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POLLEN LIMITATION OF PLANT REPRODUCTION: ECOLOGICAL AND EVOLUTIONARY CAUSES AND CONSEQUENCES

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Abstract. Determining whether seed production is pollen limited has been an area of intensive empirical study over the last two decades. Yet current evidence does not allow satisfactory assessment of the causes or consequences of pollen limitation. Here, we critically evaluate existing theory and issues concerning pollen limitation. Our main conclusion is that a change in approach is needed to determine whether pollen limitation reflects random fluctuations around a pollen–resource equilibrium, an adaptation to stochastic pollination environments, or a chronic syndrome caused by an environmental perturbation. We formalize and extend D. Haig and M. Westoby’s conceptual model, and illustrate its use in guiding research on the evolutionary consequences of pollen limitation, i.e., whether plants evolve or have evolved to ameliorate pollen limitation. This synthesis also reveals that we are only beginning to understand when and how pollen limitation at the plant level translates into effects on plant population dynamics. We highlight the need for both theoretical and empirical approaches to gain a deeper understanding of the importance of life-history characters, Allee effects, and environmental perturbations in population declines mediated by pollen limitation. Lastly, our synthesis identifies a critical need for research on potential effects of pollen limitation at the community and ecosystem levels.

Key words: *elasticities; hand pollination; plant demography; pollen; pollen limitation, causes and consequences; pollinators; seed set; supplemental pollination.*

INTRODUCTION

Plants are immobile, and therefore rely on abiotic and/or biotic vectors to transport pollen (gametes) for sexual reproduction. An inadequate quantity or quality of pollen can reduce plant reproductive success (seed quantity or quality). The term that has been used to describe this phenomenon is “pollen limitation” (hereafter “PL”). For instance, in animal-pollinated plants, pollen quantity may be reduced as a result of fewer

pollinator visits or less pollen delivered per visit, and pollen quality can be reduced if self or otherwise incompatible pollen is delivered.

Over the last two decades, determining whether seed production is pollen limited has been an area of intensive empirical study (Burd 1994). However, these empirical studies have been only weakly connected to contemporary theory developed to explain the ecological or evolutionary causes of PL (Haig and Westoby 1988, Burd 1995) or its expected evolutionary consequences (i.e., character and mating system evolution, Lloyd 1974, 1992, Maurice and Fleming 1995). In addition, the effects of PL on plant demography and population

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persistence (e.g., Calvo and Horvitz 1993, Bond 1994, Groom 1998, Lennartsson 2002), plant species coexistence (Ishii and Higashi 2001), and community structure and ecosystem functioning (Bond 1994, Amarasakare 2004) have not been fully evaluated or incorporated into our understanding of the long-term consequences of PL.

Pollen limitation has both ecological and evolutionary causes and consequences. For instance, ecological context, plant life history, mating system, and phylogenetic history may all influence or be associated with the probability or strength of pollen limitation. In turn, reproductive characters can evolve in response to pollen or pollinator limitation (i.e., plants may evolve mechanisms of reproductive assurance), reducing the potential for PL in the future. If a species' population size is limited by seed production (e.g., Turnbull et al. 2000), PL may also differentially decrease the absolute or relative abundance of that species and shift the community to one dominated by species less prone to PL, such as autogamous species. Such changes in species composition could have consequences at the ecosystem scale, and for the frequency of pollen limitation among species. Chronic PL, in particular, can have several outcomes for plant populations—reproductive or life-history characters can evolve that minimize it (or its effects), their population abundances can decline leading to local extinction, or they can evolve but not at a rate fast enough to forestall extinction. Thus determining (1) whether populations can evolve to reduce PL, and (2) whether and how PL influences population dynamics are central to our understanding of the importance of PL in the maintenance of plant diversity.

In the present paper we aim to provide an integrated review and synthesis of current understanding of PL. We acknowledge that there is likely a dynamic feedback between causes and consequences but focus our primary discussion on the causes of PL, and its ecological and evolutionary consequences. We begin by clarifying the concept of PL and reviewing pertinent evolutionary theory. We then assess the causal interpretations of an empirical finding of significant PL and critically evaluate our current methods for measuring PL. Next, we use contemporary theory (Haig and Westoby 1988, Burd 1995) as a starting point for formalizing a framework for studying the evolution of reproductive strategies in response to PL. In doing so, we outline a new approach for the empirical study of PL with the goal of improving our understanding of its evolutionary dynamics. We then turn to the ecological consequences of PL, including plant population growth rate, community structure, and ecosystem functioning, and in doing so provide a prescription for future research in these areas as well. We conclude by commenting on the need for research at the interface between the ecological and evolutionary consequences of PL.

CONCEPTS, CAUSES AND EMPIRICAL ISSUES

Concepts, theory, and frequency of pollen limitation

The application of sexual-selection theory to plant reproductive ecology and evolution (e.g., Janzen 1977, Willson and Burley 1983) led to the expectation that female reproductive success should be normally limited by resource availability and not by access to mates (receipt of pollen) (Bateman 1948). If this expectation is correct, fruit or seed set should not increase if additional pollen were delivered, because no resources would be available for maturation of the additional fertilized ovules. The contrary outcome would imply pollen limitation (PL) of female fitness. Experimental pollen supplementation has been thought to provide a straightforward test of these alternatives (Bierzychudek 1981, Young and Young 1992).

This operational definition of PL, and its detection using supplementation experiments, is illustrated in Fig. 1a. Here, seed production increases with increasing pollen receipt to a point where maximal seed production is approached and additional pollen does not result in more seeds because resources are limiting seed production (i.e., the asymptote of the pollen receipt–seed number gain curve, hereafter “ k ”; Fig. 1a). (Note that plants in higher resource sites might have higher k values). Since hand pollinations are conducted with pollen loads assumed to be in excess of what is required for full seed set, supplemental pollen loads are somewhere along the asymptote. A significant difference in seed production between natural and supplemental pollination (hereafter, “effect size” e ; Fig. 1a) is interpreted as evidence that plants are pollen limited. High values of e imply strong PL; i.e., there is a large difference between supplemental and natural pollen receipt (hereafter, S), while low values of e suggest that natural pollen levels are close to the amount required (i.e., the value of S_H is small compared to S_L).

In an important paper, Haig and Westoby (1988) suggested that the dichotomy between resource vs. pollen limitation of female reproductive success was an oversimplification. They offered a graphical model in which ovule fertilizations rise with increased allocation to pollinator attraction (“fitness gain curve”), while at the same time ovule maturation ability (seed production) declines because enhanced attraction diverts resources from seed and fruit production (“resource cost curve”). Haig and Westoby argued that plant populations will evolve traits that promote increasing rates of pollinator visits and pollen deposition until an equilibrium is reached at which female fitness is limited simultaneously by both pollen acquisition and resources. At Haig and Westoby's equilibrium, pollen supplementation would produce no response because resources limit seed set above the equilibrium level of pollen attraction, while experimental reduction in pollen receipt below the equilibrium level would reduce seed set. This model is particularly appealing because of its

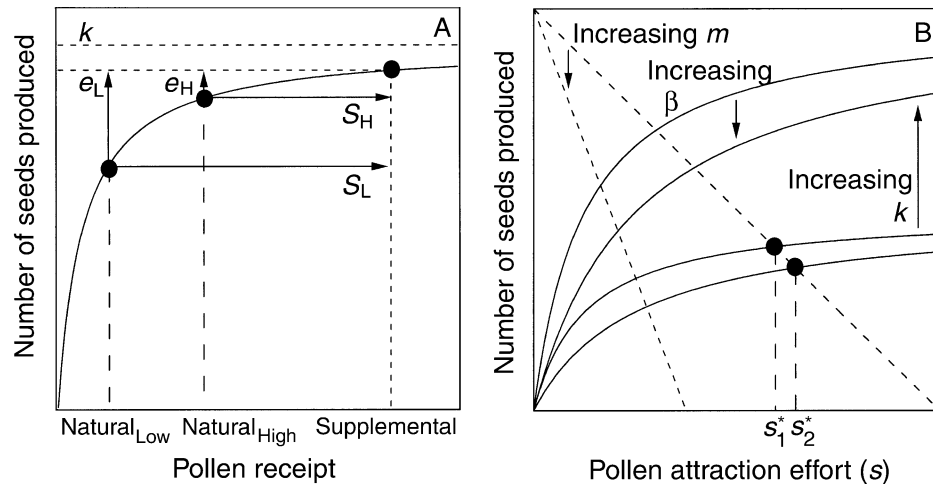


FIG. 1. Definition and theoretical representation of pollen limitation. (A) Operational definition of pollen limitation. Ovule fertilization increases with pollen receipt (self or outcross pollen) until resources become limiting at k . (Because these lines intersect the origin, apomixis is excluded.) Effect size (e) is the difference in seed production between supplemental and natural pollen receipt. Its magnitude depends in part on the difference (S) between the natural and supplemental levels of pollen receipt. Low natural levels of pollen receipt result in large effect sizes e_L ; high levels result in small effect sizes, e_H . A decelerating gain curve is drawn for convenience. All discussions and conclusions could equally use a linear relation with a maximum. (B) An extension of the Haig and Westoby (1988) model to examine the effect of variation in fitness gain and cost on optimal allocation to attraction. Two "families" of fitness gain curves (solid lines) each with varying k and β values (high k reflects greater total resources; low β , the pollination half-saturation constant, reflects rapid pollen accumulation), and two resource cost curves (dashed lines) with different m values (low m , the cost of reproductive strategy, reflects cheap attraction costs) are depicted. Variation in fitness gain and attraction cost curves determines the point at which they intersect and thus predicts different optimal allocations to attraction (s_1^* vs. s_2^*).

simplicity and because its predictions can be tested explicitly through straightforward pollen manipulations. Haig and Westoby point out, however, that stochastic environmental variation may produce apparent departures from equilibrium, so that pollen supplementation occasionally yields increased seed set even if the population is, on average, at the expected equilibrium.

However, contrary to these expectations, extensive reviews show that pollen supplementation often increases (Burd 1994, present study), and rarely decreases (Young and Young 1992), seed or fruit production. Specifically, Burd (1994) surveyed studies of 258 species, of which 62% are reported to experience statistically significant PL at some times or in some sites. In a quantitative review of studies published between 1980 and 2003, we found that in 73% of 85 cases where supplemental pollination was conducted at the whole-plant level (i.e., response in terms of number of seeds per plant) the authors reported significant PL (Appendix). Furthermore, PL was often quite strong and had an average standardized effect size of 0.35 SD units (95% CI: 0.29–0.41), which is associated with a 42% average increase in seeds per plant following supplementation (Fig. 2, Appendix). In addition, a great majority of studies conducted over multiple years (2–4 years) found a positive response to supplemental pollination in all years studied (20 out of 24; $\chi^2 = 10.7$ $P = 0.001$; T. M. Knight et al., unpublished data), indicating sustained PL in many species.

There are many possible reasons for the contrast between Haig and Westoby's (1988) expectation and the outcome of empirical studies. These include multiple potential causes of PL, issues surrounding the empirical study of PL, and biological features missing from Haig and Westoby's (1988) graphical presentation.

Causes of pollen limitation

There are at least two ultimate causes of PL (indicated by a significant e ; Fig. 1A): (1) the population is not at its Haig and Westoby (1988) equilibrium; and (2) the population is at equilibrium, but one determined by a stochastic rather than a constant pollination environment. We briefly summarize each of these below and then at the end of the *Evolutionary Consequences* . . . section (below) we discuss how we might distinguish between them.

Ecological perturbations lead to nonequilibrium situations.—Recent ecological changes in the pollination or resource environment may cause populations to diverge from their Haig and Westoby equilibrium, resulting in chronic PL. For example, introduction of highly attractive nonnative plants (Chittka and Schurkens 2001), invasion of a new habitat or habitat fragmentation (Aizen and Feinsinger 1994, Steffan-Dewenter and Tschardtke 1999), decrease in population size (Ågren 1996), or loss of native pollinators (e.g., Buchman and Nabham 1996), may reduce pollen receipt and increase PL of seed production. Some of the most extreme effect sizes are reported for plants in disturbed

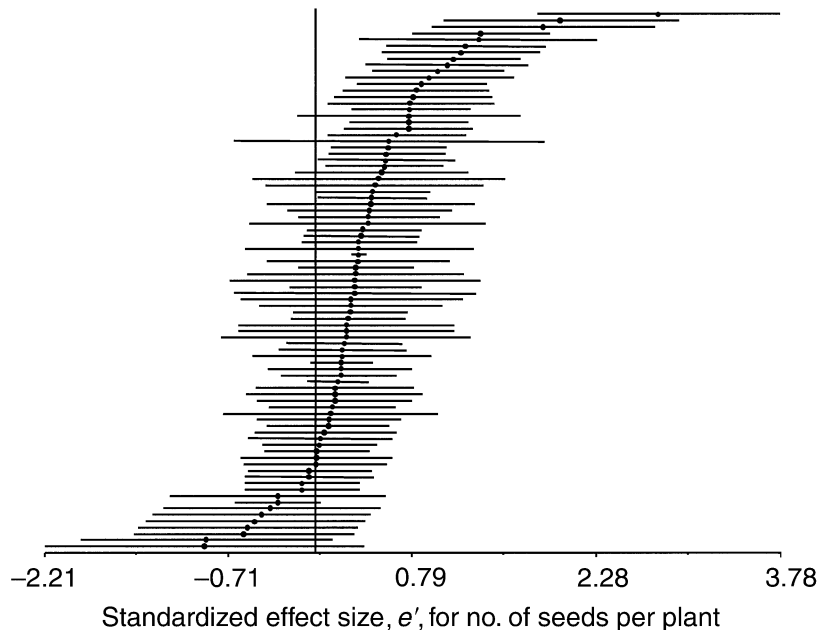


FIG. 2. Distribution of standardized effect sizes (e' ; solid dots) and sampling variances (v_e) for 85 cases where pollen supplementation was conducted at the whole-plant level (studies included are listed in the Appendix). Individual effect sizes that do not overlap 0 are significant at $P < 0.05$. We calculate e' as Hedges' d (i.e., the difference between the means of the supplement and control treatments, standardized by their pooled standard deviation and corrected for sample size bias, and sampling variance (v_e) following Rosenberg et al. (2000:14–15).

systems. For example, Parker (1997) found effect sizes of over 2000% in an invasive shrub, *Cytisus scoparius*. Anthropogenic fragmentation of habitats, climate change, and alteration of species distributions all may have wide-ranging effects on the degree to which plants exhibit optimal allocation for their resource–pollen environment. If most habitats today are influenced by some anthropogenic disturbance, or if ecosystems are naturally in rapid flux, then most plants will not be at their Haig and Westoby equilibrium.

Bet hedging in a stochastic pollination environment.—Stochastic variation among flowers in pollen receipt is a bet-hedging strategy that commonly leads to low fruit set (Stephenson 1981) or PL (Burd 1995). This hypothesis predicts that flowers should be “oversupplied” with ovules (or plants oversupplied with flowers) relative to the average pollen load received. Oversupply is adaptive in an environment with stochastic pollen receipt because plants can profit from occasional unpredictable arrival of unusually high-quantity (or high-quality) pollen on stigmas, or occasional visits from heavily laden pollinators that could pollinate many flowers. Although stocking every flower with many ovules, or every inflorescence with many flowers, entails a loss of reproductive resources to the plant, the fitness gains from the conversion of occasional “jackpot” visits into extra seeds may outweigh the cost of unutilized ovules or flowers. Burd's (1995) model of ovule packaging suggests that the fitness benefit of oversupply is greater when variation in stigmatic

pollen loads is higher, and when the cost of ovules is lower. Studies suggest that there is substantial variation in stigmatic pollen loads among flowers in natural populations (see references in Burd [1995]), indicating that there is ample opportunity for bet-hedging strategies to be adaptive. Burd's model is also appealing because it offers an adaptive explanation for what might otherwise be considered to be a maladaptive allocation of resources.

Empirical issues

Even if we better understood the cause of significant level of PL, the standard empirical approach for detecting PL remains problematic for several statistical (see Young and Young 1992, Thomson 2001) and biological reasons. Below, we elaborate on four of the latter, including (1) the level of pollen manipulation is unknown; (2) the quality of pollen differs between supplement and control treatments; (3) reallocation complicates the interpretation of fitness effect size; and (4) estimates reflect average rather than individual PL.

Level of pollen manipulation is unknown.—When performing hand pollinations most workers attempt to add pollen in excess of what is needed to fertilize all ovules. This assumes that the level applied is somewhere beyond the minimum required for full seed set (Fig. 1A), but the exact location on the curve is not usually known. In addition, because only a small percentage of studies simultaneously assess the natural level of pollen deposition (e.g., Galen et al. 1985, John-

son and Bond 1997), the magnitude of the supplementation applied (S) is unknown. Even fewer studies perform pollen reductions as well as supplementations as recommended by Haig and Westoby (1988) (but see Lawrence 1993). Thus, species could differ in effect size (e) because they differ in S or in the shape of their pollen–seed response curves. If we wish to understand the causes of variation in effect sizes among species, populations, or years, we ideally need to know both treatment level and response (S and e).

The quality of pollen differs between supplement and control treatments.—The quality and rate of delivery of pollen involved in supplemental pollination may differ from that of natural pollination. Hand pollinations often involve pure outcross pollen, whereas natural vectors deliver a mixture of self and outcross pollen (Thomson 2001). Differences in pollen quality are likely to be more extreme if natural pollinators are excluded from the hand-pollinated plants (e.g., via bagging). In addition, if only one pollen donor is used in hand pollination, and natural pollinators deliver pollen from more than one source, then hand-pollinated plants will have lower pollen diversity than control plants. Lastly, pollen delivered by hand reflects a sudden increase in pollen, whereas natural pollen delivery may be more gradual. Pollen competition may be more intense when pollen is delivered simultaneously. Thus, hand-pollination studies may falsely conclude that seed production is limited by pollen quantity when in actuality pollen quality is affecting seed production (Ramsey and Vaughton 2000, Finer and Morgan 2003). An alternative possibility is that gradual delivery of pollen in nature may be more effective at fertilizing ovules (if measured as the number of fertilizations per deposited pollen grain) than the sudden deposition of artificially large amounts of pollen, which may clog stigmas. In this case, PL may be underestimated due to the stigma-clogging effects of the hand-pollination treatment.

Reallocation complicates the interpretation of the fitness-effect size.—Because plants can reallocate resources among modules (flowers) and years, using the immediate increase in seed production due to supplemental pollination as a measure of the pollination environment is potentially confounded with several plastic responses to additional pollen.

First, plants receiving experimentally elevated levels of pollen have not “paid” the cost of attracting additional pollinators under natural conditions and therefore have more resources available for seed maturation. For example, under natural pollination most flowers may not receive adequate pollen for full seed set, but additional flowers are produced sequentially throughout the season so that partial seed set in each contributes to total seed output. In contrast, under hand pollination, individual flowers may achieve full seed set, which may lead the plant to produce fewer flowers overall. This reduced investment in flower construction

means that the increase in seed production after supplemental pollination can be a function of both increased pollen receipt and lower total investment in flowers. In addition, because pollen deposition can reduce floral longevity (Ashman 2004), hand pollination may lead to shorter flower lifetimes. Such reduced flower maintenance costs can lead to greater investment in seeds (see Ashman and Schoen 1997). Supplemental pollination, thus, may alter the efficiency at which plants can convert ovules into seeds.

Second, plants may be able to reallocate resources among flowers. If additional pollen is applied to only one flower (or one inflorescence or one branch) on a plant, resources may be shunted away from untreated flowers, causing higher seed production in the treated flower. However, at the whole-plant level, supplemented and control plants may produce similar seed numbers. Similarly, among-year reallocation can obscure resource limitation of seed production. That is, response to pollen supplementation by a polycarpic plant may come at the cost of future reproduction or survival, but because these costs are not paid within the time frame of the experiment they are not apparent. Trade-offs may also involve male fertility or seed quality, however these are often overlooked. For instance, if pollen-supplemented plants produce more fruits at the expense of producing additional flowers, they may have reduced male fertility. Similarly, hand-pollinated plants may produce larger numbers of seeds at a cost to seed size, seed germination, and subsequent seedling growth and survival (e.g., McGinley et al. 1987).

An adequate test of PL, and especially of the Haig and Westoby (1988) equilibrium, requires experimental manipulation and measurement over the entire lifetime of individuals, but such a study has been performed only for monocarpic plants. Very few studies of polycarpic plants have supplemented pollen on the same plants for many years running, and even then only over a small portion of their entire lifetime (e.g., Primack and Hall 1990, Dudash and Fenster 1997). These types of reallocation issues are at the heart of Zimmerman and Pyke’s (1988) assertion that the interpretation of supplemental pollination conducted at any level (flower or inflorescence) other than the whole plant, or for any fraction of its lifetime, can be problematic.

Estimates reflect average rather than individual pollen limitation.—The effect size most commonly reported is a population average (the mean difference between hand-pollinated vs. natural-pollinated plants). However, the shapes of resource-cost and fitness-gain curves (Fig. 1B) are properties of individuals, and selection to alter the shape of these relies on variation among individuals. Moreover, the Haig and Westoby (1988) model is based on optimizing allocation to an attractive trait associated with pollen receipt (a^* in Haig and Westoby’s model, s^* in our formalization [in next section, below]; Fig. 1B), but we rarely measure the relationship among individuals between phenotype

and the response to pollen supplementation. Exceptions include studies showing differences in PL with plant size (Dudash 1993, Lawrence 1993), petal size (Totland et al. 1998), and flower number (Ehlers et al. 2002).

EVOLUTIONARY CONSEQUENCES OF POLLEN LIMITATION

Many evolutionary arguments regarding the diversity of plant reproductive strategies incorporate pollen limitation (PL) as an important mediator of selection, and predict that plants will evolve to reduce PL. For instance, it has been argued that traits that enhance pollinator attraction (Haig and Westoby 1988), or less reliance on pollinators (i.e., obligate or delayed self-pollination; Lloyd 1974, 1992), or on sexual reproduction (i.e., increased clonal growth; Eckert 2001) may evolve. Haig and Westoby's (1988) graphical model was a pioneering effort in this pursuit, but the exclusion of many biological features and the lack of a mathematical formulation have limited its ability to guide empirical investigations into these expected evolutionary consequences of PL. For instance, the fitness-gain and resource-cost functions represented in their model are fixed in both ecological and evolutionary time, and there is no indication of how the mechanistic representation of these functions might evolve. In addition, life-history characters that could be expected to influence pollen or resource limitation of female fitness are not included. Here, we formalize and extend their conceptual framework to facilitate reasoning about the consequences of pollen-supplementation experiments, to illustrate how aspects of life history may shape fitness-gain and resource-allocation functions, and to evaluate how PL may result in the evolution of these functions.

Formalizing and extending a pollen-limitation model

Suppose a plant adopts reproductive strategy s_1 . The strategy influences the amount of pollen receipt $r(s_1) \geq 0$, and pollen receipt is necessary for female fertility gain through seed and fruit production. Increasing pollen receipt likely increases female fertility $f(r(s_1))$, but at a diminishing rate. One mathematical function capturing this idea is

$$f[r(s_1)] = \frac{kr(s_1)}{\beta + r(s_1)}. \quad (1)$$

In this expression, seed number increases with pollen receipt to a value approaching k (the asymptote of the pollen receipt–seed number gain curve), while β is the pollination half-saturation constant (larger values of β decrease the rate at which maximum seed or fruit set is approached). Individuals (and species) may differ in either k or β as indicated by the “families” of curves in Fig. 1B.

The reproductive strategy has a cost, reflecting decreased opportunities for fitness gain through other aspects of the life history. For instance, the cost might

arise because resources used in the reproductive strategy s_1 decrease resources available for survival or because enhanced female fertility occurs at the expense of male fertility. To incorporate such costs, suppose that strategy costs increase linearly with the amount of pollen receipt such that with each additional unit of pollen received, the costs increase by an amount m . Allocation strategies reflecting high or low costs are illustrated in Fig. 1B. Costs are then $c(r(s_1)) = mr(s_1)$. Fitness (w) is the difference between benefit and cost when these accrue simultaneously,

$$\begin{aligned} w(s_1) &= f[r(s_1)] - c[r(s_1)] \\ &= \frac{kr(s_1)}{\beta + r(s_1)} - mr(s_1) \end{aligned} \quad (2)$$

and is maximized when a reproductive strategy \hat{s} exists such that $dw(\hat{s})/d\hat{s} = 0$, $d^2w(\hat{s})/d\hat{s}^2 < 0$. The rate that fertility benefits and costs increase with strategy balance at this equilibrium $df(r(\hat{s}))/d\hat{s} = dc(r(\hat{s}))/d\hat{s}$, reflecting the pollination–resource trade-off in Haig and Westoby's (1988) model (“families” of s^* in Fig. 1B). The reproductive strategy \hat{s} results in a corresponding level of pollen receipt $\hat{r} = r(\hat{s})$. Supplemental pollination experiments add an amount of pollen S , so that pollen “receipt” increases from \hat{r} to $\hat{r} + S$. Female fertility then changes to $k(\hat{r} + S)/(\beta + \hat{r} + S)$, and the effect size is

$$\begin{aligned} e &= f(\hat{r} + S) - f(\hat{r}) \\ &= k \left(\frac{\hat{r} + S}{\beta + \hat{r} + S} - \frac{\hat{r}}{\beta + \hat{r}} \right). \end{aligned} \quad (3)$$

This model formulation offers the opportunity for insight into the micro- and macro-evolutionary processes operating on PL. These are discussed in the context of future empirical study in the next section.

Recommendations for future work on the causes and evolutionary consequences of pollen limitation

Over the last two decades researchers have generated a wealth of empirical data on PL at the plant level. However, we still have an incomplete understanding of when and how PL is important in plant evolution. We have suggested above that this may result from both multiple interpretations of the cause of PL, and the limitations of what has become the standard empirical approach. Here, we present suggestions for future work aimed at advancing our understanding of the causes and consequences of PL for plant evolution.

Insights on how to distinguish among multiple causes.—Distinguishing among the multiple interpretations of PL detected by supplemental pollination studies is of interest because each interpretation carries distinct evolutionary implications. For example, historical information and studies performed over multiple years will be helpful in determining whether populations are perturbed (i.e., chronic PL) or simply fluctuating

around their Haig and Westoby (1988) equilibrium. For some species, PL in pristine and disturbed sites may be compared. In addition, studies that vary pollen load above and below natural levels (supplements and reductions, e.g., Lawrence 1993) will be instructive for describing the pollen–seed-set curve (Fig. 1A) and evaluating whether a population is at its equilibrium value for traits influencing pollinator service. The stability of this equilibrium can be tested by varying the strength of perturbation (i.e., manipulated pollen level), but this also requires knowledge of natural pollen-deposition level.

On the other hand, to determine whether a bet-hedging strategy is a likely cause for PL we need to gather information on pollen-load variation and ovule and flower costs across several species. Specifically, Burd's (1995) model predicts that the degree of bet hedging (i.e., the extent of ovule or floral overproduction) will reflect the variation among modules or among years in the pollination environment, and will be influenced by ovule and flower costs. A larger response to experimental pollen supplementation should occur in populations or species that experience greater variance in pollen acquisition or have smaller costs. This prediction is amenable to comparative tests but requires that data on natural patterns of variation in pollen receipt among modules (e.g., flowers, inflorescences, or years) be collected in conjunction with results of pollen supplementation.

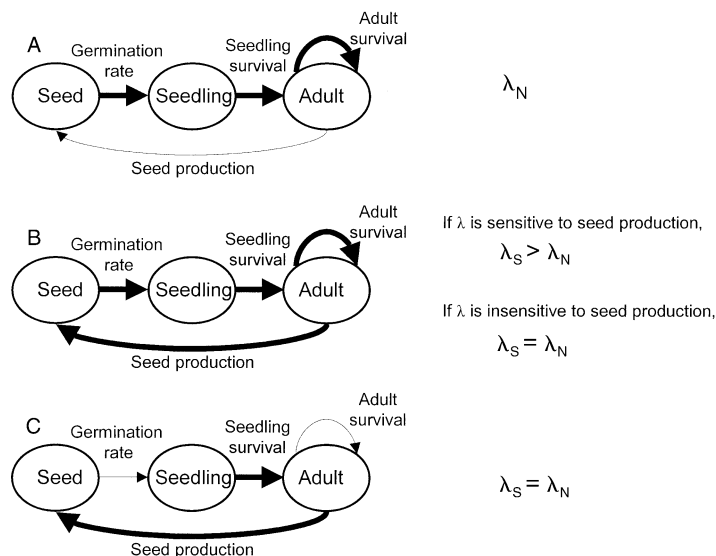
Micro-evolutionary insights from the pollen-limitation model.—While the primary means for assessing PL has been to measure the effect size (e) directly, the model presented above reveals that we can more carefully evaluate the causes of variation in PL from β , k , S , and \hat{r} . We can measure natural (\hat{r}) and manipulated levels of pollen receipt and seed production to estimate S and e . We can characterize the shape of the attractive trait vs. seed production curve (β and k) by regressing seed set on attractive traits. Individual researchers will need to determine what the most appropriate metric of attractiveness is for a given species; in some systems this may be straightforward (e.g., flower size); in others it may be more complex (e.g., a function of flower number, phenology, scent). Alternatively, we can estimate the relationship between stigmatic pollen load (natural or manipulated) and seed set in one experiment (e.g., Mitchell 1997, Kalla and Ashman 2002), and separately determine the relationship between an attractive trait and stigmatic pollen load under natural conditions (e.g., Ashman and Diefenderfer 2001). These two pieces of information can be combined to determine the relationship between attractive traits and seed set in Fig. 1B. These measures not only provide more information but also avoid several of the empirical problems associated with pollen-supplementation studies mentioned above. Specifically, by measuring \hat{r} , β , and k we obtain independent estimates of the pollination environment (\hat{r}) and plant functional response

to pollen-load sizes (β , k), and thus do not confound the effect size with allocation plasticity. Moreover, when β , k , and \hat{r} are estimated in conjunction with measures of S and e , they can provide independent validation of e as a realistic estimator of PL.

Furthermore, empirical observations of individual variation in fitness-gain and allocation curves within species quantifies the potential for evolution towards a Haig and Westoby (1988) equilibrium. For example, Mitchell (1997) found that nearly 40% of the variation in pollen-receipt vs. seed-production curves measured at the flower level was attributable to among-plant variation. We are not aware of any study exploring seed-production vs. pollen-receipt curves at the plant level, but these would circumvent reallocation problems as well as relate effect size to variation in traits that attract pollinators. In this pursuit, plants that can be clonally replicated will be particularly useful as they enable independent measures of environmental and genetic sources of variation in the shapes of the curves. Alternatively, population measures of PL combined with analyses of phenotypic selection through seed production (reviewed in Ashman and Morgan [2004]) also provide information on S , e , and β . Ideally, this information would be combined with estimates of m , the slope of the attraction-cost curve. If natural variation in attractive traits is limited, artificial selection to increase/decrease attraction may uncover a trade-off between attraction and seed production; such an approach has been successful for other floral traits (e.g., Mazer et al. 1999, Worley and Barrett 2000).

Macro-evolutionary insights from the pollen-limitation model.—The sketch of the model presented above allows assessment of pollen-supplementation studies in a macro-evolutionary context. Parameters influencing pollen receipt, k and β , might change in response to selection induced by the pollination environment or other aspects of the life history. For instance, selection for increased seed-dispersal ability might increase maximum seed production k , while selection for increased self-fertilization may decrease pollen half-saturation β . Likewise, adaptation to pollinator fauna with alternative nutrient requirements (e.g., from bees to hummingbirds) may increase the costs of pollen receipt m . Such changes provide opportunities for interpreting PL studies in a phylogenetic context. As an obvious example, decreased reliance on pollinators through the transition to substantial self-fertilization might result in a very small β , or a reduction in the slope of the cost curve m , compared to related, outcrossing taxa. The model sketched above suggests that the transition should be associated with greatly reduced effect sizes in the selfing compared to the outcrossing species. Indeed, in Burd's (1994) review, self-incompatible species were more pollen limited than self-compatible species, and this was further corroborated by Larson and Barrett (2000) in an analysis that controlled for phylogenetic history. Further,

FIG. 3. Hypothetical plant life-cycle diagram illustrating how pollen limitation may affect population growth rate, λ . (A) Seed production is pollen limited, and the population growth rate with natural levels of pollination is λ_N . (B) Population growth rate with supplemental levels of pollination, λ_S . There are two possible outcomes: supplemental pollen increases seed production and λ (i.e., $\lambda_S > \lambda_N$), or supplemental pollen increases seed production, but λ is insensitive to seed production (i.e., $\lambda_S = \lambda_N$). (C) Supplemental pollen increases seed production, but trade-offs with other life stages restrict change in λ (i.e., $\lambda_S = \lambda_N$).



if selfing and reduced effect sizes occur nested within a clade of taxa with large effect sizes, then selfing may represent a response to habitual PL. Thus, a phylogenetic analysis may allow identification of causal relationships between effect size and reproductive characters while controlling for similar evolutionary history.

ECOLOGICAL CONSEQUENCES OF POLLEN LIMITATION

In contrast to several decades of work focusing on pollen limitation (PL) at the level of the flower or the plant, the issue of how PL influences population growth has only recently received attention. We begin this section by reviewing the few published studies of PL at the population level. In doing so, we highlight why a mismatch may occur between the consequences for the individual and for the population. Second, we discuss how PL can mediate Allee effects and accelerate plant population decline. Third, we consider ways that PL at the population level can have ramifications for community composition and ecosystem functioning. We conclude this section by highlighting fundamental and emerging areas in need of additional study.

Pollen limitation and population growth

To examine PL at the population level, studies must evaluate the effect of pollen supplementation in the context of the entire plant life cycle. As an example, consider a perennial plant with a life cycle consisting of three stages; seed, seedling, and adult (Fig. 3A). On the surface it seems logical to expect that PL will have negative consequences for plant population growth because it limits the input of seeds into the life cycle (Fig. 3A vs. B). Surprisingly, even when a significant effect of pollen supplementation is found at the plant level it does not always have an effect on population growth

rate (λ ; Table 1). There are several potential reasons for this discrepancy. Two deal with the demographic role of seed production in the life cycle: (1) λ may be insensitive to changes in seed production (Fig. 3B), or (2) increases in seed production may come at a cost to other vital rates (e.g., growth, survival), owing to reallocation of resources among modules or years (Fig. 3C). We evaluate these by drawing on published data.

We evaluated whether the discrepancy between plant- and population-level responses to pollen supplementation was a result of insensitivity of λ to seed production by comparing the elasticities (proportional sensitivities) of seed production relative to other vital rates using published data for six species–population combinations (Table 1). Because elasticities sum to unity they give an index of the relative importance of changes in a particular demographic parameter (i.e., seed production) to λ (Silvertown et al. 1993). We calculated an elasticity matrix from the demographic matrices discussed in each study that linked PL to λ ; elasticities were not presented in most of the original studies, but could be calculated from the demographic data presented (using MATLAB [MathWorks 2000]). All of these studies considered one-year stage or size transitions. For each study, we considered five demographic transitions and their elasticities: (1) *seed production*—includes seed production for all reproductive life stages. In these plant species, seed production and germination often took place within a 1-yr time step, and thus the seed-production term included germination; (2) *seed and seedling survival*—includes seed dormancy, germination rate, and seedling survival (if not already included in the seed-production term); (3) *retrogression*—includes all transitions to a previous stage class or smaller size class and all transitions into vegetative dormancy (belowground dormancy of vegetative parts); (4) *stasis*—includes all transitions in which

TABLE 1. Summary of the standardized effect size (e') of pollen supplementation experiments (see Fig. 2 legend), population growth rate for plants exposed to supplemental (λ_S) vs. natural (λ_N) levels of pollen, and the summed elasticity values in five regions of the demographic matrix.

Species	e'	λ_S	λ_N	Summed elasticity values					Source
				Seed production	Seed/seedling survival	Retrogression/dormancy	Stasis	Progression	
<i>Arisaema triphyl- lum</i> †	1.22‡,§	0.97	0.90	0.02	0.02	0.16	0.54	0.26	Bierzychudek (1982)
<i>Cytisus scoparius</i> (prairie)	4.77¶,§	2.43	1.85	0.16	0.22	0.003	0.15	0.47	Parker (1997)
<i>C. scoparius</i> (urban)#	2.28¶,§	1.23	1.14	0.07	0.20	0.01	0.39	0.33	Parker (1997)
<i>Lathyrus vernus</i>	1.22‡,§	1.02 ^{NS}	1.03	0.03	0.05	0.13	0.60	0.19	Ehrlen and Eriksson (1995)
<i>Primula veris</i>	0.45¶	1.19 ^{NS}	1.21	0.01	0.01	0.15	0.43	0.40	Garcia and Ehrlen (2002)
<i>Trillium grandiflorum</i> ††	0.61#,§	0.98 ^{NS}	0.97	0.01	0.01	0.11	0.72	0.15	Knight (2004)

† Only the Brooktondale population was used (where the pollen supplementation experiment was conducted). Matrices for the two years were averaged.

‡ Data reported as number of seeds per plant.

§ Author(s) reported a significant difference between supplement and control plants at the $P < 0.05$ level.

|| The effect sizes for the two prairie populations, Johnson and 13th division, were averaged. Only the results from the 1994 pollen-supplementation experiment were used (because a demographic matrix was not available for other years at the 13th division site). The matrix was an average of values for the edge of the invading front for both sites from 1994 to 1995 (from Parker 2000).

¶ Data reported as fruit set (percentage of flowers that set fruit).

The effect sizes for the two urban populations, Discovery Park and Magnuson Park, were averaged. Only the results from the 1994 pollen-supplementation experiment were used (because a demographic matrix was not available for other years at Magnuson Park). The matrix was an average of values for the edge of the invading front for both sites from 1994 to 1995 (from Parker 2000).

†† Data from 1999 and 2000 averaged for the calculation of effect size and demographic matrix elements.

^{NS} Author(s) reported a nonsignificant difference between λ_S and λ_N .

plants remain in the same stage or size class; and (5) *progression*—includes all transitions into later stage or larger size class and all transitions out of vegetative dormancy.

A significant effect of pollen supplementation on λ is expected if (1) the supplementation results in an increase in seed production relative to the control and (2) λ is sensitive to changes in seed production. Among species in our review (Table 1), the change in λ in response to pollen supplementation— λ with supplementation minus λ with natural levels of pollen—was positively associated with the magnitude of pollen limitation (calculated as the standardized effect size, e' ; Fig. 2) ($r = 0.96$; $P = 0.002$; $N = 6$ species), and with the elasticity for seed production ($r = 0.95$; $P = 0.003$; $N = 6$ species). Both relationships were driven by the invasive species *Cytisus scoparius*, which was both highly pollen limited and highly sensitive to changes in seed production. This may not be surprising because seed production has large effects on the rate of increase of rapidly growing plant populations (Parker 1997, Crone 2001), and the elasticity of seed production is positively correlated with λ (Silvertown et al. 1993). In contrast, seed production may be less demographically important in populations that are older, and closer to their carrying capacity. This may be the case for the other species in our survey where the elasticity of seed production was very low (Table 1). For these species,

pollen limitation may have only small population-level effects.

All of the demographic matrix models we summarized here were density independent, and therefore assumed that locations for seed germination (“safe sites”) are not limiting. However, if germination is density dependent, then pollen supplementation may not increase the abundance of plants in the population, because those extra seeds will not have a place to germinate. To determine if pollen supplementation will result in more seeds and more seedlings, both a pollen-supplementation experiment and a seed-supplementation experiment should be conducted simultaneously. To date, we know of no published study that has done this.

Increased seed production might not increase λ if trade-offs with other vital rates obscure the effect of PL at the population level. Trade-offs important in determining the effect of PL on total fitness at the individual level are also important for determining the importance at the population level. For instance, increased seed production following supplemental pollination may come at a cost to seed quality, if seed number trades off with seed size. Such a trade-off may lead to decreases in vital rates associated with germination and/or seedling survival. However, to date, the direct effects of these seed trade-offs have not been explicitly examined in a demographic context. Furthermore, in

perennial plants, increased seed production may also incur costs in terms of adult survival, growth, and future reproduction. For example, Ehrlén and Eriksson (1995) found that supplemental pollen increased seed production of *Lathyrus verna* approximately three-fold but plants regressed in size and produced fewer flowers in the following year relative to control plants. Because adult stages had the highest elasticities in this species (Table 1) the net effect of supplemental pollen on λ was negligible. This discussion makes clear that information on both the magnitude of PL, the change in the vital rate, and the sensitivity of λ to that change are needed to fully evaluate the effect of supplemental pollination on λ .

Pollen limitation, population size, and Allee effects

Plant populations may be small, sparse, or declining for a variety of reasons, and PL-mediated Allee effects can accelerate the rate of decline or can exacerbate the problems of small population size. Allee effects, or positive density dependence (also known as “inverse density dependence”), occur when species benefit from the presence of their conspecifics, (i.e., due to decreased predation risk or increased mating opportunities; Allee et al. 1949). In populations where Allee effects are important, models suggest that there is a threshold size below which deterministic extinction occurs (e.g., Dennis 1989, Lande et al. 1998). Plant populations that rely on animal pollinators for reproduction are likely to experience Allee effects (e.g., Kunin 1993, Groom 1998, Hackney and McGraw 2001), and these can occur through at least three mechanisms. First, plants in low-density patches (or populations) are often less attractive to pollinators, and, therefore, receive fewer pollinator visits and less pollen than those occurring at high density (e.g., Silander 1978, Klinkhamer and Dejong 1990, Fausto et al. 2001). Second, at low density, plants may receive more heterospecific and fewer conspecific pollen grains than at high density as a result of generalist pollinators visiting multiple species within foraging bouts (e.g., Groom 1998). Third, seed quality may be affected by density. If pollinators visit more flowers per plant in sparse compared to dense patches, then there is the opportunity for more selfing in the former. In fact, several studies have shown that the selfing rate increases with decreasing plant density (e.g., Murawski and Hamrick 1991, Franceschinelli and Bawa 2000). Because self-pollinated seeds often express inbreeding depression at the germination or survival transitions (reviewed in Husband and Schemske [1996]), Allee effects brought about by pollinator behavior may be expressed in terms of both offspring quality and offspring quantity.

Population size may also affect PL in ways that are independent of population density. In particular, small population size can reduce the number of compatible mates, especially for plants with barriers to selfing (e.g., self-incompatibility alleles, dioecy, heterostyly),

and increase the relatedness among possible mates. For example, Ågren (1996) found that the degree of PL increased as the size of the population decreased in island populations of heterostylous *Lythrum salicaria*. Thus, populations with fewer individuals may experience more PL, even if they receive adequate pollinator visits, owing to incompatibility or greater relatedness among individuals.

Consequences of pollen limitation for communities and ecosystems

Pollen limitation of a focal species could also affect other members of the community. However, little attention has been paid to these “higher level” interactions. Here, we suggest that PL can affect other species irrespective of whether it affects the λ of the pollen-limited species. For example, reduced seed production owing to PL will lower resource availability for seed predators and pathogens even if it does not affect λ of the focal plant species. When PL affects the abundance of the focal species, not only is it possible that interacting species (e.g., mutualists, antagonists) will be influenced, but other community-structuring processes may also be altered. For example, if interspecific competitive interactions at the seedling stage are important among co-occurring species, reductions in the seed rain of the focal species may lead to altered competition. In addition, seed-sowing experiments show that plant community structure (e.g., species richness, evenness) is altered by seed additions (Foster and Tilman 2003), suggesting that PL may affect plant community structure when colonization of local patches is seed limited.

Population and community effects of PL may scale up to affect ecosystem processes. To the extent that the focal species uses or provides a resource disproportionately relative to its biomass, changes in its abundance ensuing from PL may have ecosystem-level effects. For example, reductions in the abundance of a nitrogen-fixing species may have strong effects on nitrogen availability for multiple species. Negative effects of PL on species that provide other ecosystem services such as water filtration or soil stabilization will also have serious ramifications. In addition, it has recently been shown that at low levels of species richness both species diversity and species composition can strongly influence a variety of ecosystem processes, such as primary productivity or invasibility (e.g., Naeem et al. 1994, Tilman et al. 2001). If PL leads to extinction of some key species from local communities, or alters community composition, then it might directly influence these ecosystem-level processes. Many of these community- and ecosystem-level consequences of PL have not been investigated theoretically or empirically, and reflect an area ripe for study.

Recommendations for future work on the ecological consequences of pollen limitation and plant population persistence

All of the studies that have evaluated the effect of pollen supplementation in the context of the entire plant life cycle have been on polycarpic perennials with limited (or no) clonal growth (Table 1). Similar studies on organisms with disparate life-history traits are necessary if we are to determine which types of species should be most likely to suffer population declines as a result of PL (Silvertown et al. 1993). Species whose population dynamics are sensitive to changes in seed production should be most likely to show population-level effects of PL (Table 1). Furthermore, we expect that plants that are incapable of clonal growth, have few reproductive episodes (Silvertown et al. 1993, Larson and Barrett 2000), and/or lack a seed bank (Bond 1994) should be more sensitive to changes in seed production than those with the opposite traits, so these characteristics may also be correlated with susceptibility to PL-driven population dynamics. Because it may be difficult to evaluate this hypothesis empirically, we suggest that a modeling approach that explores the sensitivity of λ to seed production under various life-history and environmental disturbance scenarios would provide considerable insight. Pinpointing suites of characters associated with extreme sensitivity to PL-driven dynamics would be valuable for predicting population and community changes, as well as for determining the types of plant species in need of explicit management.

Antagonists, such as seed predators and florivores, can alter the relationship between plants and pollinators (e.g., Strauss et al. 1996, Krupnick et al. 1999) and thus, PL and its importance to λ . For example, when seed predation is high, pollen-supplementation experiments may show no evidence of PL (e.g., Cunningham 1995, Parker and Haubensak 2002). The importance of other interactors in determining seed output suggests that primary emphasis on the dichotomy of pollen and resources in seed production is not justified.

Demographic trade-offs and the importance of pollen limitation to λ .—Further empirical work is necessary to determine the prevalence of trade-offs between seed production and other life-history stages and how they affect the relationship between PL and λ . To date the trade-off between seed production and germination or seedling survival rates has not been examined within a demographic framework. One approach is to simulate chronic pollen limitation (by excluding pollen or pollinators) and/or to simulate a sustained excess of pollinators (by repeatedly supplementing pollen or pollinators) and follow the adults and resultant seeds from these manipulations as well as control populations throughout a full generation. However, such an approach is not feasible for plants with very long generation times, and it may be

difficult to obtain adequate replication given the variation in response to supplemental pollination (Fig. 2). An alternative method is to conduct separate supplementation (and/or reduction) experiments for each life stage in a generation. For example, one could perform both pollen-supplementation and seed-supplementation experiments. The seed supplementation would determine the effect of increased seed production on the number of plants that germinate and survive to flowering (e.g., Turnbull et al. 2000, Moles and Westoby 2002). The source of seeds (i.e., from control or pollen-supplemented plants) for seed supplementation must also be incorporated into the experiment if one wishes to test for a trade-off between seed number and seed quality directly. Species with variation in time to reproduction or polycarpic life histories would require further information. In the case of polycarpy, adult plants should be subjected to repeated supplemental pollination to determine the effect on adult survival or reproduction.

Individual-based models that can scale up to population dynamics can also reveal how trade-offs (e.g., between seed number and seed quality) that arise at the level of individuals may translate into population-dynamic consequences. In addition, these models can incorporate the nonlinearities of PL, which, combined with the stochasticity inherent in the pollination process, can lead to fitnesses that are different from deterministic expectations. This type of approach has shown, for example, that PL and reproductive uncertainty puts dioecy at a competitive disadvantage compared to hermaphroditism (Heilbut et al. 2001, Wilson and Harder 2003). These models can be mechanistic and incorporate various biological features characteristic of particular systems, and, when appropriately parameterized, can yield insights that cannot be obtained by experimentation alone. In fact, an integrative approach of experiments in combination with mechanistic models may provide the most fruitful avenue for future investigations of PL.

Allee effects and plant population dynamics.—Despite the clear importance of plant density to pollen sufficiency and plant reproductive success (Kunin 1993, Groom 1998, Hackney and McGraw 2001), no study has incorporated these density-dependent functions into a plant population-viability analysis. A framework for incorporating density dependence exists for animal models (Dennis et al. 1995, Vonesh and De la Cruz 2002), so incorporating positive density dependence from variation in pollination into plant-population models should be relatively straightforward (see also Morris and Doak 2002). For plant species of conservation concern, knowledge of the critical threshold density and/or absolute population size at which plants will go extinct as a result of decreased pollinator visitation is essential. Similarly, for invasive plant species, the goal may be the opposite: to reduce plant density to below their critical threshold.

Community and ecosystem consequences of pollen limitation.—The consequences of PL for plant communities and ecosystems remains a largely unexplored area of research. Hypothesis generation via modeling may provide rapid progress. In addition, long-term experiments using community-level pollinator exclusions similar to those used to manipulate herbivore access would be a direct and fascinating way to assess community responses to PL.

CONCLUSIONS

Our analysis and synthesis suggest that despite a wealth of data on PL at the plant level, we remain ill equipped to assess its causes. We show that to make this conceptual advance we need to change the way we approach the question, and/or gather supplementary information in conjunction with effect size. Because data on the effects of PL on population dynamics are just beginning to accumulate, now is the time to reevaluate the meaning of effect size from standard pollen-supplementation experiments. The time is also ripe to use both theoretical and empirical approaches to evaluate the importance of plant life history, Allee effects, and environmental perturbations in generating PL-mediated population declines. Lastly, this synthesis has identified a critical need for research at the interface between the ecological and evolutionary consequences of PL in order to answer the question: Do plants evolve to minimize PL?

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APPENDIX

The list of whole-plant pollen-supplementation studies reviewed, together with plant species, sample sizes, and quantified results, is available in ESA's Electronic Data Archive: *Ecological Archives* E085-070-A1.