

Rapid report

A century of pollination success revealed by herbarium specimens of seed pods

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Received: 2 May 2019

Accepted: 9 August 2019

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New Phytologist (2019)
doi: 10.1111/nph.16119

Key words: Fabaceae, floral structure, pollination success, pollinator decline, seed production.

Summary

- A widely observed pollinator decline around the world has led to the prediction that terrestrial ecosystems could be disrupted as plant pollination suffers, but declining pollination success has not been tested rigorously in wild plants, and it still remains unclear how pollination success of plant species responds differently in the context of pollinator decline.
- By viewing the number of seeds per pod as a quantitative measure of successful pollination, we examined seed pods in 4637 herbarium specimens of 109 obligately outcrossing legumes collected over the past century.
- We found that only 13 species showed significant temporal change with nine of those as an increase. None of the three subfamilies of legumes showed a consistent trend, and the subfamily Papilionoideae with the most specialized flowers, had increasing seed number per pod more often than decreasing.
- We conclude that legume pollination in China shows no sign of disruption and the effects of plant–pollinator disruption may be more complicated than simplistic predictions have allowed.

Introduction

Pollinators are fundamental to the maintenance of biodiversity and ecosystem function in terrestrial communities (Winfree *et al.*, 2011; Ollerton, 2017), and pollination provides many benefits for agriculture (Thomann *et al.*, 2013; Dicks *et al.*, 2016; Potts *et al.*, 2016). Observed declines in pollinator abundance and diversity in the past century (Biesmeijer *et al.*, 2006; Burkle *et al.*, 2013), especially for bees (Cameron *et al.*, 2011; Ollerton *et al.*, 2014), have led to concerns about broad shifts in ecosystem function. Since more than four-fifths of wild plant species partially or fully rely on animals for pollination (Ollerton *et al.*, 2011) and *c.* 75% of food crops have production limited by pollinators (Klein *et al.*, 2007; Garibaldi *et al.*, 2013), loss of pollinators could disrupt natural ecosystems (Aguilar *et al.*, 2006; Thomann *et al.*, 2013) and reduce crop production (Klein *et al.*, 2007; Dicks *et al.*, 2016; Potts *et al.*,

2016). Though biodiversity loss and decline in yield of crops due to pollinator loss have been examined in some regions (Biesmeijer *et al.*, 2006; Cameron *et al.*, 2011; Garibaldi *et al.*, 2013; Ollerton *et al.*, 2014), there has not been any tests for widespread changes in reproductive function of wild plant species due to pollinator loss on multi-species levels. By using herbarium specimens that preserve records of past seed output in China where pollinator species are in decline (Teichroew *et al.*, 2017), we provide the first such tests.

To estimate changes in seed production in the past century, we examined specimens of legume species (Fabaceae) collected since 1900 and stored at the herbaria of the Kunming Institute of Botany (KUN) and the Institute of Botany (PE), Chinese Academy of Sciences. Seeds were counted in one pod of each specimen (see Methods section later). This was straightforward to do visually and did not damage the specimens. The family therefore provides an excellent test of historical changes of the seed production in plants. We also used the three traditional subfamilies of Fabaceae to test whether pollinator specificity predicts greater disruption of seed

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production. Improved legume phylogenetics has altered subfamily classification (The Legume Phylogeny Working Group (LPWG), 2017), but the three groups serve our purpose because the traditional Mimosoideae have open, radially-symmetric flowers (actinomorphic), while Papilionoideae have well-known pea flowers, bilaterally symmetric with a closed keel (zygomorphic); the polyphyletic Caesalpinioideae have some of both (Xu *et al.*, 2010). The zygomorphic form, which forces an insect to push open the keel, is thought to involve more specialized pollination systems, often with bees (Arroyo, 1981), while accessible actinomorphic flowers are pollinated by many insects and birds (Arroyo, 1981; Stone *et al.*, 2003). Therefore, based on seed production per pod of the legume family we asked first whether seed production (number) per pod varied over the past century, and second, whether species with more specialized flowers showed greater loss of seed output. Although this analysis does not address total reproductive output via seeds, it does specifically address pollination, because failed pollination would lead first to fewer seeds in pods.

Materials and Methods

To estimate the historical changes of seed production over the past century, we examined specimens of legumes (Fabaceae) collected since 1900 in the herbaria of the KUN and the PE, Chinese Academy of Sciences, the largest two collections of plant specimens in China. Additionally, as a partnership with the Millennium Seed Bank (MSB) Project, the Germplasm Bank of Wild Species (<http://www.genobank.org/>) was established in the Kunming Institute of Botany in 2007 with the aim to perform *ex situ* conservation of genetic resources for wild species (Li & Pritchard, 2009). In the past 10 yr, extensive collections of seeds together with specimens of wild plant species have been carried out throughout China by numerous collaborators (Sun, 2013). The number of wild species in the germplasm bank exceeds 10 000, providing additional specimens for the study (Hart *et al.*, 2014; Yu *et al.*, 2016). In total, 4637 specimens with fruits from 109 legume species were used for final analysis, all collected between 1900 and 2013 from across China (Supporting Information Fig. S1). Specimens from individual species generally span long time periods, with 65 (59.6%) out of 109 species spanning ≥ 60 yr, 82 (75.2%) species spanning ≥ 50 yr, 94 (86.2%) species spanning ≥ 40 yr, and 101 (92.7%) species spanning ≥ 30 yr (Fig. S2). *Desmodium multiflorum* had the longest span, 107 yr, and only three species had spans < 20 yr, with 18 yr for *Mucuna bracteata*, 10 yr for *Dalbergia sericea*, and 9 yr for *Vicia amurensis*.

We counted visible seeds in one intact pod on each of the specimens with fruit. If there were more than one pod on a specimen, we selected one pod to count at random after excluding the largest and smallest pods on the specimen. We searched the literatures to determine which of the species were capable of self-pollination (Arroyo, 1981; Huang *et al.*, 2014), and excluded all those capable of self-pollination. For modeling, seed number, so called 'seed production' in each pod was divided by the mean per species, so called 'relative seed production'. As a result, the mean relative seed production within taxa (species, genus, and subfamily) is fixed at one in every species, genus, and subfamily. First, a null model was utilized to detect the variation in seed production per

pod among geographic regions (100-km grid cells). The null model was unconditional, without any predictor but random intercepts assigned per grid cell. Second, a full linear mixed effect model (Pinheiro & Bates, 2000) was employed to investigate the effects of time (year) and life form (herb or wood) on seed production. The slope of the regression of relative seed production (the year effect) was allowed to vary by geographic regions and by taxa (i.e. random slopes of year). We assumed that the random slopes of year by geographic regions and by taxa were independent of each other. Biologically, the three levels of taxa: species, genus, and subfamily are nested orderly, and thus we assumed that the random slope of year assigned by the lower level were nested within the higher ones. The intercept of the regression was allowed to vary with geographic region (i.e. a random intercept) but not with taxa (because it was defined as one). Seed production was transformed using the Box–Cox technique to generate residuals as symmetric as possible (Fig. S3). The predictor, year, was standardized to a mean of zero and a standard deviation of one.

In addition, we examined the change in relative seed production through time separately for each of species with ≥ 10 samples. There were often multiple specimens within geographic regions (100-km grid cells) for individual species, which allowed the change through time, that is, the regressed slope of time, to vary across geographic regions. However, we found a very weak random effect from geographic regions (Table S1), that is, the relative seed production and the slope of time negligibly depended on geographic regions. We thus did the separate analyses per species using simple linear regression. The specimens for those individual species spanned ≥ 18 yr. We also did linear mixed effect regression as a supplement (Notes S1), which did not alter our conclusion merely with the decline in relative seed production with time becoming significant no longer in *Desmodium elegans* of Papilionoideae while the decline significant in *Acacia pennata* of Mimosoideae (Fig. S4).

We performed all analyses using the R packages 'LMERTEST' (v.2.0) (Kuznetsova *et al.*, 2015), 'MUMIN' (v.1.14.0) (Bartoń, 2015), and 'MASS' (v.7.3) (Ripley, 2017). We visualized the fixed effect with the R package 'VISREG' v.2.2-0 (Breheny & Burchett, 2015). Skewness was checked with the R package 'PERFORMANCEANALYTICS' (v.3.4.4) (Peterson *et al.*, 2018). The intra-class correlation coefficient (ICC) was calculated with the R-package 'SJSTATS' (v.0.14.1) (Lüdecke, 2018). Please refer to the Supporting Information for R scripts of our analyses (Notes S1).

Results and Discussion

We identified 109 species that are obligate outcrossers, thus incapable of self-fertilization. This includes 4637 specimens collected across much of China for > 100 yr, with the three main subfamilies all well-represented (Fig. S1). The temporal record was at least 60 yr in most species (Fig. S2). In the legume family as a whole, and in the three subfamilies each, there was no trend of declining seed production per pod through time (Fig. 1; Table S1). The average effect across species (the fixed effect from a linear mixed effect model) was an increase of seed per pod through time, but it was not significantly different from zero (Fig. 1; Table S1).

Individual species varied in change through time, but roughly equal numbers of species showed increasing vs decreasing seed production (Table S2). Only four out of 95 species with ≥ 10 samples showed significant decline in seeds per pod through time, while nine showed a significant increase (Fig. 2; Table S2). The subfamily Papilionoideae, with a more specialized pollination system, showed significant increases in seven species and declines in two species, while Mimosoideae had significant increases in two species and a decline in one species. Only one species of Caesalpinioideae had a significant trend. Changes of seed production per pod did not differ between herbaceous and woody species (Fig. 1; Table S1).

We find reasonably firm evidence that the family Fabaceae in China has suffered no loss of seed output per pod over the past century, even in subfamily Papilionoideae with its specialized flowers. Since we excluded species capable of selfing, and wind is not relevant in Fabaceae pollination (Arroyo, 1981), we conclude that there is no evidence for reduced pollination via animals, though pollinators are declining in China (Teichroew *et al.*, 2017). Either these plants are not pollinator limited, or pollinator populations have remained adequate in the past years in China. Pollen limitation of seed production occurs widely in flowering plants (Burd, 1994; Larson & Barrett, 2000; Ashman *et al.*, 2004;

Knight *et al.*, 2005; Rosenheim *et al.*, 2016), and thus we suggest that pollinator populations to legumes could be adequate in the past year in China, despite the fact that we cannot identify the changes of pollinator species and/or abundance. Our results of nonsignificant changes in mutualisms between legumes and their pollinators are actually parallel to constant conspecific pollen deposition on stigmas from herbarium species collected in the past century (Johnson *et al.*, 2019).

In fact, although pollinator decline has been actively advocated (Biesmeijer *et al.*, 2006; Burkle *et al.*, 2013), several empirical observations suggests pollinator visitations to plant species do not decrease. For an instance, a generally significant increase in pollinator functional abundance was found on plant-community level from undisturbed montane habitats of the Sierra de Cazorla in the past two decades, despite the fact that different pollinator functional groups showed different patterns of changes in timescale (Herrera, 2019). Moreover, index of pollen limitation of fruit production also did not show temporal increase in outcrossing *Erythronium grandiflorum* (Liliaceae) over a 26 yr period (J. D. Thomson, pers. comm. from University of Toronto), suggesting that seed production of naturally pollinated flowers did not decrease in the past years, although index of pollen limitation increased in a 17 yr period since 1993 (Thomson, 2010). Accordingly, in natural ecosystems, plant–pollinator relationships could be complicated because plant species could recruit multiple pollinators, and this might offset the decline of some pollinators (Kaiser-Bunbury *et al.*, 2010). This recruitment of new pollinators has been confirmed by the increased proportions of heterospecific pollen deposition on stigmas in recent 50 yr after examinations of herbarium flowers over a century period (Johnson *et al.*, 2019). Furthermore, rapid cultivation of nectariferous crops and the resultant development of apiculture in China (Wu *et al.*, 2007) might have contributed pollination due to the important role of honeybees in plant–pollinator interaction in natural habitats (Duan & Liu, 2007; Hung *et al.*, 2018). However, we cannot distinguish these explanations presently since we have no direct evidence on pollinators of the species we studied.

The principal caveat to our conclusion is that we did not study total plant reproduction since only seed set per pod is available in specimens. We contend that this is a valid measure of pollination success (Dafni *et al.*, 2005), since pollinator loss is likely to mean fewer seeds per flower and thus per pod. We cannot draw any conclusions on total pod production per individual plant, but that is outside the realm of pollinator mutualisms. Another caveat about resource limitation on seed production might not be neglected since changes of resource availability could affect both seed quantity and quality (Zhang *et al.*, 2011). We cannot estimate resource availability of involved plant species presently, but we consider that pollen limitation might be more important in limiting seed production than resource limitation because of the widely observed pollen limitation in flowering plants (Burd, 1994; Larson & Barrett, 2000; Ashman *et al.*, 2004; Knight *et al.*, 2005; Rosenheim *et al.*, 2016). Collectively, our results suggest that the pollination success of legumes generally maintains constant in the past century, indicating the stable pollinator service to legumes. Given our results and widely reported pollinator decline, we highlight the need for establishing

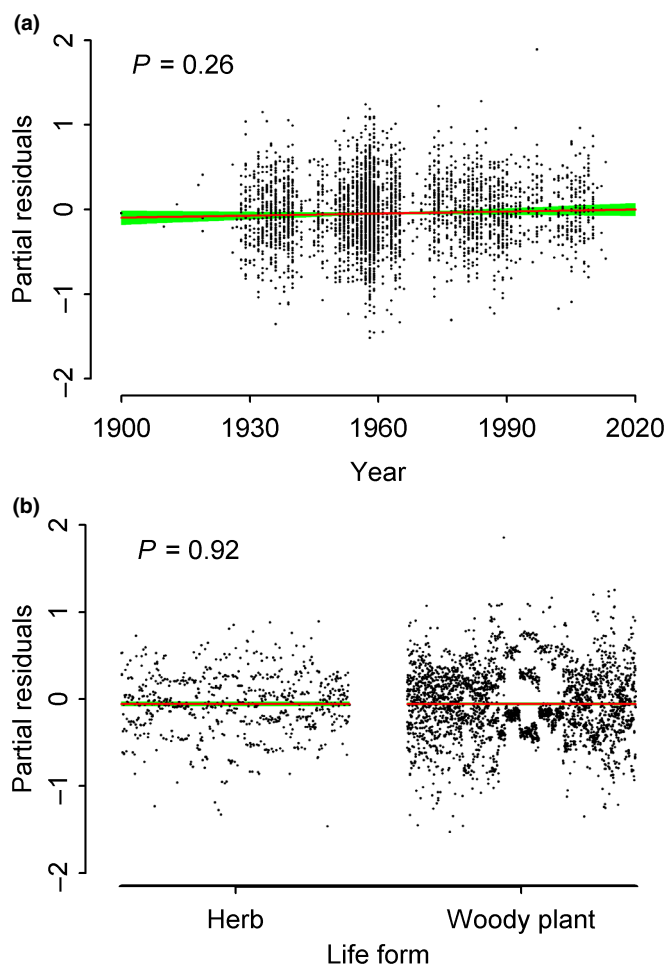


Fig. 1 Changes of partial residuals in relative seed production as a function of time (a) and life form (b), from the linear mixed effect model. Fitted lines are in red and 95% confident intervals in green.

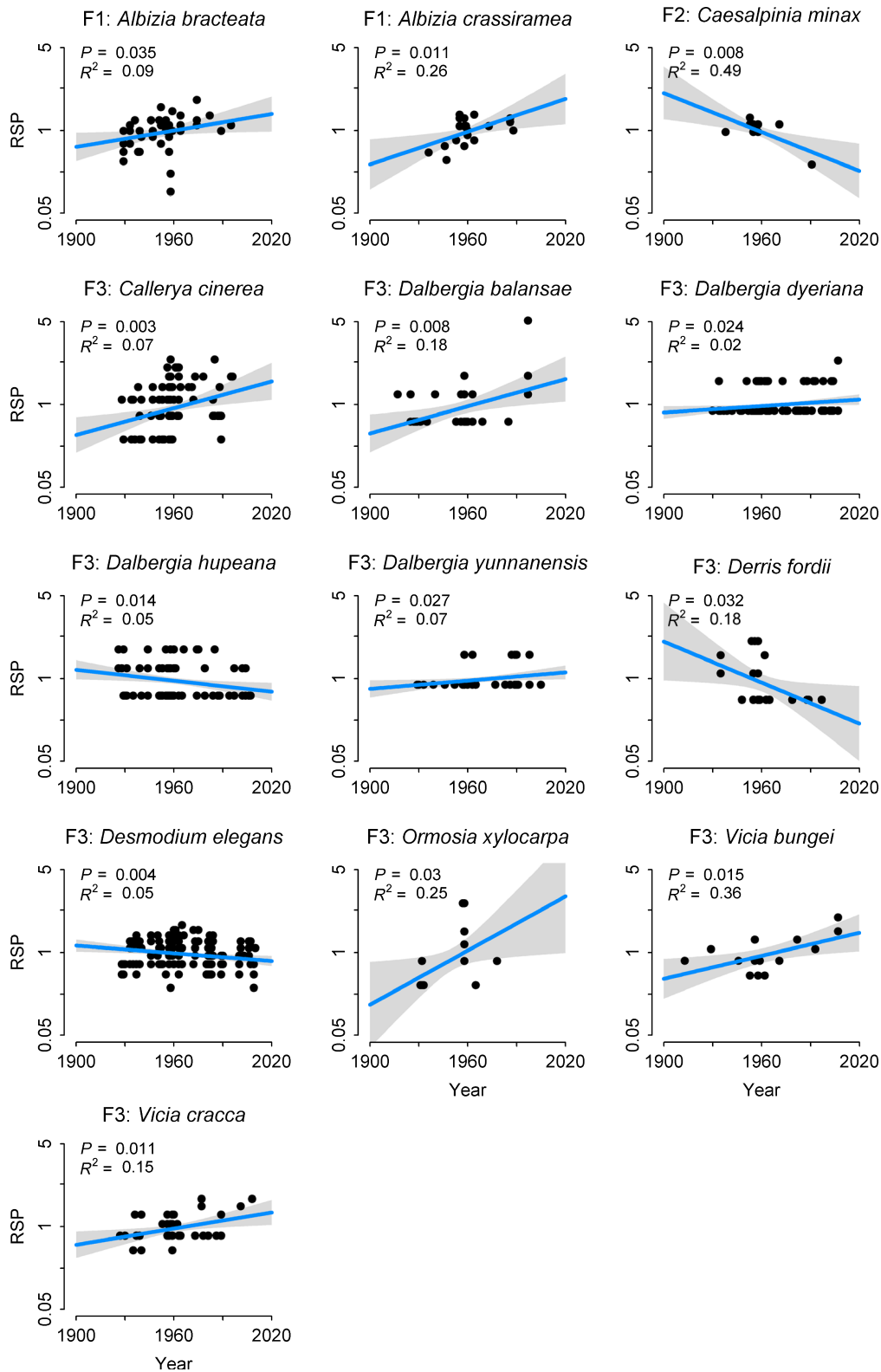


Fig. 2 Significant changes of relative seed production (RSP) per pod over time (year) for each of the 13 species with > 10 samples. Seed production is Box–Cox transformed, and regression lines (blue) are fitted with 95% confident intervals (gray). F1, F2 and F3 refer to the subfamily Mimosoideae, Caesalpinioideae, and Papilionoideae, respectively. After considering random effects explained by geographic regions, the change becomes nonsignificant for *Desmodium elegans* but remained significant for the other 12 species, while *Acacia pennata* of Mimosoideae turns significant in the decline through time.

long-term monitoring of wild pollinator populations and their ecosystem effects in China and globally, in order to make more precise prediction about the dynamics of complex pollinator–plant interactions.






Acknowledgements

The authors are grateful to Prof. Richard Condit for his constructive suggestions and improvement of the manuscript, and Prof. Jens-Christian Svenning and Dr Zachary Y. Huang for their comments. This work was financially supported by the Strategic Priority Research Program of Chinese Academy of Sciences (grant nos. XDA20050000, XDA19050503), the Natural Science Foundation of China (grant nos. 31570385, 31590820). The authors declare no competing interests.

Author contributions

Y-WD and Y-PY supervised the project. TL, Z-QZ, L-LW and Y-LT collected the data from specimens. Y-WD, H-BR and Y-PY performed the analysis and wrote the manuscript. Y-WD and H-BR contributed equally to this work.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Geographic distribution of specimens for 109 legume species.

Fig. S2 Distribution of time period (year) over which 109 legume species span.

Fig. S3 Histograms of relative seed production, Box–Cox transformed relative fitness, and residuals of linear mixed effect model, and corresponding normal QQ plots for them.

Fig. S4 Simple linear regression and linear mixed effect model of relative seed production (RSP) per pod against year for *Acacia pennata* and *Desmodium elegans*.

Notes S1 R scripts for the main statistical analyses in the present study.

Tables S1 Variation of relative seed production per pod between 100-km grid cells and change in relative seed production through year and against life form.

Tables S2 Linear regression of relative seed production per pod against year in three subfamilies of Fabaceae, with significant change at the 0.05 level in gray shade.

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