

Global meta-analysis shows that threatened flowering plants have higher pollination deficits

Received: 9 February 2024

Accepted: 10 June 2025

Published online: 01 July 2025

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Most flowering plant species rely on animal pollinators to reproduce, but insufficient pollen receipt, or pollen limitation, commonly occurs and is mediated by plant traits. Pollen limitation could either exacerbate extinction threat or arise as a consequence of population and range declines in threatened plants, leading to the expectation that pollen limitation should be higher in threatened compared to non-threatened plants. To test this, we perform a meta-analysis on a global dataset of pollen limitation from 2633 pollen supplementation experiments, integrating plant threat status and thirteen reproduction and life history traits. Threatened plant species have 26% higher levels of pollen limitation than non-threatened species. This pattern is moderated by plant traits and geographic location: we find higher levels of pollen limitation for threatened compared to non-threatened species for pollinator-dependent plants and for plants found in Asia and temperate zones. Using path analysis, we find that plant traits, study region, and threat status are causally linked to pollen limitation. We suggest that plant traits such as auto-fertility, which strongly predict pollen limitation, should be considered in global databases on plant threat. Further, preventing pollen limitation through habitat and pollinator management is a promising path to preventing plant extinction.

Many plant species are threatened by extinction from anthropogenic disturbances, including climate change, land use change, biological invasions, and overharvesting^{1,2}. It is estimated that nearly 45% of angiosperm plant species are threatened with extinction³, and this number is expected to rise as it is estimated that more than 100,000 plant species are yet to be discovered⁴ and newly discovered species are more likely to be classified as threatened⁵. Understanding the main threats to plant species is key to developing scientifically informed conservation practices^{6,7}.

Receipt of pollen in low quantity or quality can lead to decreased reproductive success despite adequate resources such as water and nutrients, since flowering plants are sessile organisms that depend on biotic or abiotic agents to transport pollen for sexual reproduction⁸. This phenomenon is referred to as pollen limitation^{8–11}, and it is well known that many plant species experience pollen limitation¹¹. However, it is currently not known whether threatened plant species have similar or higher levels of pollen limitation than non-threatened species. In addition to documenting patterns of pollen limitation based on

plant threat status, it is equally important to understand the potential processes involved. For example, it could be that anthropogenic factors result in plant species becoming threatened, which in turn may increase pollen limitation as population and range sizes decrease (i.e., threat status causes pollen limitation). Alternatively, plant functional traits might make plants more vulnerable to becoming both threatened and pollen-limited, resulting in a non-causal association between threat status and pollen limitation (i.e., plant traits cause pollen limitation and threat status). Finally, pollen limitation might act as an extinction threat itself and cause plants to become threatened (i.e., pollen limitation causes threat status).

Taxon-focused empirical studies have demonstrated the existence of strong pollen limitation for threatened and locally rare plant species^{12–17}. These studies worldwide have largely suggested that anthropogenic disturbances, such as habitat fragmentation or degradation, are the primary threats, and that pollen limitation then occurs due to reductions in plant population size^{18,19}. In contrast, studies that have taken a meta-analysis approach have shown only weak associations between pollen limitation and indicators of threat, such as abundance and endemism^{20,21}. This suggests that a global examination of the direct association between pollen limitation and threat status is needed, as well as consideration of the direction of causality.

Reproductive traits, such as self-incompatibility, dichogamy (male and female reproductive organs mature at different times), and herkogamy (the spatial separation of anthers and stigmas within flowers), have evolved to prevent self-fertilization and promote outcrossing in many flowering plants^{8,22–27}. However, these traits also make plants more dependent on animal pollinators, and thus more prone to pollen limitation following natural and anthropogenic changes to their pollinators^{8,10,11,28,29}. In contrast, plants that are autotetraploid (the ability to autonomously self-fertilize) and/or self-compatible have greater reproductive assurance, which makes them less dependent on animal pollinators and less prone to pollen limitation^{10,11,29}. Furthermore, these reproductive traits are often associated with plant life histories: short-lived plant species with limited temporal reproductive opportunities often have traits that assure successful pollination, are less pollinator-dependent and have lower pollen limitation, whereas longer-lived plant species more often have traits that promote outcrossing, are more pollinator-dependent and have higher pollen limitation^{10,29–32}. In addition, plants have evolved suites of floral traits (i.e., pollination syndromes) to attract certain pollinators³³, which may offer higher pollination efficiency due to trait matching and high fidelity. However, plants with specialized flowers, such as restrictive floral shapes or hard-to-access rewards, have been shown to have higher pollen limitation than those with more generalized flowers, potentially because anthropogenic activities disrupt the specialized pollinators these plants depend on or disrupt the potential for the interaction to take place (e.g., temporal mismatches due to climate change)^{11,34–39}.

These same reproductive and life history traits might also determine whether or not plants are likely to become threatened by anthropogenic changes. For example, plants that are self-compatible and/or autotetraploid can establish a population from a single individual. These traits allow these species to more easily establish new populations and shift their range distribution in response to anthropogenic threats such as climate and land use change^{40–42}, provided that suitable habitats are available. Plant longevity might also be associated with threat status. Longer-lived plants recruit offsprings over a longer period of time, and factors that cause even a small increase in adult mortality can cause significant population declines because it takes populations of these species such a long time to replace lost adult individuals through new recruitment⁴³.

Path analysis provides a way to disentangle the relationships among multiple variables and to elucidate direct and indirect pathways. Here we use this approach to compare a baseline model, representing no relationship between pollen limitation and threat

status, but incorporating the known effects of traits on pollen limitation, against alternative models capturing the possibilities that (1) pollen limitation causes threat status, (2) threat status causally influences pollen limitation, and/or (3) pollen limitation and threat status are non-causally associated because the same traits influence them both. An updated global database of pollen limitation (GloPL⁴⁴) provides the opportunity for a global meta-analysis to test whether threatened plants exhibit stronger pollen limitation than non-threatened ones and to elucidate the causal relationships between plant traits, pollen limitation, and threat status. We specifically addressed the following questions: (1) Do reproductive and life history traits differ between threatened and non-threatened plant species? (2) Do threatened plants have greater pollen limitation compared to non-threatened plants, and does this difference depend on plant traits? (3) What are the paths that best describe the causal relationships among plant traits, pollen limitation, and threat status?

In this work, we leverage a global phylogenetic meta-analysis of 2633 pollen supplementation experiments to examine the association between plant traits, pollen limitation, and extinction risk. We find that threatened plants experience significantly greater pollen limitation than non-threatened plants, which is mediated by reproductive and life history traits and biogeographic origins. Path analysis supports that pollen limitation is causally influenced by threat status as well as plant traits and the studied regions. These findings reveal a link between plant reproductive ecology and extinction vulnerability, offering insights for biodiversity conservation.

Results

Frequencies of threat status do not differ across plant traits or major phylogenetic clades

For all 13 traits, we found similar trait frequencies for threatened and non-threatened plant species (Supplementary Data 1 and Supplementary Fig. 1; all χ^2 p -values > 0.05). Likewise, we found a similar frequency of threat status among the major phylogenetic clades, i.e., the magnoliids, the monocots, and the eudicots (Fig. 1; $\chi^2 = 4.24$, $df = 2$, p -value > 0.05).

Stronger pollen limitation in the monocots

We observed higher pollen limitation in the monocots ($n = 640$; 0.75 ± 0.04) compared to the eudicots ($n = 1964$; 0.39 ± 0.02) (Fig. 1; $F = 48.56$, p -value < 0.001), but similar values amongst all other pairwise comparisons (magnoliids vs. monocots p -value = 0.890; magnoliids vs. eudicots p -value = 0.136).

Stronger pollen limitation in threatened plants

Threatened plant species exhibited 26% higher pollen limitation ($n = 458$; 0.58 ± 0.04) than non-threatened species ($n = 1670$; 0.46 ± 0.02) ($t = 2.79$, $df = 703.16$, p -value = 0.0054) (Supplementary Table 1 and Fig. 2a). The following factors moderated the relationship between threat status and pollen limitation: autotetraploidy (AF), self-compatibility (BS1), growth form (LH3), overall floral structure (FS), reward type, continent and region (Table 1 and Fig. 2).

Among species that depend on pollinators, those that are threatened ($n = 331$) exhibited greater pollen limitation compared to non-threatened species ($n = 1310$) (0.70 ± 0.05 vs. 0.53 ± 0.02 ; $t = 3.19$, $df = 501.47$, p -value = 0.0015; Fig. 2b); however, threatened ($n = 89$) and non-threatened ($n = 344$) autotetraploid species showed similar magnitude of pollen limitation (p -value > 0.05). In partially self-compatible plants, threatened species ($n = 91$) had greater pollen limitation than non-threatened species ($n = 235$) (0.68 ± 0.11 vs. 0.36 ± 0.05 ; $t = 2.78$, $df = 135.77$, p -value = 0.0063); nevertheless, no difference in pollen limitation was determined between threatened and non-threatened species in other BS1 categories (p -value > 0.05) (Fig. 2c). For herbaceous plants, we found that the threatened species ($n = 238$) had greater pollen limitation than non-threatened species ($n = 1178$) (0.61 ± 0.06

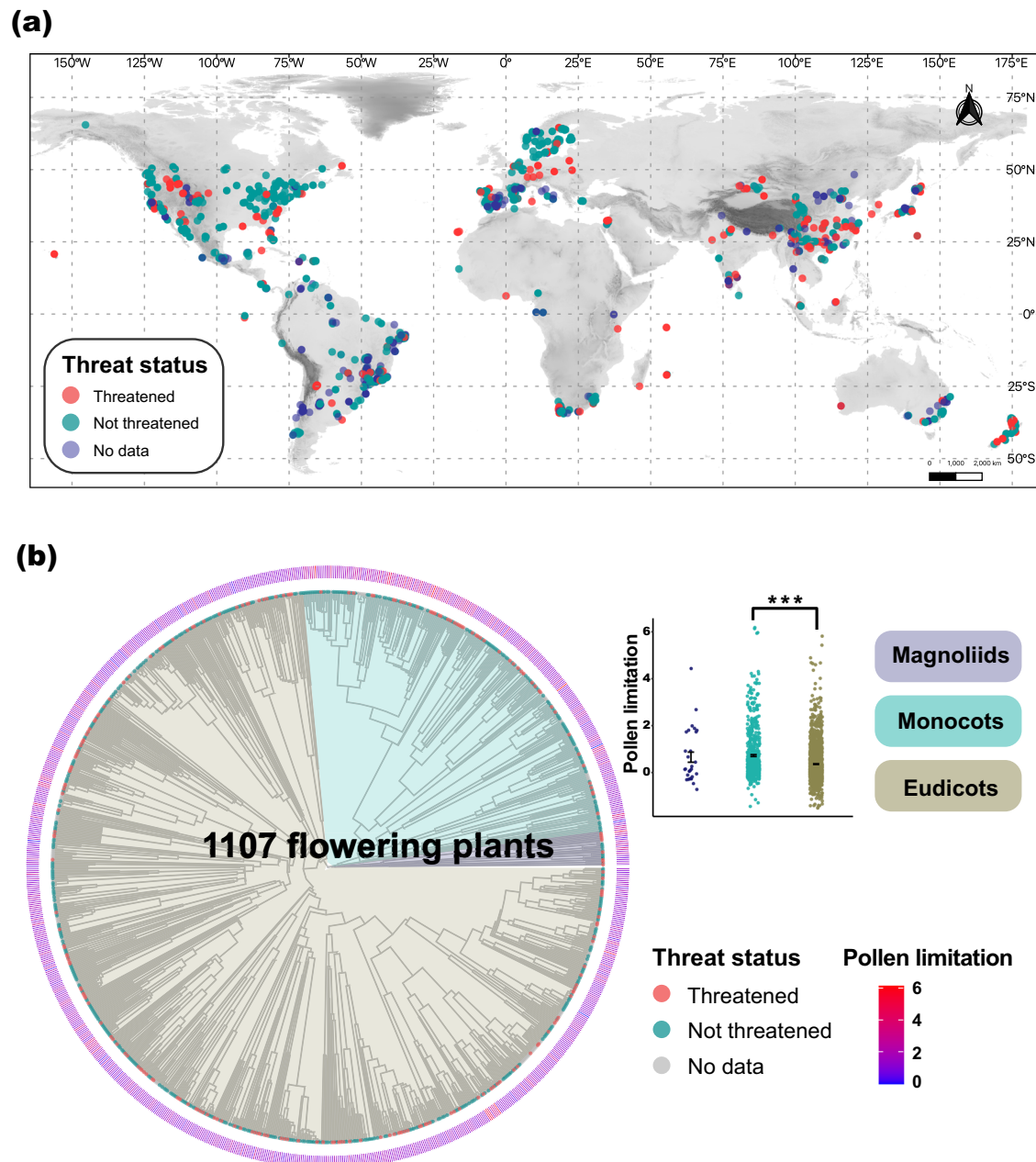


Fig. 1 | Global distribution and phylogenetic patterns of pollen limitation in flowering plants. **a** The distribution map of 2633 pollen supplementation experiments from the GloPL database. On the map, each record of a pollen supplementation experiment is colored in accordance with the threat status of the studied species. The world map with elevation data was downloaded from the WorldClim database⁷⁴. Among the 1107 species, 224 of them are considered threatened, 602 of them are considered non-threatened, and the remaining 281 species lack sufficient threat status data (see tip color). **b** The phylogeny of 1107 studied flowering plant

species. Major angiosperm groups are denoted. The mean pollen limitation effect size for each species is given in a heatmap (the outer circle). The mean value $\pm$ standard error of the pollen limitation effect size of three major phylogenetic clades is shown (upper-right panel). The one-way ANOVA and post-hoc analysis suggested a higher pollen limitation in the monocots than the eudicots (p -value $< 2e-16$). Significant differences are indicated: *** p -value < 0.001 . Source data are provided as a Source Data file.

vs. 0.44 ± 0.02 ; $t = 2.67$, $df = 314.19$, p -value = 0.0081), while no pollen limitation difference was found between woody threatened and non-threatened plants (p -value > 0.05) (Fig. 2d). Among plants with generalized floral structures, the threatened species ($n = 253$) showed greater pollen limitation than their non-threatened counterparts ($n = 1072$) (0.60 ± 0.06 vs. 0.35 ± 0.02 ; $t = 4.07$, $df = 317.17$, p -value < 0.0001), while no pollen limitation difference was found between plants with specialized floral structures (p -value > 0.05) (Fig. 2e). For plants offering only pollen as reward, threatened plants ($n = 37$) showed greater pollen limitation compared to the non-threatened ones ($n = 143$) (0.89 ± 0.20 vs. 0.44 ± 0.08 ; $t = 2.08$, $df = 46.89$,

p -value = 0.0428) (Fig. 2f). Similarly, threatened plants that offer nectar and pollen ($n = 142$) exhibited stronger pollen limitation than those non-threatened plants ($n = 500$) (0.53 ± 0.06 vs. 0.35 ± 0.03 ; $t = 2.64$, $df = 214.38$, p -value = 0.0089). No pollen limitation difference appeared between threatened and non-threatened species with more specialized rewards (p -value > 0.05).

In the continent of Asia, threatened plants ($n = 136$) showed stronger pollen limitation than the non-threatened plants ($n = 178$) (0.83 ± 0.09 vs. 0.58 ± 0.07 ; $t = 2.16$, $df = 283.88$, p -value = 0.0314) while no pollen limitation difference was found between threatened and non-threatened species in the other continents (p -value > 0.05).

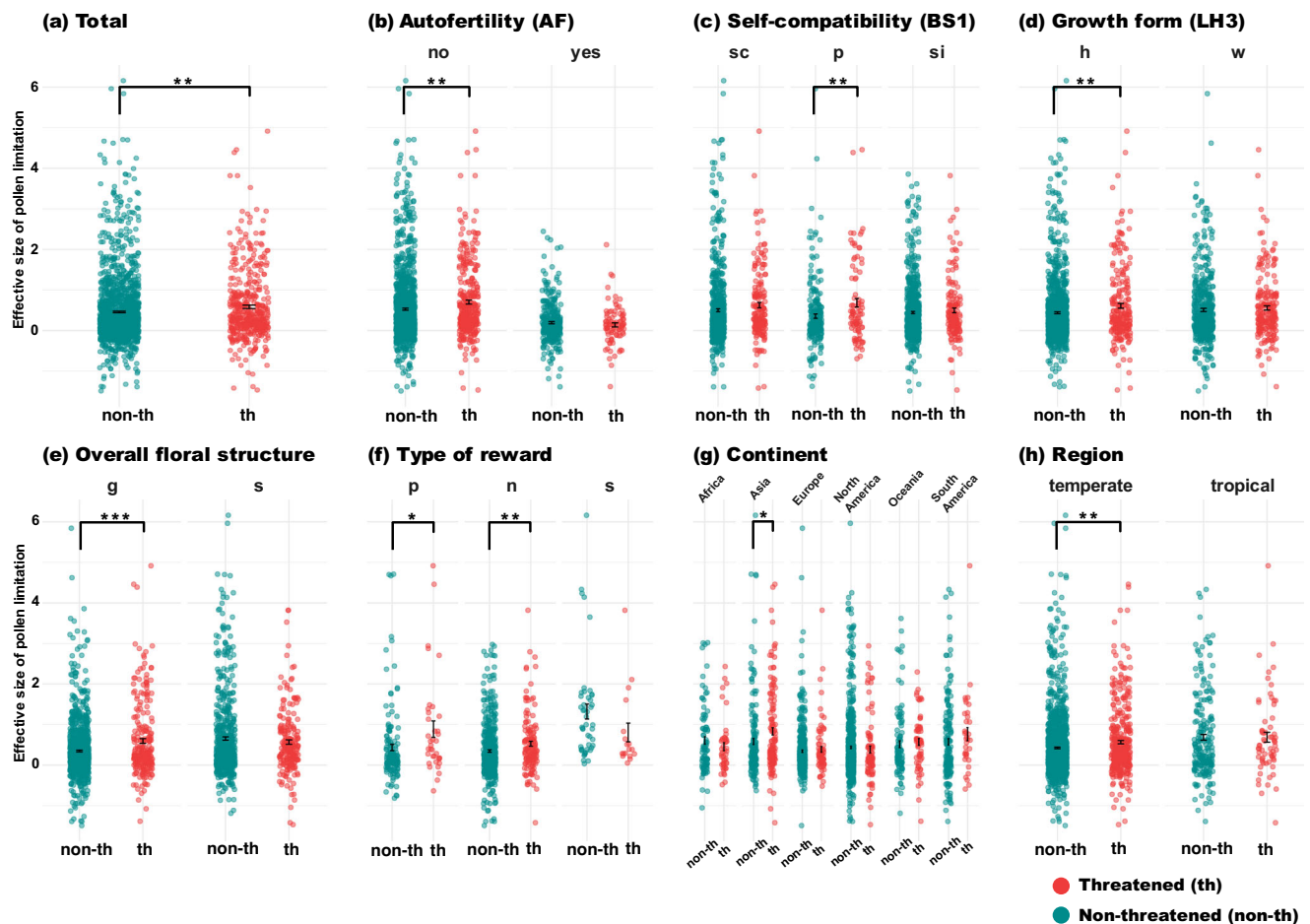


Fig. 2 | Pollen limitation effect size for records (pollen supplementation experiments) in each combination of threat status and trait category. **a** Total (n of threatened plants = 458, n of non-threatened plants = 1670, p -value = 0.0054); **b** Autofertility (AF-no: n of threatened plants = 331, n of non-threatened plants = 1310, p -value = 0.0015; AF-yes: n of threatened plants = 89, n of non-threatened plants = 344, p -value = 0.3272); **c** Self-compatibility (BS1), sc = self-compatible (n of threatened plants = 175, n of non-threatened plants = 697, p -value = 0.0995), p = partial self-compatible (n of threatened plants = 91, n of non-threatened plants = 235, p -value = 0.0063), si = self-incompatible (n of threatened plants = 160, n of non-threatened plants = 717, p -value = 0.4078); **d** Growth form (LH3), w = woody (n of threatened plants = 220, n of non-threatened plants = 492, p -value = 0.4686), h = herbaceous (n of threatened plants = 238, n of non-threatened plants = 1178, p -value = 0.0081); **e** Overall floral structure, g = generalized (n of threatened plants = 253, n of non-threatened plants = 1072, p -value = 5.93×10^{-5}), s = specialized (n of threatened plants = 205, n of non-threatened plants = 598, p -value = 0.2098); **f** Type of reward, p = pollen (n of threatened plants = 37, n of non-threatened plants = 143, p -value = 0.0428), n = nectar (n of threatened plants = 142, n of non-

threatened plants = 500, p -value = 0.0089), s = specialized (n of threatened plants = 18, n of non-threatened plants = 47, p -value = 0.0874); **g** Continent (Africa: n of threatened plants = 47, n of non-threatened plants = 87, p -value = 0.2536; Asia: n of threatened plants = 136, n of non-threatened plants = 178, p -value = 0.0314; Europe: n of threatened plants = 82, n of non-threatened plants = 422, p -value = 0.5535; North America: n of threatened plants = 91, n of non-threatened plants = 704, p -value = 0.5660; Oceania: n of threatened plants = 66, n of non-threatened plants = 106, p -value = 0.6328; South America: n of threatened plants = 36, n of non-threatened plants = 173, p -value = 0.2983); **h** Region (temperate: n of threatened plants = 392, n of non-threatened plants = 1455, p -value = 0.0027; tropical: n of threatened plants = 66, n of non-threatened plants = 215, p -value = 0.9862). The points show the data for all records, and the mean value $\pm$ standard error of pollen limitation effect size is shown for each category. Labels of the x-axis were simplified to th (stands for threatened) and non-th (stands for non-threatened). Two-tailed t -tests with Holm adjustment were performed for pairwise comparisons. Significant differences are indicated: * p -value < 0.05; ** p -value < 0.01; *** p -value < 0.001. Source data are provided as a Source Data file.

(Fig. 2g). Threatened plants living in temperate zones (n = 392) showed stronger pollen limitation than the non-threatened counterparts (n = 1455) (0.57 ± 0.04 vs. 0.43 ± 0.02 ; t = 3.01, df = 587.21, p -value = 0.0027), while no pollen limitation difference was found between threatened and not threatened species in the tropical region (p -value > 0.05) (Fig. 2h). All statistical results are available in Supplementary Table 1.

Causal relationships between traits, region, pollen limitation, and threat status

All hypothesized path models were not rejected (Bollen-Stine bootstrap p -value > 0.1). The baseline structural equation modeling (SEM) analysis (Fig. 3) indicated that plants with specialized flowers (path

coefficient = 0.27, p -value < 0.001) and plants that are pollinator-dependent (path coefficient = -0.44, p -value < 0.001) would have higher pollen limitation than those with the opposite traits, that woody species were less likely to be classified as autofertile (path coefficient = -0.07, p -value < 0.05), and that the tropical region showed a higher pollen limitation than the temperate region (path coefficient = 0.16, p -value < 0.05). We found no support for the idea that pollen limitation leads to threat status (Model A, Bollen-Stine bootstrap p -value = 0.14), or for the idea that plant traits and region lead to both threat status and pollen limitation. However, we found significant evidence that threat status can lead to high pollen limitation (Model E, Bollen-Stine bootstrap p -value = 0.17; path coefficient = 0.16, p -value < 0.05) (Fig. 3).

When considering the SEM models only for pollinator-dependent plants (Supplementary Fig. 2) and only for the continent of Asia (Supplementary Fig. 3), the causal relationship of threat status leading to pollen limitation becomes stronger. When considering maximum pollen limitation rather than average pollen limitation as the response variable, the causal relationship between threat status and pollen limitation becomes non-significant (Supplementary Fig. 4).

Discussion

The goal of this study is to quantify the relationship between threat status and pollen limitation globally and to investigate the paths in the relationship between plant traits, threat status, and pollen limitation. We find that threatened species have greater pollen limitation

Table 1 | Results of the phylogenetic meta-analysis models revealing the interaction of traits and threat status in moderating pollen limitation

Trait	n	QM	p-value of QM	p-value of the likelihood-ratio test
AF	2074	98.25	<0.0001	<0.0001
BS1	2075	95.46	<0.0001	0.0006
BS2	1147	6.03	0.1104	0.0708
BS3	2128	4.13	0.2478	0.1555
BS4	840	2.59	0.4595	0.2772
BS5	608	8.64	0.0345	0.0710
LH1	2128	3.43	0.3302	0.1831
LH2	2128	5.21	0.1567	0.1120
LH3	2128	25.29	<0.0001	0.2048
Overall floral structure	2128	74.80	<0.0001	<0.0001
Flower symmetry	1661	7.78	0.0508	0.1357
Type of reward	887	46.58	<0.0001	0.1055
Reward accessibility	610	0.49	0.9210	0.8948
Continent	2128	88.71	<0.0001	0.1773
Region	2128	18.67	0.0003	0.0145

n sample size, AF autofertility; BS breeding system, BS1 self-compatibility, BS2 heterostyly, BS3 sexual system, BS4 dichogamy, BS5 herkogamy, LH life history, LH1 life span, LH2 reproductive frequency, LH3 growth form, QM test statistic of the omnibus test of moderators in the two-tailed phylogenetic meta-analysis, the two-tailed likelihood-ratio tests showed the relationship between threat status and pollen limitation variation.

compared to their non-threatened relatives. While it is already known from previous studies that plant traits are strongly associated with pollen limitation, the causal relationships between plant traits, threat status, and pollen limitation were not known prior to this study. There are mechanisms that make all possible causal paths feasible: that plant traits can lead to pollen limitation and threat status, that pollen limitation can cause plants to become threatened, or that declines in range and abundance associated with heightened threat status can lead to pollen limitation. We find evidence for the latter, that plant threat status can lead to pollen limitation. Our results are in line with those shown previously, that there is a strong relationship between plant traits and pollen limitation. Plants that are long-lived are less likely to be autofertile, and plants that are autofertile are less likely to be pollen-limited. Plants with specialized flower structures are more likely to be pollen-limited. In this study, we also show a causal path that threatened plant species have higher pollen limitation. Finally, we show that plants occurring in tropical regions show higher pollen limitation than those in temperate regions.

Based on the results from previous studies, we expected and did find that plant traits are associated with pollinator dependence and pollen limitation^{10,11,37,45}. Using a dataset from 224 species, Larson & Barrett⁴⁵ found evidence that self-incompatible, non-autogamous, and woody plants showed higher levels of pollen limitation compared to their counterparts. Focusing on plants from the Brazilian Atlantic forests, Wolowski et al.³⁷ found that plants with specialized (zygomorphic) flowers showed stronger pollen limitation than those with less specialized flower structures. These results align well with both theory and empirical evidence that plant traits, such as self-compatibility, autofertility, and flower structure, determine pollinator dependence. The pattern that woody plants are more pollen-limited also aligns with the results here when it is considered that woody plants typically have longer lifespans. In this study, our path analysis shows a negative association between life history and autofertility, specifically that long-lived plants are less likely to be autofertile. Plants with longer lifespans can compensate for poor pollination services in one reproductive season during other reproductive seasons with better conditions, whereas short-lived plants often evolve reproductive assurance (e.g., autofertility, self-compatibility) to avoid pollen limitation^{10,46}.

We hypothesized that these same plant traits might influence threat status as well as pollen limitation, but find no support for this idea. Specifically, we find that threatened plant species have similar frequencies of reproductive and life history traits as non-threatened species (Supplementary Fig. 1) and that these traits are not associated

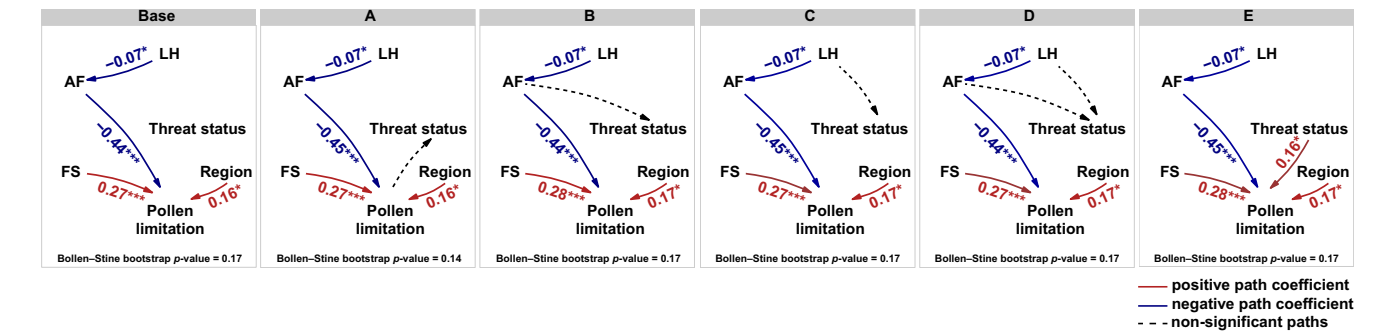


Fig. 3 | The conceptual structural equation modeling (SEM) showing significant pathways among traits, region, pollen limitation, and threat status. Base The baseline model assumed the direct effects of autofertility (AF), the overall floral structure (FS), and region on pollen limitation, and growth form (LH) directly affects AF and then affects pollen limitation; **A** Model A assumed an additional (compared to the base model, hereafter) direct effect of pollen limitation on threat status; **B** Model B assumed an additional direct effect of AF on threat status;

C Model C assumed an additional direct effect of LH on threat status; **D** Model D assumed additional direct effects of both AF and LH on threat status; **E** Model E assumed an additional direct effect of threat status on pollen limitation. Only significant paths are colored red (positive paths) or blue (negative paths), where the path coefficients are shown nearby. Significance levels: *p-value < 0.05; ***p-value < 0.001.

with threat status. This is somehow in contrast with a review study using a compilation of matrix population models of plant demography (the COMPADRE database), which demonstrated that plants with slower life histories were more likely to be classified as threatened⁴⁷. However, tests using relatively small databases of plant abundances, such as GloPL and COMPADRE (with their different limitations in power and biases), suggest that the influence of longevity may be present but is only detectable with detailed data beyond our simple categorizations of plant traits and threat status, but the generalities of the findings will require more data than are currently available.

We specifically hypothesized that autofertile species might be better able to avoid becoming threatened compared to pollinator-dependent species because these species can more easily establish new populations from a single individual and respond to changing environments by shifting their range^{40,41,48,49}. Our results do not support this idea. One possible reason is that although autofertile plants exhibit lower pollen limitation due to their reduced dependence on pollinators, they still face significant threats from habitat loss, which remains the most critical global threat to plants^{50–52}. Meanwhile, suitable, unoccupied habitats are not often available for plants to colonize, even for autofertile species. Additionally, self-incompatible plants have higher genetic variation⁵³, and might be better able to adapt locally to changing environments and to avoid becoming threatened. These results highlight that while autofertility can reduce pollen limitation, it does not necessarily translate to a lower risk of becoming threatened.

We find evidence for a causal relationship between threat status and pollen limitation, but not vice versa. Habitat fragmentation and small plant population sizes are associated with pollen limitation^{19,54}, but some species are threatened in part due to naturally limited distributions (e.g., single-island endemics). The IUCN Red List uses different criteria for listing species, and we might expect pollen limitation to be more common in species listed under criterion A (recent population declines) if plant population declines are the causal factor. With criterion B (limited range size), plant species can persist with limited distributions and/or small population sizes, yet are also experiencing continuing declines, possibly via habitat degradation and/or declines in pollinators. However, we do not analyze criterion types for two reasons: (1) criterion B listings are more common (76% of assessed plants³) because distribution data are more readily available than detailed population surveys required for criterion A; and (2) dividing the 63 threatened species into finer categories would reduce sample size and statistical power. We highlight that most of the publications that make up GloPL do not report habitat size, plant population sizes, pollinator abundances and diversity, or many of the other factors that could help assess the causes of plant endangerment and the mechanisms that might lead to pollen limitation. We encourage authors of original studies to include this relevant information in future studies that present the results of pollen supplementation experiments.

Our study shows important patterns that require more data (new pollen supplementation experiments) to explore further. Specifically, we find higher pollen limitation in tropical compared to temperate regions. However, the relatively small sample size in tropical regions ($n = 281$) highlights the need for more extensive data collection in this area, especially given the high plant biodiversity in the tropics. We find no pollen limitation difference in magnoliids compared to monocots and eudicots. However, with only 22 magnoliid species in this study, very little can be concluded at this time. Further, we specifically advocate for new pollen supplementation experiments on threatened plants of South America and Africa, as these are less frequent in GloPL which limit our ability to dive deeper into testing hypotheses related to threat status and pollen limitation.

In addition to having more studies, it is also important to consider the response variable used in the analysis. In this study, we considered both average pollen limitation and maximum pollen limitation. Our

path analysis shows that threat status causes pollen limitation when we use average pollen limitation, but not maximum pollen limitation, as a response variable. We suspect that this is because non-threatened species are more likely to have multiple estimates of pollen limitation (i.e., studies conducted in multiple populations and years) than threatened plant species, and thus are more likely to capture an incidence of high pollen limitation (Supplementary Figs. 5, 6). Our measure of pollen limitation cannot distinguish whether plants receive an inadequate quantity of pollen (too few pollen grains) or low-quality pollen (self-pollen and heterospecific pollen)⁵⁵. Some pollen supplementation experiments are designed with extra treatments to manipulate pollen quality (e.g., treatments that add self-pollen vs. outcross pollen on emasculated plants), but the low sample size of studies with these extra treatments and the lack of standardized methodology for these treatments currently prevents distinguishing between quantity and quality limitation in a global meta-analysis.

Our results show that threatened plant species suffer higher pollen limitation deficits. Thus, conservation interventions that reduce pollen limitation through management are critical. The IPBES report on pollinators delivers the concerning message that populations of both wild and managed pollinators are declining and provides an overview of 39 strategies for conserving pollinators, including transforming agricultural landscapes and regulating pesticides²⁸. Many countries worldwide have adopted or intend to introduce national pollinator conservation strategies⁵⁶. These approaches differ among regions and countries, as some focus on protecting specific pollinators (e.g., the honey bee) while others claim to protect all pollinators^{57,58}. We note that a holistic approach to pollinator conservation is always desired, and factors depending on the plant-pollinator relationship should be accounted for, especially in the face of global climate change^{59,60}. Therefore, we suggest that studies evaluating the effectiveness of these strategies should directly measure pollen limitation. Likewise, we suggest that pollen supplementation experiments would be a useful addition to current monitoring schemes, as pollen limitation might be an early warning sign of plant endangerment.

One important implication of our results is that pollination services and pollen limitation should be an important consideration in conservation assessments of plant species. As an important trait governing pollen limitation, autofertility could be the target trait to predict the potential for pollination deficits. BGCI currently manages ThreatSearch⁶¹, a global database of all known conservation assessments of plants. It is an important future direction to add relevant traits to this database, such as autofertility, that might be useful to determine relevant conservation actions. Our GloPL dataset could be used as a first source to populate a new autofertility feature in this database. Further, in the current IUCN red listing process, assessors are asked to choose threat levels to the species from a list of possibilities. Currently, disruptions in mutualistic interactions, including pollination, are not mentioned as one of the possible threats despite the high proportion of pollinator-dependent species and the potential vulnerability of such interactions. Although our results do not indicate that threat status is likely the primary cause of pollen limitation, the occurrence of pollen limitation in threatened plants alone highlights the critical need to incorporate pollination issues into the IUCN red listing process. Explicitly acknowledging disruptions in pollination as a potential threat would enhance the accuracy of extinction risk assessments and better guide conservation priorities. In summary, our results highlight the necessity and importance of assessing plant traits such as autofertility and disruptions in mutualistic interactions for threatened plant species.

Methods

The GloPL database and trait data

The present study was conducted with the GloPL database⁴⁴ (accessed on July 19th 2019), which contains 2969 pollen supplementation

experiments on 1265 plant species worldwide and provides the pollen limitation effect size of plant populations (separately for different years) as the log response ratio of the reproductive output of pollen-supplemented flowers (hand) compared to open-pollinated controls (natural): pollen limitation effect size = $\log_e(\text{hand}) - \log_e(\text{natural})$ ⁴⁴. Given that a meta-analysis requires estimates of sampling variance, we calculated the variance of pollen limitation effect size for each record⁶². We removed records when the calculation of variance was unavailable ($n=186$) or when variance was zero ($n=6$). Our previous work demonstrated that global mean values and comparisons of pollen limitation were robust to whether or not these cases are included⁴¹. Furthermore, we restricted our analysis to native species and excluded records from species in their non-native ranges ($n=132$). We excluded records with extremely low pollen limitation effect size (<-1.5 ; $n=12$), which might reflect damage to the plant during the pollen supplementation experimentation. Thus, we considered 2633 records from 1107 flowering plant species (including 32 infra-species taxa) for analysis (Fig. 1; Supplementary Fig. 7). These records include both animal and wind-pollinated species, but the latter category is rare in our dataset.

We obtained data for a total of 13 traits with potential influence on pollen limitation^{39,44}: autofertility (AF), five traits related to the breeding system (BS), three traits related to the life history (LH) strategy, and four traits related to floral specialization. We considered a species either autofertile or not (i.e., pollinator-dependent) based on the ratio of seed number in the bagged (pollinators excluded) treatment compared to seed number in the supplemental pollination treatment or author-stated information following Burns et al.³⁹. Based on this ratio, species were coded as AF-yes if this ratio was ≥ 0.2 or AF-no if this ratio was < 0.2 . For the breeding system (BS1), we coded species as self-compatible (sc), self-incompatible (si), or partially self-compatible (p), based on the index of self-incompatibility (ISI)^{39,44}. Whether each species exhibits stylar polymorphisms (heterostyly) or not (BS2; yes vs. no), bisexuality or not (sexual system, BS3; yes vs. no), dichogamy or not (BS4; yes vs. no), and herkogamy or not (BS5; yes vs. no) were coded in GloPL. Data of the three LH traits describing (1) life span (LH1; perennial (p) vs. annual or biennial (a or b)); (2) reproductive frequency (LH2; polycarpic (poly) vs. monocarpic (mono)); and (3) growth form (LH3; woody (w) vs. herbaceous (h)) were also coded in GloPL. Floral traits include (1) overall floral structure (FS), as proxied by flower shape: generalized (bell, funnel, brush, inconspicuous, open, or dish) or specialized (chamber, flag, gullet, keel, or spurred); (2) flower symmetry: generalized (actinomorphic) or specialized (zygomorphic); (3) type of reward offered by the plant: pollen only, pollen and nectar, or specialized (heat, oil, floral parts, scent, resin); and (4) accessibility of reward to pollinators: generalized (flowers have no evident restriction to reward collection or pollinators do not need complex body structures or mechanisms to collect rewards) or specialized (trigger flowers, or when pollen is in poricidal anthers and requires buzz pollination)³⁹. Information on plant location (continent and region) was also provided in GloPL. The species names were validated with the R package Taxonstand (version 2.4)⁶³. The phylogenetic clade (the magnoliids, the monocots, or the eudicots) was assigned for each species with the R package taxize (version 0.9.100)⁶⁴. Since not all trait data are available for every species, the final numbers of analyzed records varied (see Table 1).

Threat status

We classified 1107 plant species into two threat status categories: (1) threatened and (2) non-threatened, with the following steps. First, we queried the species against the IUCN Red List using the R package taxize. Then, for those species not assessed by IUCN, we queried the ThreatSearch database based on the species name and the exact sampling locality. For example, *Cephalanthera falcata* is listed as least concern in China while being listed as vulnerable in Japan. Given that

the *Cephalanthera falcata* population in our dataset was studied in Japan, we coded this species as threatened.

The BGCI and IUCN conservation status for each species was merged into two categories for our analyses: threatened (which includes the IUCN categories of critically endangered, endangered, and vulnerable and the BGCI categories of threatened and possibly threatened) and non-threatened (which includes the IUCN category of least concern and the BGCI category of not threatened). Our final sample sizes included 224 threatened species (ca. 20%; 63 species assigned by the IUCN Red List, 161 species assigned by the BGCI's ThreatSearch database) and 602 non-threatened species (ca. 54%). Among the threatened species recognized by the IUCN Red List, 25 species meet criterion A, two meet criteria A + B, 25 meet criterion B, two meet criteria B + C, one meets criteria B + D, one meets criterion C, four meet criterion D, and the criteria based on which the remaining three being assigned threatened were not reported (<https://www.iucnredlist.org/>; accessed on May 20th, 2024). The threat status of 281 species was unavailable (data deficient according to BGCI), and these species were excluded from the subsequent analyses (Fig. 1).

Data analysis

Frequencies of threat status across traits and major phylogenetic clades. To determine whether threatened and non-threatened plant species differ in the 13 traits described above, we compared the proportional distribution of threatened versus non-threatened species across trait categories for each measured trait using the χ^2 test via the `chisq.test` function in the R package stats (version 4.1.2)⁶⁵. Similarly, we compared the frequency of threat status among major phylogenetic clades (i.e., the magnoliids, the monocots, and the eudicots) using the same method.

Pollen limitation across major phylogenetic clades. We tested whether pollen limitation differed among the three major phylogenetic clades using one-way ANOVA (the `aov` function) and a post-hoc analysis (the TukeyHSD function) available in the R package stats.

Threat status, moderators, and pollen limitation. To determine whether threatened and non-threatened plant populations differ in their pollen limitation, and whether this was mediated by plant traits or plant location (continent, region), we performed a phylogenetic meta-analysis on pollen limitation effect size using the R package metafor (version 3.8-1)⁶⁶. For each of the 13 traits, we tested whether the trait and the threat status (threatened and non-threatened) of the plant interactively influence pollen limitation using the `rma.mv` function. For significant interactions between the plant trait and threat status, we conducted all possible comparisons among means within each interaction, using the Holm adjustment for pairwise comparisons with the R package stats. We then applied likelihood-ratio tests to examine the presence of a relationship between threat status and pollen limitation by comparing the full model (where moderators included the interactions between the threat status and the trait) to the reduced model (where the trait was the sole moderator) using the `anova` function from the R package metafor. Likewise, we tested whether the continent (Africa, Asia, Europe, North America, South America, or Oceania) or the region (temperate or tropical) would influence the relationship between threat status and pollen limitation using the same method.

All models included random effects of plant species and the study ID (proxied by the author's name and the year of publication) to account for differences in effect sizes across species and/or across studies that often contain multiple experiments^{39,67}. We controlled for possible non-independence of effect sizes from species with shared evolutionary history by considering phylogeny in the analysis⁶⁷. The phylogeny of the plant species in our study was reconstructed using the seed plant phylogeny of Smith & Brown⁶⁸ and the R package V.PhyloMaker2 (version 0.1.0)⁶⁹ (the most commonly used scenario 3).

Later, we modeled the phylogeny as a variance-covariance matrix using the `vcv` function from the R package `ape` (version 5.6.2)⁷⁰.

Structural equation modeling. We used SEM to analyze hypothetical pathways that may explain causal relationships among plant traits, pollen limitation, and threat status. Based on results showing associations between moderators and pollen limitation (phylogenetic meta-analysis; Table 1), and correlations among some of the trait variables, we considered four factors in the SEM: autofertility (AF), growth form (LH3), overall floral structure (FS), and region. While both AF and BSI influence the relationship between threat status and pollen limitation (Table 1), these factors provide overlapping information (e.g., all autofertile plants are also self-compatible), and thus only AF was considered in the SEM. Both the type of reward and floral structure influence pollen limitation, but only floral structure was considered in the SEM due to its moderating effect on the effect of threat status on pollen limitation (Table 1), and due to the relatively low sample size available for type of reward ($n=887$). Life history is well known to influence pollen limitation through AF¹¹, and only LH3 significantly affected pollen limitation in this study (Table 1). Region but not continent moderated the effect of threat status on pollen limitation (Table 1).

The baseline model assumed the direct effects of AF, FS, and region on pollen limitation, and the possibility that LH3 directly affects AF and then affects pollen limitation (Fig. 3). Model A considered an additional (compared to baseline) direct effect of pollen limitation on threat status. Thus, model A considers the possibility that plant traits directly affect pollen limitation, and then pollen limitation directly affects threat status. The next three models (B, C, D) consider the possibility that plant traits affect both threat status and pollen limitation. In model B, we considered the additional direct effect of AF on threat status. In model C, we considered the additional direct effect of LH3 on threat status. In model D, we considered the additional direct effect of both AF and LH3 on threat status. Finally, model E considered the possibility that threat status influences pollen limitation. The SEM analysis included 788 species for which all variables were available (Supplementary Data 2). For each species, the mean pollen limitation value across all unique entries (e.g., pooled across different populations and years) was calculated.

To examine the robustness of our relationships between threat status and pollen limitation in the SEM, we considered subsets of the data. First, we considered SEM analyses for pollinator-dependent (not AF) and AF plants separately to test whether the causality could change depending on the AF status. Second, we considered only the continent of Asia, since this was the only continent for which threatened plants were significantly more pollen-limited than non-threatened plants. Finally, we considered the SEM analysis when maximum pollen limitation rather than average pollen limitation was used as the pollen limitation response variable, as high pollen limitation observed in some populations or years within a species might not be captured using the average pollen limitation response variable.

The SEM was implemented using the R package `lavaan` (version 0.6-13)⁷¹. Finally, we used the nonparametric Bollen-Stine bootstrapping to estimate the robustness of the models⁷². A good model fit was indicated by a Bollen-Stine bootstrap p -value > 0.1 .

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

Data are openly available in GloPL (Bennett et al.⁴⁴; <https://datadryad.org/dataset/doi:10.5061/dryad.dt437>), IUCN red list (<https://www.iucnredlist.org/>), and BGCI threat search (<https://www.bgci.org/resources/bgci-databases/threatsearch/>). The specific data that

support the findings of this study are available from the figshare repository⁷³ with the identifier doi: 10.6084/m9.figshare.27123633. Source data are provided as a Source Data file with this paper.

Code availability

The R codes used to generate the results of this study are available from the Zenodo repository with the identifier doi:10.5281/zenodo.13852683.

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Acknowledgements

This paper is the result of a working group supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig (DFG FZT 118). Additional funding was provided by a recruitment initiative to T.M.K. from the Alexander von Humboldt Foundation and the Helmholtz Association. Early support was received as part of a Pollen Limitation Working Group supported by the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (DEB-00-72909). T.L.A. was supported by the Alexander Humboldt Foundation and NSF DEB-2027604. J.M.B. is supported by a Discovery Early Career Award (DE220100144) funded by the Australian Government.

Author contributions

H.L. and J.L. conceived the idea. J.L. and T.M.K. supervised the project and led this work. H.L. and Y.Y. performed the analyses. H.L. wrote the manuscript with input from Y.Y., J.L., J.M.B., T.-L.A., G.A.-G., M.B., L.A.B., J.H.B., W.D., A.G.E., L.F., J.G.R., J.C.V., M.W., J.X. and T.M.K.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-025-61032-5>.

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Peer review information *Nature Communications* thanks Renate Wesselingh, Catarina Siopa, and the other anonymous reviewer(s) for their contribution to the peer review of this work. A peer review file is available.

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