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OUT-OF-THE-BOX

Intraspecific competition might reduce pollen productivity of grassland plants on the Tibetan Plateau

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Land cover, shaped by the joint effects of climate and human activities, has critical biogeophysical and biogeochemical feedback paths to the atmospheric and climate system. Knowledge of the long-term changes in land cover, and decomposing the contributions of climate change and human activities, is the scientific foundation for predicting future trends in land cover and for achieving harmony between humans and nature. Past pollen assemblages archived in sediment contain information about plant communities and human land use and can be used to investigate past land-cover change. However, the difference in pollen productivities of plants biases the estimated plant abundance and community evenness.[1]

The Landscape Reconstruction Algorithm is a state-of-the-art approach for pollen-based land-cover reconstruction, converting pollen percentages into plant relative abundances through pollen productivity corrections; with the pollen productivities assumed to be stable for all plants in space and time.[2] However, pollen productivities can be influenced by climate, soil, and species competition, with significant regional peculiarities,[1] which challenges the reliability of the land-cover reconstruction. Hitherto, how the pollen productivity of a plant taxon varies across its ecological contexts, and whether intraspecific competition affects it, remains unresolved. This question is critical for both quantitative land-cover reconstruction and qualitative

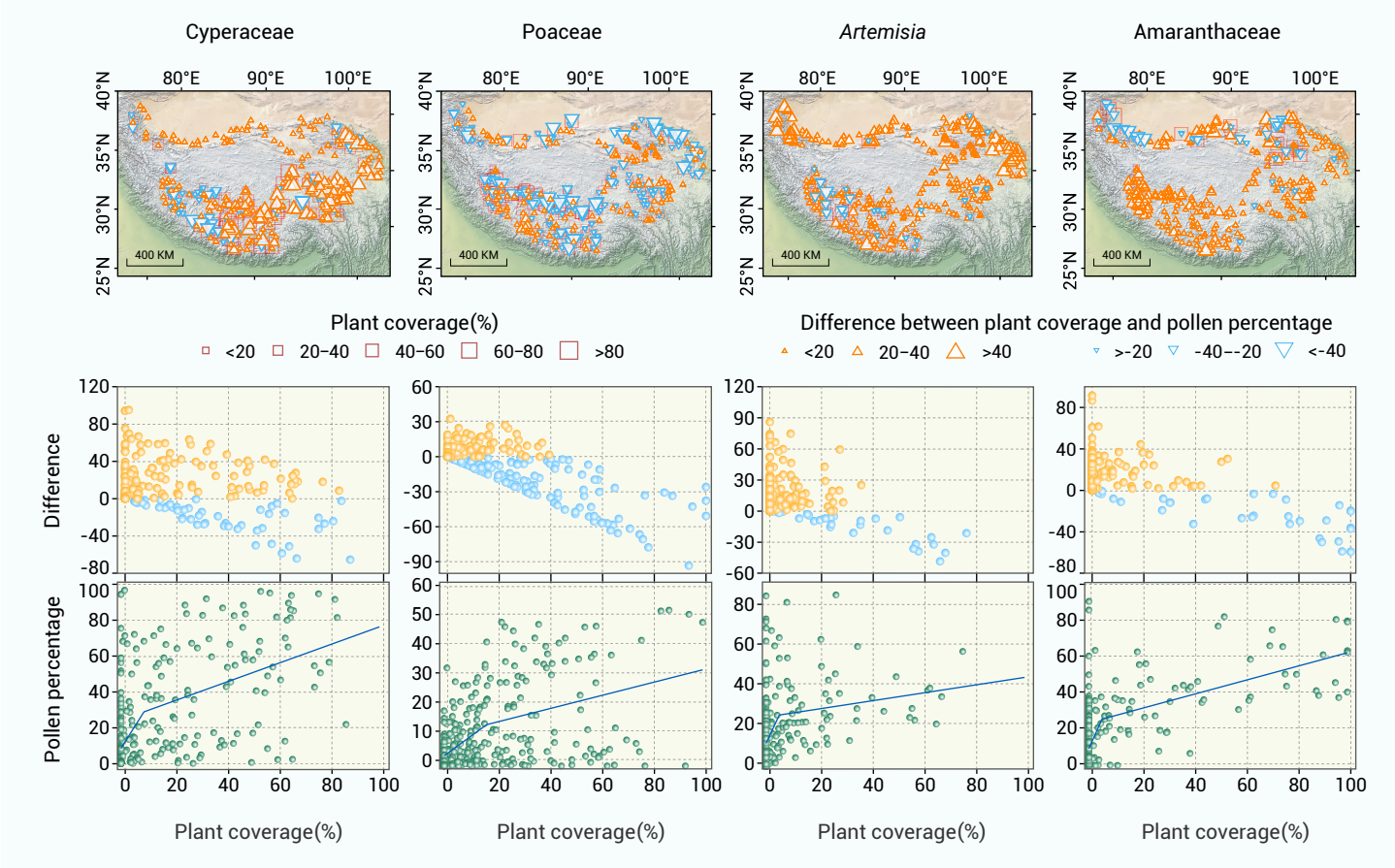

Figure 1. Relationships between pollen percentage and plant cover for four dominant pollen taxa on the Tibetan Plateau First row: spatial distribution of the differences between pollen percentage and plant cover (upward-pointing orange triangles signify under-representation in the pollen assemblage; downward-pointing blue triangles signify over-representation). Second row: distribution of the differences between pollen percentage and plant cover along plant cover gradients (orange: positive values indicating under-representation; blue: negative values indicating over-representation). Third row: response changes of pollen percentage to plant cover as revealed by segmented linear regression (R^2 value for Cyperaceae is 0.37; Poaceae, 0.27; *Artemisia*, 0.19; Amaranthaceae, 0.48).

pollen-sequence interpretation.

Due to its high elevation and continental climate, the Tibetan Plateau is predominantly covered by alpine grasslands, including alpine meadows, alpine steppes, and alpine deserts, which have lower plant diversity compared to lowland temperate grasslands. The relatively limited number of dominant and common plant species results in pollen assemblages (both from modern and late Quaternary samples) being dominated by a few herbaceous taxa, such as Cyperaceae, Poaceae, *Artemisia*, and Amaranthaceae. This makes

the Tibetan Plateau an ideal region for studying pollen–vegetation relationships, as few plant species are represented by an individual pollen taxon. During the summers of 2018 to 2021, our research team carried out vegetation surveys and soil-surface sample collection across the grasslands on the Tibetan Plateau.[3,4] This study investigates the relationship between pollen percentages and plant cover for four dominant taxa at 307 sites, aiming to determine whether pollen productivity varies with changes in plant cover. Exogenous arboreal pollen grains were excluded from percentage calculations. Plant cover for each site was calculated as the mean values from 2 or 3 plots, with proportion of bare ground excluded from the calculation; then the cover of plants belonging to the four selected taxa were combined to ensure comparability with the pollen percentages.

Pollen taxa can generally be classified as over- or under-represented based on their pollen percentage relative to plant cover. A higher pollen percentage than plant cover indicates over-representation, and vice versa. Our evidence from the Tibetan Plateau suggests that pollen representation may depend on the plant's status within its community. For the four dominant taxa, pollen percentages are generally higher than plant cover at sites where the plants are sparse, while lower than plant cover at sites where plants are numerous. For instance, the difference between *Artemisia* pollen percentage and plant cover indicates that it is an over-represented taxon at sites with less than 30% plant cover, while it shows under-representation at sites with higher plant cover. Although Poaceae is generally considered an under-represented taxon by previous studies, our data show it is over-represented at sites with low plant cover (Figure 1).

In traditional palynology, a linear relationship between pollen percentage and plant cover is commonly hypothesized, where the slope and intercept represent pollen productivity and background pollen, respectively.[5] We used segmented linear regression to evaluate the relationship between surface pollen samples and plant cover and to determine the location of any breakpoint (using the segmented package for R). Our evidence from the Tibetan Plateau indicates that pollen percentages exhibit a non-linear response to plant cover: higher cover appears to inhibit pollen productivity, while lower cover might stimulate plants to produce more pollen grains. This over-representation under low cover conditions could also be attributable to the relatively low pollen productivity of dominant plants. The results of the segmented linear regression reveal that all four dominant pollen taxa exhibit steeper slopes at sites with lower plant cover and lower slopes at sites with higher plant cover (Cyperaceae, 2.28 vs. 0.52; Poaceae, 0.65 vs. 0.23; *Artemisia*, 2.80 vs. 0.20; Amaranthaceae, 3.23 vs. 0.39), with different breakpoints of plant cover (Cyperaceae, 8.9%; Poaceae, 16.5%; *Artemisia*, 5.1%; Amaranthaceae, 5.1%). The breakpoints suggest that pollen productivity varies with population density; however, further research is needed to determine any ecological significance.

Based on this case study from the Tibetan Plateau, we hypothesize that intraspecific competition can affect a plant's pollen productivity. This phenomenon will bias pollen-based land-cover reconstructions and overestimate community evenness inferred from pollen data. To validate this hypothesis, future studies should investigate modern pollen–vegetation relationships for woody plants and other geographical regions beyond the current herbaceous-dominated study area, which will require more reliable pollen monitoring (e.g. pollen influx obtained from traps) and vegetation surveys. In addition, this competitive effect on pollen productivity should be incorporated into both quantitative land-cover reconstruction and the qualitative explanation of pollen spectra. Corresponding models and approaches also need to be refined by considering the variation of pollen productivity.

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AUTHOR CONTRIBUTIONS

Xianyong Cao: Conceptualization, Visualization, and Original draft. Mengna Liao, Kai Li, Yili, Jin, Lina Liu and Jian Ni: Field work and Data preparation. Wenjia Li, Zitong Wang and Lina Song: Numerical analysis and Editing. All authors contributed to and approved the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

DATA AND CODE AVAILABILITY

The plot-based dataset of plant community can be found in Jin et al.' paper[3] at http://doi.org/10.17521/cjpe.2022.0174; and detailed information about the modern pollen dataset can be found in Liao et al.' paper,[4] which is openly available from the National Tibetan Plateau Data Center (DOI: 10.11888/Paleoenv.tpdc.302015).