Meta-analysis reveals severe pollination limitation for the flowering plants growing in East Himalaya-Hengduan Mountains region.

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Abstract

Pollination limitation widely occurs and has an important effect on flowering plants. East Himalaya-Hengduan Mountains region is one of the 24 biodiversity hot spots around the world. However, no study as we known has synthetically assessed the degree of pollination limitation in this area. The present study aims to reveal the degree of pollination limitation for the flowering plants growing on East Himalaya-Hengduan mountains, and test if the reproductive features, the floral traits or the elevation are closely correlated with the degree of pollination limitation. We complied data from 76 studies, with 96 species and 108 independent data records included. We found that flowering plants in this area undergo severe pollination limitation (overall hedges'd=2.004, with the 95% confident interval [1.3264, 2.6743]), which is much higher than the flowering plants growing in many other regions around the world. The degree of pollination limitation was tested to be related to the capacity of autonomous self-reproduction and the pollination pattern (generalized vs. specialized pollinated) of plants. In addition, we found a clear relationship between elevation and the degree of pollination limitation, which indicates that plants might undergo severe pollination limitation in higher places.

Background

Pollination limitation widely occurs and has been an essential clue for determining whether flowering plants undergo limitation from pollination services in natural habitats [1,2]. Flowering plants, especially those obligately cross-fertilized, strongly rely on external pollination services for their sexual reproduction [3, 4]. On the one hand, pollination limitation exerts an essential selection on plants [5, 6, 7]. Within a life-history cycle, severe pollination limitation during a flowering season would cause the failure of sexual reproduction in given year, which might therefore cause reproductive resources discounting for plants [8]. Over the long term, plants might evolve favorable strategies that ensure their reproductive success, i.e., autonomous self-reproduction, clonal growth or apomixis, if they undergo long-term pollination limitation [9]. On the other hand, the pollination services in nature are largely provided by pollinator animals (bees, butterflies, birds, etc.) [4]; thus, the degree of pollination limitation could indicate the abundance and variability of the pollinators in nature to some extent.

Various independent studies have reported that many plant species do suffer from pollination limitations in nature. For example, *Primula modesta*, an obligate heterostylous outcrossing plant that is not pollination limited in domestic environment, suffers severe pollination limitation in natural habitats [10]. In general, plants growing in harsh environments, i.e., deserts and arctic and alpine areas, are more frequently pollination limited [11, 12]. This is probably because the abundance and vitality of pollination insects in these areas are generally lower than those of pollination insects in tropical and subtropical areas. Several synthetic reviews have assessed the frequency and degree to which pollination limitation occurs in different areas around the world [13]. For example, pollination limitation has been studied among alpine flowering plants (24 species) [14] and plants of the Atlantic forest in Brazil (132 species) [15]. In García-Camacho and Totland's synthetic study, an investigation of the degree of pollination limitation in the alpine areas around the world revealed no severe pollination limitation for alpine

flowering plants (the overall effective size was no more than 1); however, only 24 species were included in their analysis.

The East Himalaya-Hengduan Mountains region locates in southwestern China and includes northwestern Yunnan Province, western Sichuan Province and southeastern Tibet. In Chinese, “Hengduan” means lands separated by mountains and rivers transversely. The Mekong River, Yangzi River and Salween River, along with many different mountains, go across this area from north to south, dividing this region into pieces. The East Himalaya-Hengduan Mountains region varies in elevation from 1200 meters to more than 6000 meters; therefore, this area contains various climates and vegetation types, from tropical seasonal forests to subtropical forests and temperate meadows. Benefiting from its various habitats and vast elevational span, many plant species in this area are differentiated by the Quaternary glacial and interglacial periods [16, 17]. For instance, the East Himalaya-Hengduan Mountains are the biodiversity and evolutionary center of the families Primulaceae [18], Ericaceae and Gentianaceae [19].

Previous synthetic studies on the degree of pollination limitation in the tropical forest in Atlantic Brazil and in alpine flowering plants from around the world focused on various flower traits, for example, the capacity for autonomous self-reproduction, the vegetation type and the flower shape [14, 15]. Given that the abundance and vitality of pollinators decreases with increasing elevation [20, 1], elevation is probably an important factor affecting the degree of pollination limitation [21]. Therefore, the degree of pollination limitation would be expected to increase with increasing elevation. However, to our knowledge, no study has synthetically assessed the relationship between elevation and the degree of pollination limitation. Considering that the elevation of the East Himalaya-Hengduan Mountains region varies substantially, this area is an ideal model to study the relationship between elevation and the degree of pollination limitation.

In the present study, we aim to answer the following specific scientific questions: (1) What is the degree of pollination limitation for the flowering plants growing on the East Himalaya-Hengduan Mountains? (2) Which plant reproductive features significantly affect the degree of pollination limitation that a plant suffers? (3) Does the degree of pollination limitation show an obvious correlation with elevation in the East Himalaya-Hengduan Mountains region?

Methods

Literature review and dataset

A search for the focal publications was primarily conducted in the Web of Science database (webofknowledge.com) and Google Scholar (scholar.google.com) using the keywords “Yunnan” or “Tibet” or “Sichuan” or “Himalaya” or “Hengduan” in combination with the terms “pollination” or “fruit set” or “seed set” or “hand poll*” or “supp* poll*”. To include more published pollination works conducted in this area, we also searched the Chinese publications database, CNKI (Chinese National Knowledge Infrastructure, www.cnki.net), using the keyword combinations mentioned above in Chinese. Some unpublished papers, theses and personal data graciously given by the authors were also added to this

analysis. The following criteria were used to select the focal publications: (1) studies of flowering plants growing on the East Himalaya-Hengduan Mountains, including plants in northwestern Yunnan Province, western Sichuan Province, southern Gansu Province and southeastern Tibet; (2) studies that applied hand pollination on the studied plants and assed the reproductive success of both hand- and open-pollination treatments; and (3) studies whose results included average seed set/seed production, standard deviation and sample size and fruiting proportion and sample size. For the fruit data recorded, we extracted the numbers of flowers with and without fruit in both hand- and open-pollinated treatments. For the seed set or seed production data, we extracted the mean, standard deviation and sample size of both treatments. For those data exhibited in graphs, we extracted the dataset from the graphs with ImageJ 1.31 [22].

To understand the effects of plant reproductive features on the degree of pollination limitation, several key traits were extracted, including the capacity for autonomous self-reproduction, pollination type (generalized vs. specialized pollination) [23], flower shape (restricted vs. nonrestricted) [24], rewards (unique vs. various) [25] and flowering time [26], from the collected studies or from the Flora of China. We assessed the capacity for autonomous self-reproduction by the reproductive success of bagged treatments and hand-pollination treatments. If the seed production/fruit set of the bagged treatment vs. hand-pollination treatments was over 50%, the species, which would otherwise be thought to be incapable of autonomous self-reproduction, was viewed as being capable of autonomous self-reproduction. The flowering time was separated into three categories: early spring (before May), summer (May to August), and after summer (August). The pollination pattern was assessed by the number of pollination functional groups. Specialized pollination plants had only one kind of pollination functional group; otherwise, a plant was regarded as having generalized pollination. We extracted the elevation from the publications if the authors provided it; otherwise, we extracted it from Google Maps based on the geographic coordinates or names the authors provided. The elevation was arranged as a continuous variable from 1213 meters to 4600 meters.

Given that studies of heteromorphic species had more than one data entry, we took the average of records as the final number for a species if the data did not differ significantly in elevation, pollination type, flowering time or flower feature. In total, 108 datasets from 94 species and 26 families were collected from 76 studies, and Primulaceae (14.04%), Gentianaceae (8.77%), Scrophulariaceae (10.53%) and Orchidaceae (14.91%) represented most of the collected species in our study.

Data Analysis

For the binary data, i.e., fruit set, we calculated the effect size with log odds ratios (ln(o)) obtained from a 2 X 2 table of the flowers with and without fruit in the hand- and open-pollinated treatments [27]. For the continuous data, i.e., seed set and seed production, we calculated the effect size by Hedges' d with the mean, standard deviation and sample size of the hand- and open-pollinated treatments [27]. The standard error recorded in studies was transformed to standard deviation by dividing by the sqrt of the

sample size. The effect size of each study was calculated in OpenMEE, a free meta-analysis software for ecology and evolution research [28]. To include as many datasets as possible, we transformed the log odds ratios to Hedges' d following Coopers' method [27]. The degree of pollination limitation was viewed as the reproductive success of hand-pollination treatment vs. open-pollination treatment, and the plant species were viewed as pollination limited if the effect size was positive and its 95% confidence interval did not overlap zero [29]; otherwise, it was not viewed as being pollination limited.

The overall effect size was calculated by the traditional method and phyloMeta method separately. For the traditional meta-analysis, we used a random model to calculate the overall effect size, which took into account the deviation from the true effect size that may be generated by differences between the studies. We calculated Rosenthal's fail-safe numbers to test the presence of publication bias in the datasets [30]. These numbers represent the number of nonsignificant, unpublished, or missing studies that would need to be added to a meta-analysis to change the results from significant to nonsignificant. If the fail-safe number is larger than five times the sample size plus 10, it is safe to conclude that the results are robust with the consideration of publication bias [30]. Because the Rosenberg fail-safe number was 80721 in the present study, which was much larger than the critical value (1080), there was no evidence of publication bias in the dataset. The classical meta-analysis, as well as the calculation of Rosenberg fail-safe number, was conducted with the "metaphor" package [31] in R 3.6.0.

For the phylogenetic meta-analysis, we constructed a list of plant species (family/genus/species) with the aid of the "plantlist" package [32]. The angiosperm APG III consensus tree was constructed [33], and the branch lengths were calibrated from the "ape" package [34], which is used for phylogenetic analysis. After that, the overall effect size of the phylogenetic meta-analysis was tested the by the "metafor" package [31] with the aid of the constructed phylogenetic tree mentioned above. Since the heterogeneity of the dataset was significant, several explanatory variants were added in the analysis. In the analysis, the flowering time, the capacity of autonomous selfing, the pollination type, the flower shape and the reward type were set as discontinuous explanatory variables, and the elevation was set as a continuous explanatory variable. The Q_m and p values were calculated for each explanatory variable, and the different categories within an explanatory variable were significantly different if the p value did not exceed 0.05. The correlation between the continuous explanatory variable (elevation) and the degree of pollination limitation was also calculated.

Results

- The degree of pollen limitation of the flowering plants in the East Himalaya-Hengduan Mountains

The overall effect size inferred by the traditional meta-analysis was 2.0004, with a 95% confidence interval [1.3264, 2.6743]. The overall heterogeneity was Q=4792.3756, P<0.001. The effect size inferred by the phylogenetic meta-analysis was consistent with the results of the traditional meta-analysis, and

the sigma value of the “species” in the analysis was zero, which indicated that a phylogenetic signal was not present in the calculated effects sizes. Moreover, 90% of the species exhibited pollination limitation (i.e., a positive effect size and the confidence intervals that did not overlap zero). These results indicated a severe pollination limitation for the flowering plants growing in the East Himalaya-Hengduan Mountains.

- Pollination limitation associated with plant features, flowering time and elevation

Five explanatory variables were included in the present analysis, and we did not find that the flower shape, reward type or flowering time accounted for the heterogeneity in the dataset. Elevation, the capacity for autonomous selfing and the pollination type accounted for a significant amount of the heterogeneity in the dataset (fig. 2). The degree of pollination limitation showed a significant correlation with elevation (fig. 3).

Discussion

Pollination limitation is frequently reported in various flowering plants in different places around the world [35.36]. Severe pollination limitation could cause a decrease in resources for flowering plants [6]. The present study reveals a severe pollination limitation for flowering plants growing in the East Himalaya-Hengduan Mountains region. We found that floral features, including the capacity for autonomous self-reproduction and the pollination pattern, accounted for a significant amount of the variation in the pollination limitation. We also found a statistically significant correlation between elevation and the degree of pollination limitation, which indicates that pollination limitation was more frequent among the flowering plants in high elevation places compared to those growing in low elevation places.

For the present dataset, we used a funnel plot and tested its symmetry to indicate publication bias. The p value of the symmetry test was greater than 0.05, which indicated there might be a possibility for publication bias. Several studies used an influence plot to exclude outliers, thus making the dataset perfectly fit the symmetry test [15]. The seed productions of the hand- and open-pollination treatments were generally not the key results for most publications, and studies with different degrees of pollination limitation would not be treated differently for publication. Moreover, the Rosenberg fail-safe number is 80721 in the present study, which is much larger than the critical value (1080); thus, it is safe to conclude that the results are robust with the consideration of publication bias [30]. Considering that a high degree of pollination limitation would most likely be the reality for flowering plants in the East Himalaya-Hengduan Mountains region [37], we would not eliminate specific values to make the data fit the symmetry test.

As expected, the capacity for autonomous self-reproduction accounts for a significant amount of the heterogeneity in the dataset. This is because the plants that are capable of autonomous self-reproduction

would largely rely on themselves for sexual reproduction; thus, the reproductive success of most autonomous selfing species does not rely on external pollination services; in other words, autonomous selfing could provide reproductive assurance for the plants [38]. In fact, many alpine plants rely on autonomous selfing for their reproduction success [39.40]. We also found that the pollination pattern, i.e., plants with generalized vs. specialized pollination, accounts for a significant amount of the heterogeneity in the dataset. This result indicates that the plants with generalized pollination that rely on various pollination functional groups could more effectively avoid pollination limitations in nature [23]. At some extent, specialized pollination system is unstable since the plants could not get pollination service if the specific pollinator was missing [23]; however, generalized pollination system could provide reliable pollination service for the plants in many cases, and is regarded to be more commonly found in plants than the specialized pollination system [41].

Our results showed a clear correlation between elevation and the degree of pollination limitation, which has been a common view for most scientists but was lacking statistical evidence. The richness, abundance and variability in pollinators are commonly thought to decline from low to high elevation areas [42, 43]. However, no studies have quantitatively assessed the correlation between elevation and the degree of pollination limitation. Our results provide clear evidence that pollination limitation, and probably the abundance of pollinators also, decrease from the low to high elevation areas. Pollinators are scarce in high elevation area, which cause severe pollination limitation for most alpine plant species. Under such condition, many alpine flowering plants may evolve to autonomous selfing or other strategy for their sexual reproduction.

In conclusion, we revealed severe pollination limitation for the flowering plants growing in the East Himalaya-Hengduan Mountains, which is one of the global biodiversity hotspots. In addition, we found a clear relationship between elevation and the degree of pollination limitation; that is, plants grown in high elevation places suffer more severe pollination limitations. The present study is the first to synthesize an analysis of the degree of pollination limitation in this area and to quantitatively assess the relationship between elevation and the degree of pollination limitation.

Declarations

Ethics approval and consent to participate

Not applicable

Consent to publish

Not applicable

Availability of data and materials

The original data from this paper are presented in the supporting information table S1.

Competing interests

The authors declare that they have no competing interests.

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Authors' Contributions

All authors have read and approved the final manuscript. JXF collected the data, applied the meta-analysis and prepared the manuscript for publication, and XYP was responsible for figure 1 and figure 2 and gave advice on revising the manuscript.

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Figures

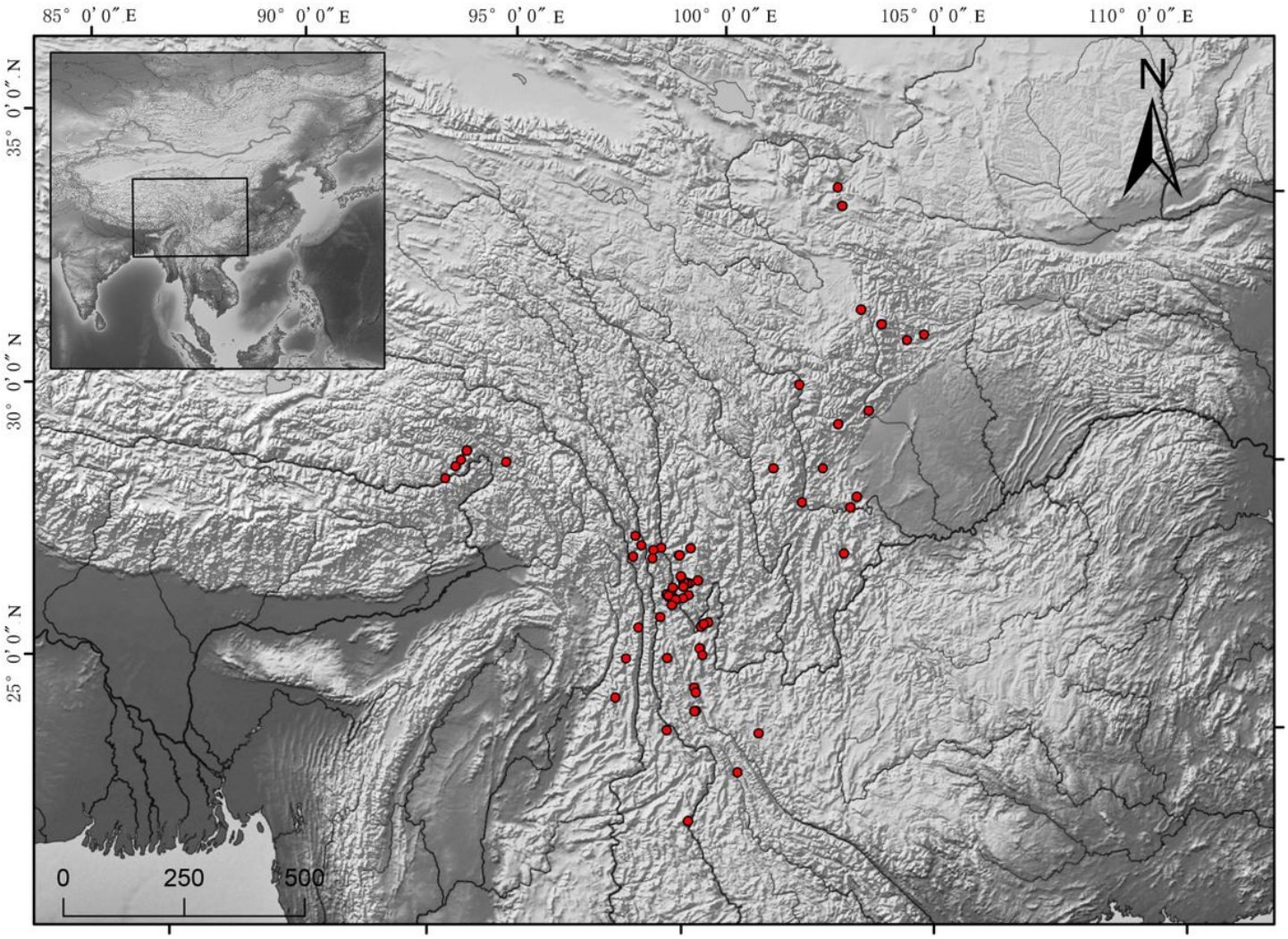

Figure 1

The locations of the plant species collected in this synthetic analysis. All the plant species are distributed within the East Himalaya-Hengduan Mountains region. Note: The designations employed and the presentation of the material on this map do not imply the expression of any opinion whatsoever on the part of Research Square concerning the legal status of any country, territory, city or area or of its authorities, or concerning the delimitation of its frontiers or boundaries. This map has been provided by the authors.

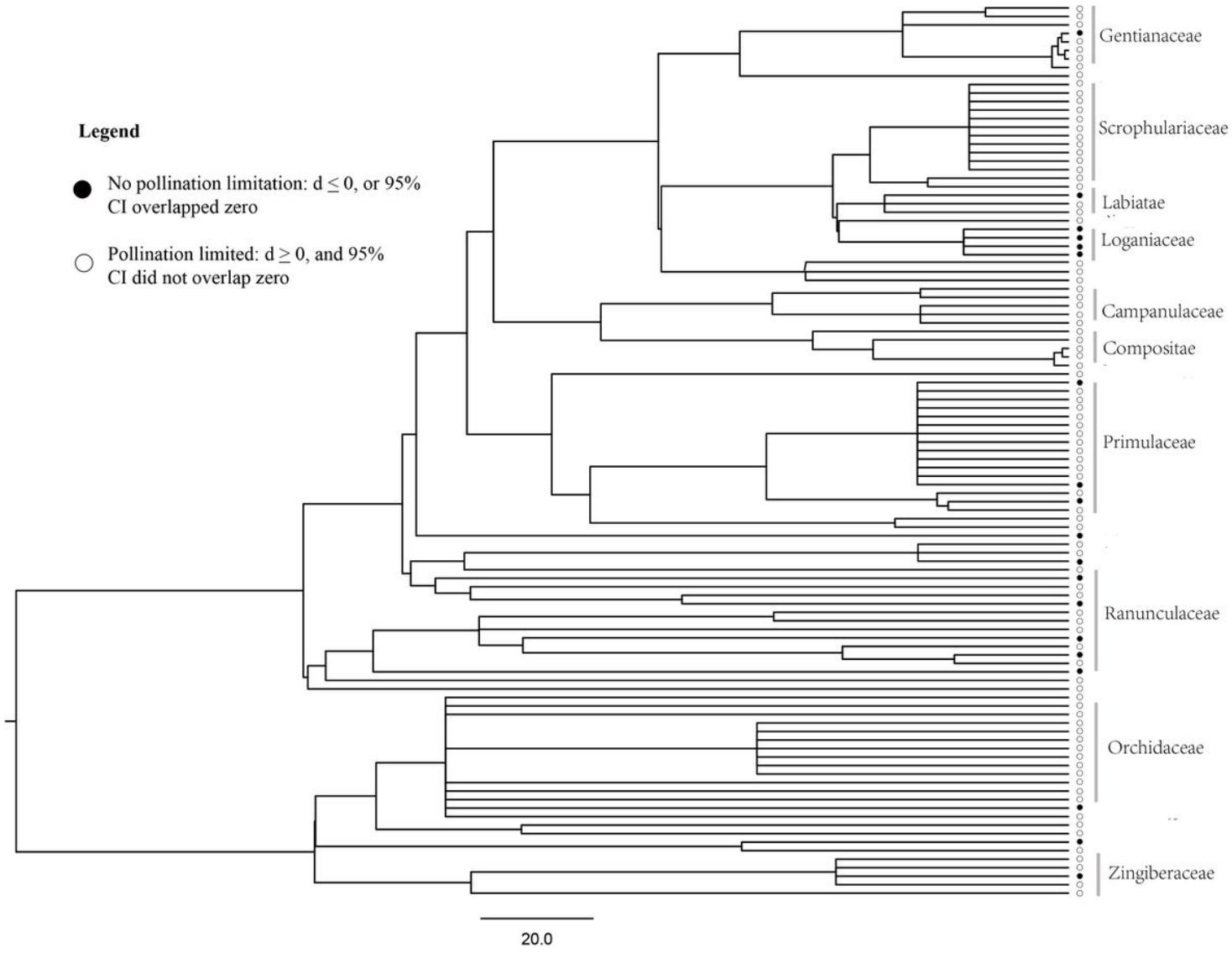

Figure 2

Distribution of pollination limitation across the phylogeny of plants in the East Himalaya-Hengduan Mountains. The black circles represent the species that were not pollination limited (the effect size is negative or the 95% confidence interval overlap zero), and the white circles represent pollination-limited species (the effect size is positive and the 95% confidence interval did not overlap zero).

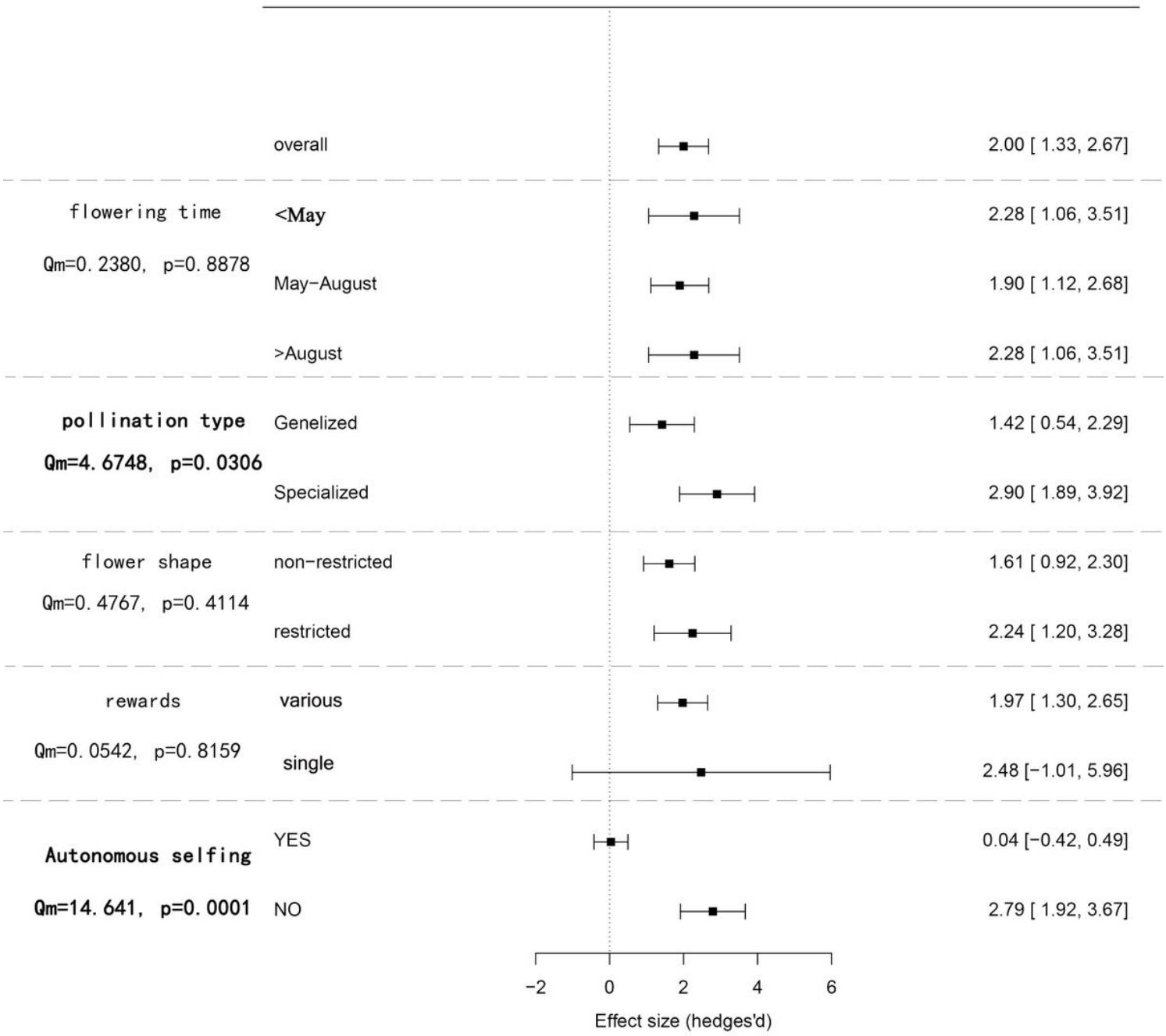

Figure 3

Effect size and the 95% confidence interval of the pollination limitation in the East Himalaya-Hengduan Mountains. The within-category heterogeneity (Qm) and P value are presented.

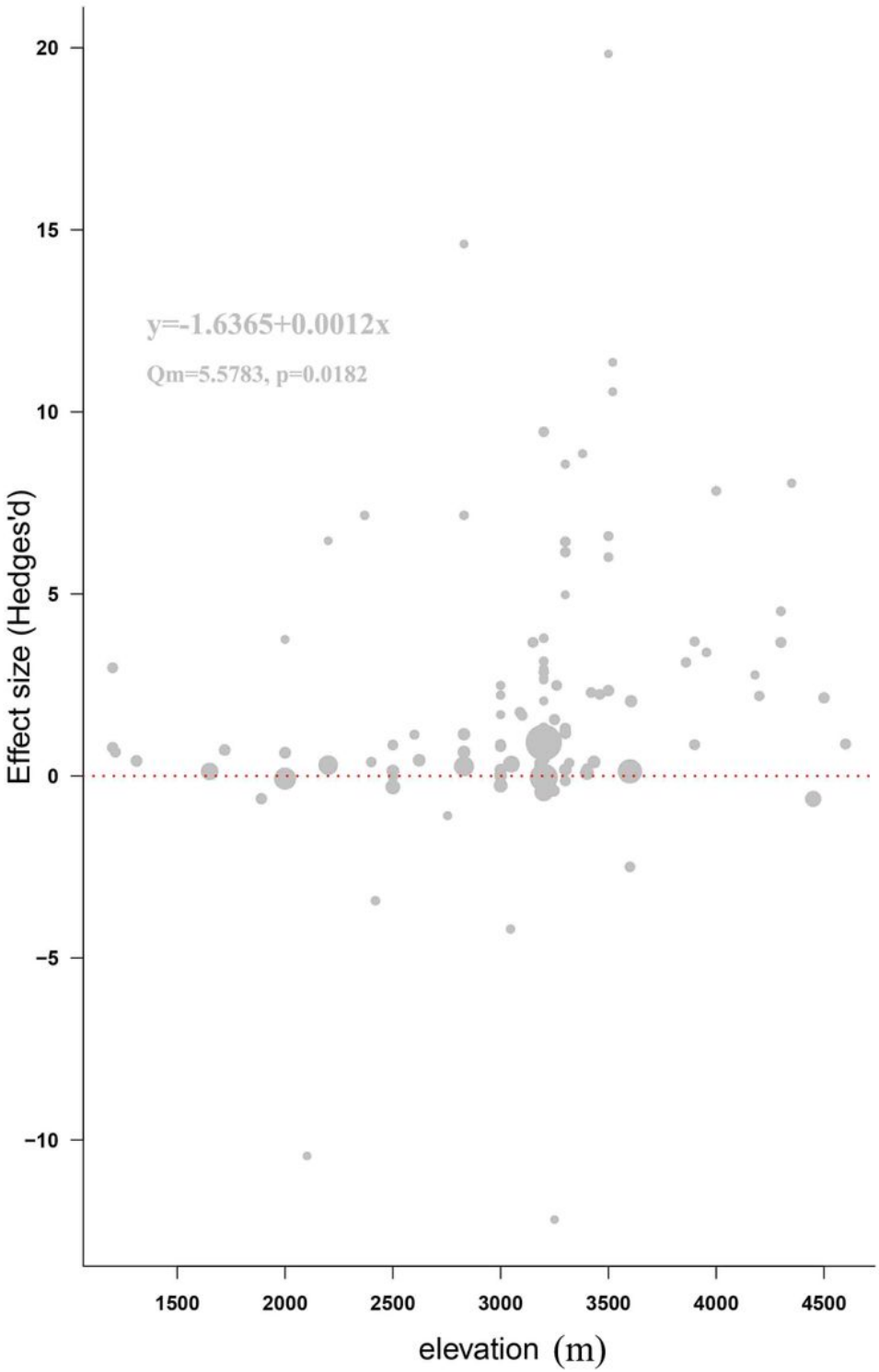

Figure 4

Correlation between elevation and the degree of pollination limitation. The within-category heterogeneity (Qm), P value and correlation coefficient are presented.

Supplementary Files

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- tables1pollinationlimitation.csv