PLANT SCIENCES

Widespread vulnerability of flowering plant seed production to pollinator declines

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Despite evidence of pollinator declines from many regions across the globe, the threat this poses to plant populations is not clear because plants can often produce seeds without animal pollinators. Here, we quantify pollinator contribution to seed production by comparing fertility in the presence versus the absence of pollinators for a global dataset of 1174 plant species. We estimate that, without pollinators, a third of flowering plant species would produce no seeds and half would suffer an 80% or more reduction in fertility. Pollinator contribution to plant reproduction is higher in plants with tree growth form, multiple reproductive episodes, more specialized pollination systems, and tropical distributions, making these groups especially vulnerable to reduced service from pollinators. These results suggest that, without mitigating efforts, pollinator declines have the potential to reduce reproduction for most plant species, increasing the risk of population declines.

INTRODUCTION

Most of the world's approximately 350,000 flowering plant species engage in mutualistic relationships with animal pollinators to reproduce (1). It is estimated that 82% of species are pollinated exclusively by insects and 6% are pollinated by vertebrates compared to only 12% pollinated by wind (1, 2). However, declines in the abundance and diversity of pollinators have been reported from multiple continents (2–8), consistent with declines in wild animals overall (9, 10). If these trends are representative, plant reproduction could be reduced by pollinator declines globally. For example, parallel declines in pollinators and the plants they pollinate suggest that reduced

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pollinator service already constitutes an extinction threat to some plant species (5, 11, 12). However, the risk to plant populations from pollinator declines depends on the contribution of pollinators to seed production. This has remained an open question because the majority of plants can produce at least some seeds without pollinators via autofertility (AF) (i.e., by self-fertilization or asexual embryo formation) (13) and the amount by which pollinators increase seed production above this level has not been assessed from a global dataset of plants (1, 3, 14).

To quantify the contribution of pollinators to seed production, it is necessary to compare seed production in the absence of pollinators to seed production with pollinators present (i.e., under natural pollination). The pollinator contribution (PC) metric (fig. S1) therefore estimates PC by comparing seed or fruit production when pollinators are experimentally excluded (f_{exc}) with that in naturally pollinated control flowers (f_{nat}) as PC = ($f_{nat} - f_{exc}$)/f_{nat} (15). Until now, PC data have been synthesized only for vertebrate-pollinated plants, indicating that these animals contribute on average 63% of seed production for the plants they pollinate (14). The importance of all animal pollinators (i.e., including insects) across flowering plants thus remains unknown.

Although previous studies imply that pollinator visitation improves seed production in most plants (13, 16–18), the metrics analyzed in those studies do not quantify this benefit (fig. S1). A global dataset of the index of AF (19) suggests that visits from animal pollinators should increase seed production in 81% of plants (13). Also, a global dataset of the pollen limitation (PL) index (16) shows that reproduction is limited by pollen supply in 62 to 73% of plants (17, 18). However, unlike PC, AF and PL do not compare seed production between naturally pollinated and pollinator-excluded flowers, so they do not assess the realized benefit of pollinators in natural populations (14, 15). Thus, filling the knowledge gap on the contribution of pollinators to seed production has awaited a synthesis of the PC metric (fig. S1).

Pollinator declines may influence future patterns of plant diversity through greater impacts on plants and geographic regions with

higher PC. In general, PC should be higher in plants that have lower AF or that receive better service from pollinators. As AF is higher in smaller, shorter-lived plants than in larger, longer-lived plants (13, 20, 21), we expected PC to show the opposite pattern. Among plant-functional groups, we therefore expected the rank order of PC would be trees > shrubs > polycarpic (reproducing more than once) herbs > monocarpic (reproducing once) herbs. We also expected invasive alien plants to have lower PC than native plants as AF is higher in invasive species (13). As plants with more specialized pollination relationships may have more effective pollinators (22), we expected higher PC in specialized compared to generalized plant species. Geographically, we expected PC to increase with decreasing latitude because the higher abundance and diversity of pollinators at lower latitudes could result in higher pollinator visitation (23) and because asexual AF (apomixis) is thought to be less frequent at lower latitudes (24). If PC is greater in more specialized plant lineages, greater specialization in pollination relationships at lower latitudes (25) could also reinforce a pattern of greater PC in more tropical ecosystems.

To make a global assessment of PC across all flowering plants, we assembled a dataset of fruit and seed production in pollination experiments for animal-pollinated plant species. We did this by extracting data from 1528 separate experiments, representing 1392 plant populations and 1174 species from 143 plant families, from three previously assembled datasets (13, 26, 27). These data are drawn from pollination experiments carried out on all continents except Antarctica, over four decades (1975 to 2015), and across the angiosperm (flowering plant) tree of life (Fig. 1 and data file S8).

RESULTS

Our global dataset estimates that 50% of flowering plant species need animal pollinators for at least 80% of their seed production (PC ≥ 0.8). This includes 33% of species that would produce no seed without pollinators (PC = 1) (Fig. 1). Pollinators make at least some contribution to seed production in 79% of species (PC > 0) and no contribution in 21% of species (PC = 0) either because they are wind-pollinated (12% of species) (1) or because pollination experiments indicate that their seed production is currently not affected by pollinators (9% of species; Fig. 1). We estimate that, across flowering plants, the mean PC is 0.60 [95% confidence interval (CI) = 0.58 to 0.63] and the median is 0.80 (95% CI = 0.75 to 0.84; interquartile range = 0.08 to 1). These estimates capture the full current value of pollinator services for plant reproduction and provide an upper bound on the impact of future pollinator declines.

To understand how the impact of pollinator decline may vary geographically, and among plants with different traits, we investigated the geographical and trait associations of PC (table S1, A to C). PC exhibited significant phylogenetic signal (Pagel's λ = 0.452, $P < 0.001$) demonstrating that some variation in PC across flowering plants is due to shared evolutionary history. Phylogenetically controlled analyses showed that PC increased as latitude decreased (Fig. 1C and fig. S2) and was not affected by year of study (fig. S3). Monocarpic herbs (mainly annuals and biennials) had lower PC than other plants (polycarpic trees, shrubs, and herbs), and trees had higher PC than other plants (Fig. 2). Plants with more specialized pollination relationships (pollinated by one pollinator functional group) had higher PC than plants with more generalized pollination relationships (pollinated by multiple pollinator functional groups) (Fig. 2).

Plants with morphologically specialized flowers had higher PC than those with generalized flowers (Fig. 2). Naturalized and invasive aliens had lower PC than natives (Fig. 2).

To evaluate the potential influence of AF on geographic and trait associations of PC, we analyzed geographic and trait associations of AF, coded as a binary variable with AF absent (i.e., PC = 1) versus AF present (i.e., PC < 1). Results for the presence of AF were largely congruent with results for PC [i.e., variable coefficients have opposite signs in the two analyses; compare table S1 (A to C) with table S2 (A to C)], indicating that variation in PC is at least partially driven by variation in AF. Likelihood ratio tests and Akaike information criterion (AIC) values supported relationships of plant functional group, latitude, and number of pollinator functional groups (but not alien status and flower morphological specialization) with the presence of AF (table S2, A to C).

To understand how plant reproductive strategy may affect resilience to pollinator declines, we cross-classified species in our dataset by number of reproductive events (single versus multiple) and PC category (low versus high). We estimate that very few species— only 2%—have high PC (PC ≥ 0.8) and reproduce only once, while 48% have high PC and reproduce in multiple years (Fig. 3). Furthermore, 6% of species reproduce once and have low to moderate PC (PC < 0.8), while 32% reproduce in multiple years and have low to moderate PC (Fig. 3).

DISCUSSION

Global contribution of pollinators to seed production

We estimate that pollinators contribute to seed production in 79% of flowering plant species, including about half of species that rely on pollinators for most or all (80 to 100%) of their seed production (Fig. 1). Although AF is common (13), our results show that the amount of seed produced in this way is usually small compared to seed produced via pollinator visitation, so reductions in pollinator visitation could reduce seed production in most (i.e., 79%) plant species. This aligns well with PL analyses, which show that improved pollinator visitation could increase seed production in most (62 to 73%) species (17, 18). Therefore, results for PL and PC together show that changes in pollinator visitation have the potential to cause large changes in seed production for many plant species. This brings into focus the importance of pollinators for maintaining viable plant populations and the potential vulnerability of plants to pollinator declines.

Vulnerability and resilience of plants to pollinator declines

Pollinator declines, documented mainly in North America and Europe (3–5, 7, 8) but potentially more widespread (2, 6), seem likely to reduce pollinator species richness, alter functional composition, and reduce total pollinator abundance in many pollinator faunas. Although some plant species may show resilience to altered pollinator faunas by switching pollination relationships on ecological time scales (i.e., through network rewiring) (28, 29), plants that are more specialized to their pollinators would be less able to make such accommodations (30). Moreover, in the event of community-wide reductions in pollinator availability, visitation to at least some plant species will surely be reduced [e.g., (29)], especially those that compete less strongly for pollinator visitation. For some plants, evolution of increased AF or increased attractiveness to pollinators may mitigate the consequences of reduced pollinator abundance (31). However, evolutionary rescue may not be possible for lineages with high levels of inbreeding
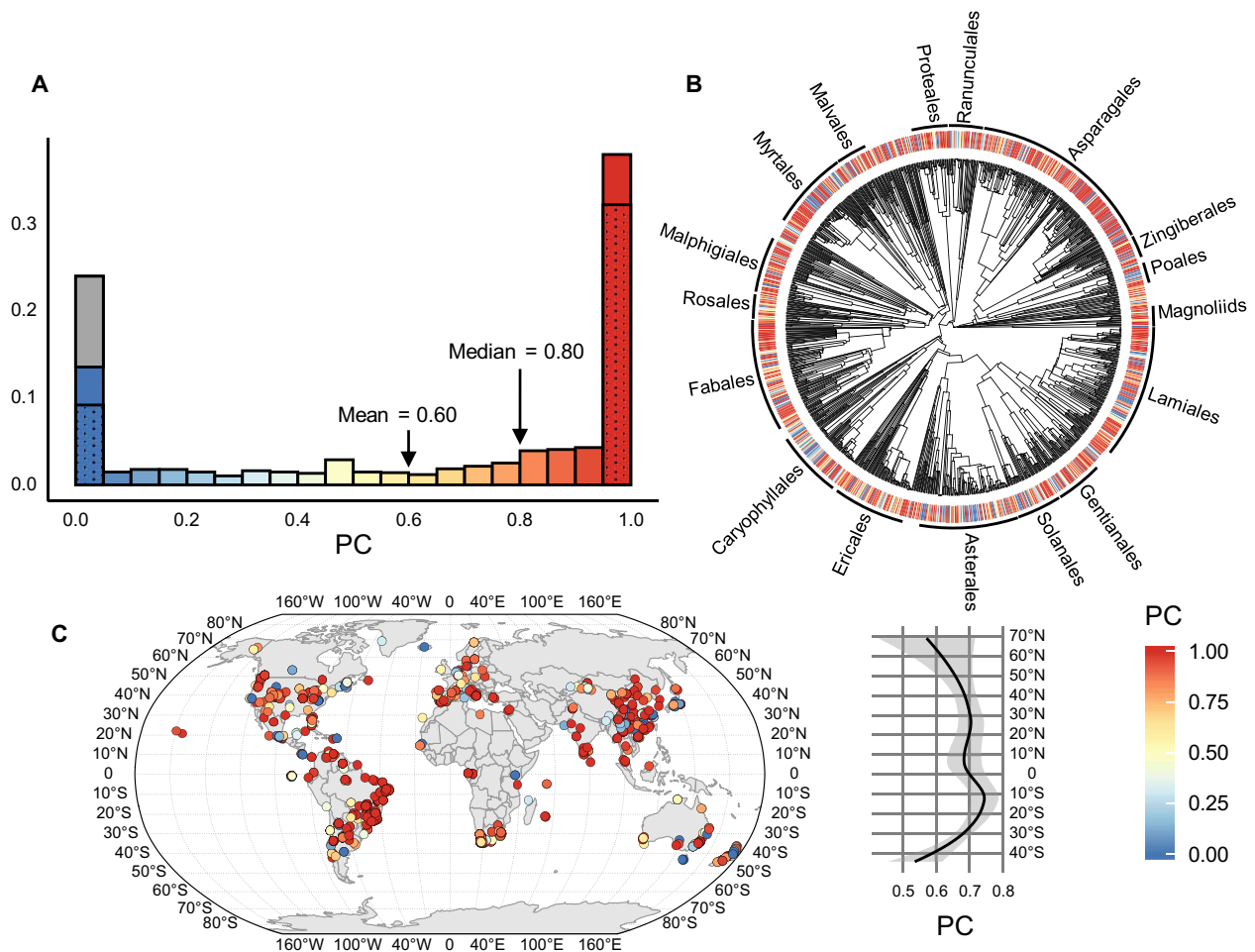
Fig. 1. Global dataset of pollinator contribution (PC) in wild flowering plants. PC measures the proportion of seed production that is attributable to pollinator visitation, with values of 0 indicating that pollinators do not affect seed production and values of 1 indicating that seed production only occurs when pollinators visit flowers. (**A**) Frequency distribution, (**B**) phylogenetic distribution, and (**C**) geographical distribution of PC in our dataset. The frequency distribution (A) is based on our dataset of 1174 animal-pollinated species adjusted for 12% of angiosperm species being wind-pollinated (1). First quartile = 0.08; third quartile = 1. For the left-hand bar, colors represent species as follows: gray, PC = 0 due to wind pollination; stippled blue, PC = 0 although visited by animal pollinators; solid blue, 0 < PC < 0.05. For the right-hand bar, colors represent species as follows: stippled red, PC = 1; solid red, 0.95 < PC < 1. For other colored bars, colors represent PC as indicated in the legend at bottom right. On the phylogeny (B), angiosperm orders and the Magnoliid clade are shown with segments around the outside and PC values are depicted by the color of the bars. There is significant phylogenetic signal in PC ($\lambda = 0.452$, $P < 0.001$). The points on the map (C) represent study locations, with color indicating population PC values and the line graph to the right indicating the latitudinal pattern in PC in animal-pollinated species from a loess fit (not controlling for phylogeny or any additional variables). Wind-pollinated species are not represented on the phylogeny (B) and map (C).

depression (e.g., most trees) or low levels of genetic variation (21). Ecological and evolutionary shifts in pollination systems are thus likely to only partially mitigate pollinator declines.

Variation in PC across geographic distribution and plant traits suggests that uneven effects of pollinator declines may influence future patterns of plant diversity. As plants constitute habitat for animals and the base of food chains, impacts of pollinator declines on plant diversity and vegetation structure are also likely to cause further cascading effects on animals (3, 32, 33). Higher average PC in plants with longer life span, greater stature, and greater pollinator specificity (Fig. 2) indicates that pollinator declines will tend to be more detrimental to plant lineages with these traits, potentially leading to decreases in their relative or absolute abundance compared to lineages with contrasting traits and lower average PC. Likewise, lineages

with high AF or wind pollination, which will not be directly affected by pollinator declines, may become more abundant at the expense of lineages with high PC. Higher PC in natives than naturalized and invasive aliens indicates that native species should on average be more severely affected by pollinator declines than aliens. The latitudinal gradient in PC suggests that the consequences of pollinator declines for seed production will be more severe closer to the equator, potentially exacerbating an existing latitudinal gradient in extinction risk (34). This pattern is reinforced by the concentration at lower latitudes of animal-pollinated lineages (1), especially some groups with higher PC—trees and pollination-specialized plants (Fig. 2) (25, 35). Thus, while studies on long-term trends in pollinators are strongly biased to temperate North America and Europe, our results add weight to the call to assess trends in pollinators and pollination
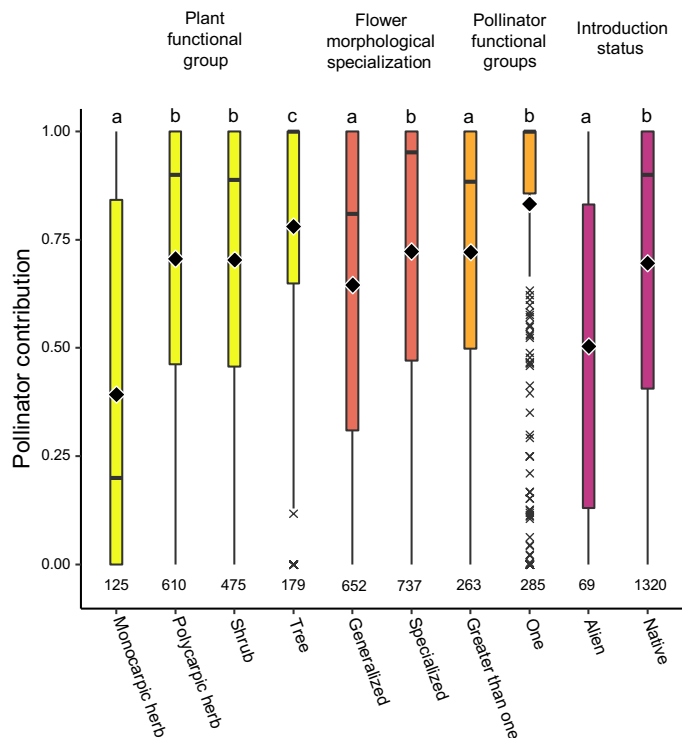
Fig. 2. Pollinator contribution is related to plant functional group, flower morphological specialization, number of pollinator functional groups, and alien status. All trees and shrubs analyzed are polycarpic (having multiple reproductive episodes). Specialized flowers are those with bilateral symmetry, specialized shapes, specialized rewards, and/or restricted access to rewards. Examples of pollinator functional groups are bats, nonflying mammals, and hymenopterans (bees and wasps). Different levels of the same factors are shown in the same color, and different letters above boxes of the same color indicate significant differences between factor levels in phylogenetic generalized least squares analyses. Numbers below boxes indicate sample sizes (populations). Diamonds indicate means and horizontal lines across boxes indicate medians. Tops and bottoms of boxes indicate quartiles and whiskers that extend to the last value within 1.5 times the interquartile range.

in the tropics (*36, 37*). More broadly, these results highlight that altered biotic interactions should be factored into global change projections of future species richness and ecosystem function.

The overall congruence between geographic and trait associations for PC (table S1) and those for the presence of AF (table S2) (*13*) indicates that AF is an important driver of patterns in PC. Nevertheless, because PC arises from an interaction between plant traits (including AF) and the environment (including pollinators), PC will not necessarily mirror AF in its relationships with other variables (fig. S1) and analysis of PC is thus vital to make sound inferences on variation in vulnerability to pollinator declines.

There may be a time lag between pollinator declines and their effects on plant diversity because species that are highly vulnerable to reductions in seed production tend to be long-lived with multiple reproductive events (*30, 38*). Of the 50% of flowering plants with high PC (PC ≥ 0.8), most are relatively long-lived (48% of species in our dataset; Fig. 3) and could persist for decades to centuries even without producing seed (*30, 39*). Many trees, shrubs (e.g., *Rhododendron calendulaceum*; Fig. 3), and bulbs fall into this group for which multiple reproductive events and longevity provide resilience to pollinator

declines. Relatively few species—2% of our dataset—reproduce only once (mainly annuals and biennials) and have high PC (e.g., *Digitalis purpurea*; Fig. 3). Pollinator declines are likely to cause steeper population declines in this group (*40*). Alternatively, due to short generation time, such lineages may also rapidly evolve toward increased AF or enhanced attractiveness to the remaining pollinators (*41*). Short-lived species with high PC should therefore be prioritized for monitoring of population size, AF, and reproductive morphology to test for effects of pollinator declines. However, demographic projections (*40*) give hope that timely action to restore pollinator communities (*42*) may mitigate losses, especially for long-lived species. Identification of plant species that would benefit from such actions would be aided by accounting for vulnerability to pollinator declines (Fig. 3) when making conservation assessments, such as red listing.

Robustness of our dataset

Most large, predominantly animal-pollinated plant families are present in our dataset (data file S8). Although some families are underrepresented (e.g., *Orchidaceae*) or overrepresented (e.g., *Iridaceae*), in general, we regard this first global assessment of the contribution of pollinators to seed production as conservative. We may underestimate the proportion of vulnerable plants because two categories of plants with relatively high PC are underrepresented: trees (13% in our dataset, 20% globally) (*35*) and species that have separate male and female flowers, and are therefore unlikely to self-pollinate (3% in our dataset, 12% globally) (*43*). Moreover, when lineages that have historically reproduced mainly by cross-fertilization are forced to reproduce by self-fertilization, the offspring frequently suffer from inbreeding depression; i.e., they perform poorly compared to those from cross-fertilization (*44*). Therefore, the effects of pollinator decline on demography and natural selection for such lineages may be even greater than implied by our analysis of PC. Because the PC values synthesized here do not account for any reductions in seed production due to pollinator declines before experiments were carried out, we may also underestimate the combined impact of historical and future pollinator declines.

MATERIALS AND METHODS
Experimental design
We obtained records including pollinator exclusion and natural pollination treatments from three previously assembled datasets of breeding-system and pollen-supplementation experiments. These source datasets are the GloPL Dataset (*26*), the Konstanz Breeding System Dataset (*13*), and the Stellenbosch Breeding System Dataset (*27*). The GloPL Dataset and the Konstanz Breeding System Dataset are global in scope, whereas the Stellenbosch Breeding System Dataset focuses on South Africa but also includes some records from outside South Africa (table S3). A record refers to a row in a dataset containing reproductive output for different treatments from a pollination experiment, as reported in the original study, together with associated explanatory variables, and details of the study. Reproductive output was reported in all studies as one or more of the following: fruits per flower, seeds per flower, seeds per fruit, seeds per plant, seeds per ovule for all flowers treated, or seeds per ovule for flowers that set fruit.

Source datasets were assembled mainly from keyword searches of electronic databases, but theses were also included (details provided in table S3). For our PC dataset, we extracted records from the three
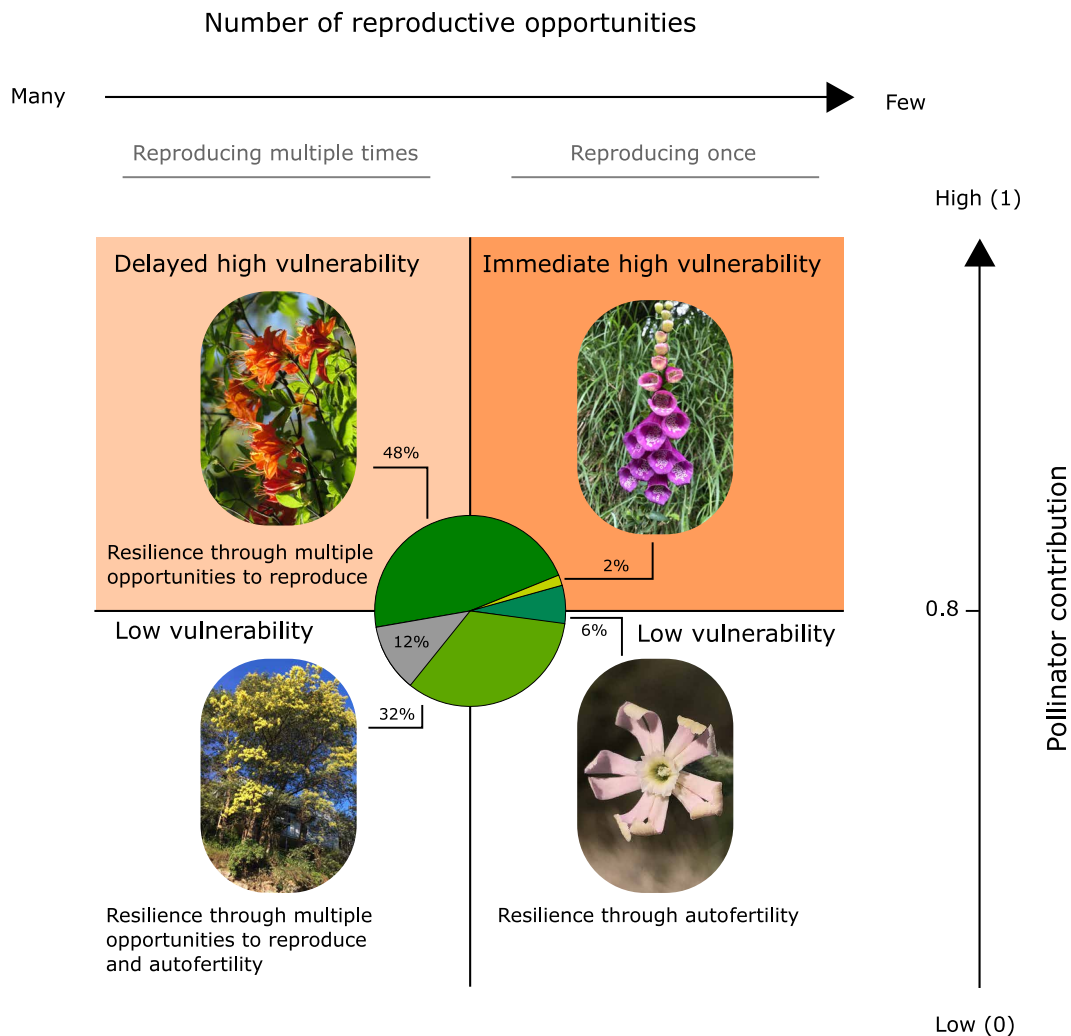
Fig. 3. Vulnerability of flowering plants to future pollinator declines through pollinator contribution and opportunities for reproduction. Pollinator declines will have little impact on seed production of species with low PC (bottom two quadrants). Plant species with high PC (top two quadrants) will experience reduced seed production if their pollinators decline. However, those that are longer lived and have multiple opportunities to reproduce (top left quadrant) are only expected to experience population declines after a lag period, while short-lived species that reproduce only once in their lives (top right quadrant) may experience more rapid population declines when their pollinators decline. The 12% of angiosperm species that are resilient to pollinator decline due to wind pollination are shown by the gray slice. The photographs show representative species for each category of animal-pollinated angiosperm species, clockwise from top right: *Digitalis purpurea*, *Silene noctiflora*, *Acacia dealbata*, and *Rhododendron calendulaceum*. Images from inaturalist.org by L. Jiang (CC-BY 4.0), C. Altmann (CC-BY 4.0), J. Sullivan (CC-BY 4.0), and E. M. Eraskin (CC-BY 4.0).

source datasets that had both a pollinator exclusion treatment and an unmanipulated treatment, provided these pollination treatments were not combined with other manipulations potentially affecting reproductive output (table S4). For example, we excluded records where there was also an application of nutrients. Where the same study was present in one or more of the source datasets, we usually used the records from GloPL, as this dataset was the most complete for explanatory variables.

We obtained 1658 records from 1509 populations, 1263 species, and 662 studies after excluding duplicates between source datasets (table S4). Furthermore, 32 records were excluded as experiments were carried out on cultivated plants, 78 records were excluded as they belonged to species regarded as entirely or partially wind-pollinated, 10 records were excluded due to lack of identification to species level, and 10 records

were excluded because fewer than three plants received each pollination treatment. The final dataset consisted of 1528 records from 1392 populations, 1174 species, 143 plant families, and 614 studies (table S4). Data handling and all analyses were performed in R version 4.0.3 (*45*).

We obtained the following explanatory variables for PC records in our dataset: geographical coordinates, plant functional group (monocarpic herb, polycarpic herb, shrub, or tree), alien status (invasive/naturalized alien or native), floral specialization (generalized or specialized), and number of pollinator functional groups (ant, bat, beetle, bird, fly, hymenopteran, lepidopteran, nonflying mammal, wasp, and other). In the case of PC records from GloPL, explanatory variables were provided from the GloPL dataset itself (*26*). Explanatory variable data for the Konstanz and Stellenbosch datasets were obtained either from the datasets themselves or, if missing in those

datasets, by searching the original papers and other literature sources. However, number of pollinator functional groups was only available for records from GloPL. Flowers were classified as morphologically specialized as opposed to generalized following Burns *et al.* (*46*), if they fulfilled any of the following conditions: bilateral as opposed to radial symmetry, specialized (chamber, flag, keel, orchid, spur, and gullet) rather than generalized (bell/funnel, open/dish, brush, inconspicuous, and tube) shape, presence of specialized rewards (e.g., oil and fragrance), a floral tube longer than 10 mm, or otherwise restricted access to rewards (e.g., poricidal anthers).

Where geographical coordinates were not reported, we obtained these by searching for study sites on Google Earth using descriptions in the original papers. For 16 records, the study site location was not described, and we used an approximate centroid of the range depicted in The Red List of South African Plants (*47*) or the Australian Virtual Herbarium (*48*). Growth form and life history were combined into a single plant functional group variable, as only herbs contained both monocarpic (having a single reproductive episode in life) and polycarpic species (having multiple reproductive episodes), except for a single monocarpic shrub. Number of pollinator functional groups was treated as a categorical variable with two levels, one versus more than one functional group. Geographical coordinates of study location were used to obtain mean annual temperature and precipitation Bioclim variables (BIO1 and BIO12) using the raster package in R (*49*).

Species accepted names were obtained by checking names in our dataset against The Plant List (*50*). We used the ape package (*51*) in R for handling phylogenetic trees. A phylogeny was obtained by pruning the ALLMB tree of Smith and Brown (*52*) down to only the taxa that were also in our dataset (accounting also for infraspecific classification, if present). All genera in our dataset were included in the ALLMB tree. There were 122 taxa in our dataset that were not present in the ALLMB tree. These taxa were bound into the phylogeny using the function congeneric.merge from the Pez package in R (*53*). Where multiple populations were present per species, these were represented as polytomies with branch lengths of 100 years (*54*).

Statistical analysis

We estimated PC, the proportional contribution of pollinators to plant reproduction for each record, as PC = $(f_{nat} - f_{exc})/f_{nat}$ for $f_{nat} > f_{exc}$, where f_{nat} and f_{exc} represent measures of reproductive output (fruit or seed production) for natural pollination and pollinator exclusion treatments, respectively, following Melathopoulos *et al.* (*15*).

Where $f_{nat} = 0$, which was the case for 24 records in our dataset, PC cannot be calculated using this formula (as this would mean dividing by zero). For these records, we treated PC as zero. This is appropriate when there is no reproductive output due to pollinator failure (although some of these cases may also be due to resource limitation). Although the lower limit for PC is theoretically zero because excluding pollinators should not improve reproductive output, the above formula produces negative values when $f_{nat} < f_{exc}$. This was the case for 133 values in our dataset. These cases are probably mainly due to observational (random) error in plants with complete AF (i.e., true values are $f_{nat} = f_{exc}$) but, in some cases, may be due to experimental error, for instance, if bags favored seed development by protecting against seed predators. Thus, we estimated PC as PC = 0 for $f_{nat} < f_{exc}$ or $f_{nat} = 0$. Qualitatively identical results are obtained (i) if all records with $f_{nat} < f_{exc}$ are excluded and (ii) if the formula PC = $(f_{nat} - f_{exc})/f_{nat}$ is used for all records with $f_{nat} > 0$.

Previous studies have referred to the PC metric as "pollinator dependence" (*15*). However, because this term has also been used for another metric (*15*), we here introduce the term "pollinator contribution" to avoid confusion (fig. S1).

Pollination experiments are generally concerned with differences in seed production between treatments, but often report fruit production, on the assumption that relative values of pollination treatments will be similar across measures. For the 241 records that reported both seeds per flower and fruits per flower, the Pearson correlation coefficient between PC calculated from fruits per flower and PC calculated from seeds per flower was $r = 0.89$. Similarly, for the 200 records that reported both seeds per fruit and seeds per flower, the Pearson correlation coefficient between PC calculated from seeds per fruit and PC calculated from seeds per flower was $r = 0.89$. This indicates that fruit production is a reasonable index of seed production for PC. Where a study reported multiple measures of reproductive output, we chose only one to calculate PC. Our order of preference, based on how well the measure estimates plant-level seed production, was as follows: seeds per plant, seeds per ovule for all flowers treated, seeds per flower, fruits per flower, seeds per fruit, and seeds per ovule for only flowers that set fruit (see "Robustness of our dataset" below). As PC differed between measures of reproductive output, we included the measure of reproductive output used to calculate PC as a factor in phylogenetic generalized least squares (PGLS) analyses (see below). This had to be included as a fixed factor as PGLS does not accommodate random factors.

We assessed the frequency distribution of PC in animal-pollinated flowering plants from 1174 species-level PC values, representing 1392 populations. Here, we used the average PC for species represented by more than one population in our dataset. We calculated the percentage of species in our dataset in the following ranges: PC = 0; PC > 0.8; PC = 1. To estimate the percentage of all flowering plants in these different PC ranges, we multiplied frequencies of species in our dataset by 0.875, as an adjustment for only 87.5% of plants being pollinated by animals (*1*). We treated the 12.5% of plants that are wind-pollinated as a separate category and assumed that, for all of these, pollinators do not contribute to reproduction (PC = 0). This is a conservative assumption, as some species have combined wind and animal pollination systems (ambophily), although this is thought to be rare relative to pure wind pollination (*55*) (see "Robustness of our dataset" below). To categorize vulnerability to extinction arising from future pollinator declines, we calculated the proportions of monocarpic and polycarpic species in our dataset with PC < 0.8 and PC ≥ 0.8. We again multiplied these proportions by 0.875, assuming that 87.5% (*1*) of both monocarpic and polycarpic plants are animal-pollinated. Note that this procedure only accounts for vulnerability to future pollinator declines. Some species may have low PC because they have already experienced pollinator declines, and these are not differentiated from those that have low PC due to high production of seeds without pollinators (i.e., high AF; see fig. S1). We thus assess the impact of future pollinator declines relative to a baseline provided by historical data.

To estimate the mean and median PC values across flowering plants, we appended 168 zero values representing the 12.5% wind-pollinated flowering plant species (*1*), which, we assume, have zero PC to the 1174 species-level PC values in our dataset and took the mean and median of all 1342 values (168 is 12.5% of 1342) (Fig. 1). We bootstrapped 95% CIs for the mean and median with r package boot using the bias-corrected and accelerated approach.

To understand how the impact of pollinator decline may vary geographically, and among different groups of plants, we investigated geographical and trait associations of PC in phylogenetically controlled least squares analyses (*56*). For these analyses, we replaced PC = $(f_{nat} - f_{exc})/f_{nat}$ with the log ratio $\ln(f_{nat}/f_{exc})$ because log ratios are closer to the normal distribution, and changes in numerator and denominator have equal effects on log ratios, in contrast to ratios (*57*, *58*). For records with PC = 1 (because $f_{exc} = 0$), calculating the log ratio in this way would involve taking the log of zero (which is undefined). To avoid this, we treated 557 such records (in the total dataset of 1528 records) as having $f_{exc} = 0.01 \times f_{nat}$. Although zeros in the denominator are sometimes remedied by adding a small constant to the numerator and the denominator for ratio variables (*57*), such an approach generates considerable noise and bias for a log ratio because the effect of the added constant on the logarithm of a number depends on the size of that number. Population average values of the log ratio were used for populations represented by more than one record, for instance, because the population was studied in multiple years or results for different sexual morphs were reported separately. For these analyses, we excluded two populations belonging to species for which flower morphological specialization was not known and one population of a monocarpic shrub species because it was the only one in this functional group in our dataset. After this, 1389 populations remained in the analysis. We estimated phylogenetic signal of the log ratio with the "lambda" method in the function phylosig in the package phytools in R, testing significance from the log-likelihood ratio (*56*). This showed significant phylogenetic signal ($\lambda = 0.452$, $P < 0.001$). Furthermore, to assess whether phylogenetically controlled analysis was warranted, we tested phylogenetic signal of Pearson residuals (*56*) from a nonphylogenetic analysis with the following explanatory variables: reproductive output measure, plant functional group, alien status, flower morphological specialization, latitude, temperature, and precipitation. As residuals of the nonphylogenetic model had significant phylogenetic signal ($\lambda = 0.319$, $P < 0.001$), we proceeded with phylogenetically controlled analyses.

Phylogenetic least squares analyses were carried out with the function pgls in the package phytools in R (*56*). For each analysis, we estimated phylogenetic signal (λ) by maximum likelihood for the full model and used this as the value of λ for all reduced models. Before significance testing, we conducted model selection to decide whether to combine some measures of reproductive output (fruits per flower, seeds per flower, seeds per fruit, seeds per plant, seeds per ovule for all flowers treated, and seeds per ovule for flowers that set fruit) into a single level for analysis, as sample size was small for some measures, and to assess whether temperature, precipitation, and latitude all needed to be included in the model, as these variables are strongly correlated. We compared AIC between a model in which all six measures of reproductive output were included as factor levels, and one with two levels: fruit set (fruits per flower) and seed set (seeds per plant, seeds per flower, seeds per fruit, seeds per ovule for all flowers treated, and seeds per ovule for only flowers that set fruit). The comparison showed that using two levels was preferable to six levels (ΔAIC >2). To assess which environmental measures should be included, we compared AIC between models that all contained reproductive output measure, plant functional group, alien status, flower morphological specialization, and year of study but included different combinations of latitude, temperature, and precipitation (table S5). The model with latitude only had the lowest AIC

score but was similar (ΔAIC <2) to models with only temperature or temperature and latitude. We therefore retained only latitude.

We tested significance of the effects of reproductive output measure, plant functional group, alien status, flower morphological specialization, year of study, and latitude in an analysis of data from 1389 populations, in which we dropped variables one at a time from the full model. Significance was assessed from an *F* test (a one-sided test) on the change of sum of squares. The R^2 value for the full model was 0.060. The effect of number of pollinator functional groups was assessed in a separate analysis for the 538 populations with data for this variable, where the full model also included all the variables mentioned above. In this case, the R^2 value for the full model was 0.098. Residual plots for these PGLS analyses did not show appreciable heterogeneity or departure from normality. Although the R^2 is relatively low, inspection of AIC values of the full model and reduced models (*59*) showed that inclusion of all the significant effects was justified (ΔAIC >2; table S1A). Thus, although we find well-supported effects of plant traits and the environment on PC, these are not of great value for predicting PC.

PC depends jointly on AF and pollinator visitation. Unfortunately, we could not quantify the effect of AF on PC because the indices PC and AF are calculated with a common ratio-element f_{exc}: AF = $f_{exc}/f_{hand\ cross}$, while PC = $(f_{nat} - f_{exc})/f_{nat}$. This introduces a spurious correlation, so that the coefficient of correlation *R* (and the coefficient of determination R^2) between AF and PC may indicate a relationship when there is no biological relationship (*60*, *61*). We therefore refrain from presenting the correlation coefficient between AF and PC and from using AF as a covariate in analyses of PC. However, given the formulas for AF and PC, when $f_{exc} = 0$ (no ability to produce seeds without pollinators), AF = 0 and PC = 1. As $f_{exc} = 0$ for a large proportion of populations in our dataset (Fig. 1), the influence of AF on PC should be strong. To test whether associations of PC with plant traits and geographical distribution are at least partially driven by AF, we analyzed the relationships of these variables with presence of AF (AF > 0) as a binomial response variable derived from the PC dataset with PC = 1 (i.e., AF = 0) versus PC < 1 (i.e., AF > 0) using the phyloglm function with the "logistic_IG10" method in the phylolm package in R (*62*). Significance of variables was tested with the likelihood ratio test, dropping variables one at a time from a full model, including all variables found to be significant in the analyses for PC.

We estimated the proportion of plants able to benefit from pollinator visitation (0.81) as the product of the proportion of plants in the Konstanz Breeding System dataset (*13*) in which fruit set or seed set in the pollinator exclusion treatment is lower than in a hand cross-pollination treatment (0.92) and the proportion of flowering plants regarded as animal-pollinated (0.88) (*1*).

Robustness of our dataset

The 1174 species analyzed here make up 0.4% of the estimated 295,383 species of described flowering plants (*63*). Our dataset shows generally good geographic representation, although with poor coverage for western Asia, eastern Europe, and Africa, except South Africa (Fig. 1).

To assess phylogenetic biases, we compared the frequencies of species in our dataset to those in the angiosperm (flowering plant) flora as a whole (*63*). We used totals available from work (*63*), which follows the Angiosperm Phylogeny Group IV (APG IV) classification, except for families affected by changes in family concepts

between APG III and APG IV (*64*), for which we obtained totals by manually checking the plant list website (*50*). Using the proportion each family makes up in the angiosperm flora, we calculated the expected number of species of each family our dataset would contain if we had randomly sampled all angiosperms and the difference between the observed and expected numbers of families.

Phylogenetic coverage in our dataset is good with most large, predominantly animal-pollinated plant families represented, although basal angiosperms are absent. Most of the very large plant families (>500 species) (*63*) that are absent or poorly represented in our dataset are predominantly wind-pollinated (e.g., *Poaceae*, as we excluded wind-pollinated species), or dioecious or monoecious (e.g., Urticaceae, as these species are seldom subject to pollinator exclusion experiments) (data file S8). Overrepresentation and underrepresentation of other families likely reflect underlying geographic biases in our dataset and biases among pollination biologists for studying certain taxonomic groups (data file S8). For instance, underrepresentation of *Orchidaceae*, a group favored by pollination biologists, may be due to concentration of orchid species richness in the tropics and possible poorer representation of tropical species in our dataset (Fig. 1), while overrepresentation of *Iridaceae* appears to arise from a taxonomic bias of pollination biologists, including a single study involving 26 species (Fig. 1).

We explicitly excluded species with wind pollination from our dataset, and when we assessed the distribution of PC across angiosperms, we assumed PC = 0 for all wind-pollinated species, including ones with combined wind and animal pollination (ambophilous species). This makes our estimates of mean PC more conservative. We made this assumption because it is difficult to experimentally quantify relative contributions of animal pollinators versus wind in ambophilous species and because ambophily is thought to be a rare condition, although there is no precise estimate of its prevalence (*55*).

Our dataset is biased for plant functional type, in that trees are underrepresented and monocarpic plants are overrepresented. An estimated 20% of all flowering plant species are trees (*35*) but only 13% of species in our dataset are trees. Our dataset contains 9% monocarpic species, which are mostly annuals, whereas annuals make up approximately 4% of the global flora (*65*). As PC is higher in trees than in other groups, and lower in monocarpic plants than other groups, this would bias our estimates of PC downwards.

Our dataset is biased for sexual system. About 12% of flowering plant species have separate male and female flowers, either borne on separate male and female individuals (dioecy) or borne on the same individuals (monoecy) (*43*). However, only 3% of species in our dataset are monoecious or dioecious. Average PC is likely very high across dioecious and monoecious species, because they can only achieve AF through leakiness (occasional production of hermaphrodite flowers) and apomixis (asexual seed production), both of which are regarded as rare. Nevertheless, the mean level of AF in monoecious and dioecious species is not well quantified by our dataset, which contains only 30 species in these two categories, so we do not attempt to correct for this bias, which likely leads to underestimation of the mean and median PC.

Our estimate of PC may be biased by the measures of reproductive output that were available. Where studies provided multiple measures of reproductive output, our order of preference in choosing which one to use to calculate PC was seeds per plant, seeds per ovule for all flowers treated, seeds per flower, fruits per flower (fruit set), seeds per fruit, and seeds per ovule for only flowers that set fruit. Seeds per plant is the best measure to use because it directly estimates total reproductive output. Calculating PC from seeds per ovule for all flowers treated, or seeds per flower should be equivalent to using seeds per plant, as the ratio between the two treatments should stay the same. However, calculating PC from fruits per flower (fruit set), seeds per fruit, or seeds per ovule for only flowers that set fruit may underestimate PC. This is because seeds per flower is the product of seeds per fruit and fruits per flower, while seeds per ovule for all flowers treated is the product of seeds per ovule for flowers that set fruit and fruits per flower. Pollinator exclusion is expected to reduce all of fruits per flower (fruit set), seeds per fruit, and seeds per ovule for flowers that set fruit due to reduced pollen transfer, self-incompatibility, and early acting inbreeding depression. Our PC estimate will also underestimate the consequences of pollinator failure across the plant life cycle because it does not account for inbreeding depression after seed production, in survival, growth, and subsequent reproduction of offspring (*44*).

SUPPLEMENTARY MATERIALS

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Citation: J. G. Rodger, J. M. Bennett, M. Razanajatovo, T. M. Knight, M. van Kleunen, T.-L. Ashman, J. A. Steets, C. Hui, G. Arceo-Gómez, M. Burd, L. A. Burkle, J. H. Burns, W. Durka, L. Freitas, J. E. Kemp, J. Li, A. Pauw, J. C. Vamosi, M. Wolowski, J. Xia, A. G. Ellis, Widespread vulnerability of flowering plant seed production to pollinator declines. *Sci. Adv.* **7**, eabd3524 (2021).

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