader spatial extents and longer temporal scales to reveal the spatiotemporal patterns and driving mechanisms of land-cover change in drylands. Their incorporation into large-scale pollen-based land-cover datasets would also provide a stronger basis for assessing the role of dryland land-cover change in land–atmosphere feedbacks through climate and Earth system modelling. Such efforts will also improve our understanding of dryland ecosystems and provide scientific support for ecological conservation, desertification control, and vegetation restoration.

6. Conclusions

Based on surface pollen and vegetation survey data from Akesai and Ejina in the temperate deserts of inland Asia, we examined modern pollen–vegetation relationships, estimated RPP values for major plant taxa, and evaluated an RPP-based reconstruction–correction framework for quantitative land-cover reconstruction in arid inland Asia. The main conclusions are as follows.

(1) We estimate RPP values for eight major plant taxa in the temperate deserts of arid inland Asia using the ERV model. In Akesai, with Chenopodioideae as the reference taxon, RPPs decreased in the order *Nitraria* (1.305 ± 0.171), Chenopodioideae (1), *Calligonum* (0.913 ± 0.069), Asteraceae (0.577 ± 0.041),

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Ephedra (0.543 ± 0.020), Poaceae (0.337 ± 0.039), *Gymnocarpos* (0.197 ± 0.026), and Tamaricaceae (0.001 ± 0.005). In Ejina, with *Ephedra* as the reference taxon, RPPs decreased in the order *Calligonum* (3.508 ± 0.073), *Nitraria* (1.125 ± 0.038), *Ephedra* (1), and Tamaricaceae (0.006 ± 0.025).

(2) Based on Davis indices and RPP estimates, we found marked taxon-specific differences in pollen representation in temperate deserts. Chenopodioideae, *Ephedra*, *Nitraria*, and *Calligonum* showed a strong ability to indicate the local occurrence of their parent plants, whereas Tamaricaceae was strongly under-represented in pollen assemblages. These results suggest that taxon-specific differences in pollen representation should be carefully considered when interpreting fossil pollen records, with particular attention to the vegetation information carried by under-represented or low-percentage pollen types.

(3) Comparisons with RPP estimates from other arid region studies indicate that regional differences in RPP are mainly related to plant community composition and landscape characteristics. Dominant taxa with high cover and broad spatial distributions, or taxa receiving substantial extra-local pollen input, tend to show higher pollen percentages and higher RPP estimates.

(4) We proposed and evaluated an RPP-based reconstruction–correction framework for quantitative land-cover reconstruction in arid regions. The reconstructed results from Akesai and Ejina closely matched the vegetation survey data, suggesting that this approach can capture vegetation landscape patterns under high bare-ground cover. Future applications to fossil records could improve large-scale pollen-based land-cover datasets and support assessments of dryland land–atmosphere feedbacks through climate and Earth system modelling.

Data availability

Research data from this study are available in the Supporting Information and on Zenodo (https://doi.org/10.5281/zenodo.23755213).

Author contributions

https://doi.org/10.5194/egusphere-2026-7103
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Jingyi Liu: Writing – original draft, Methodology, Investigation, Formal analysis. **Yuanhao Sun:** Writing – review & editing, Conceptualization, Investigation, Formal analysis, Supervision, Funding acquisition. **Jiaqi Pang:** Investigation. **Jiheng Shi:** Investigation**. Qinghai Xu:** Writing – review & editing, Investigation. **Ruchun Zhang:** Investigation. **Linyuan Ma:** Methodology**. Jianhui Chen:** Writing – review & editing, Conceptualization, Formal analysis, Supervision, Funding acquisition.

Competing interests

The authors declare that they have no conflict of interest.

Financial support

This work was supported by the National Natural Science Foundation of China (423B2103, 42601280), the Science and Technology Leading Talent Program in Gansu Province (24RCKB007), and the Postdoctoral Fellowship Program of China Postdoctoral Science Foundation (GZC20260187).

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