Parental Optimism versus Parental Pessimism in Plants: How Common Should We Expect Pollen Limitation to Be?

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ABSTRACT: Many organisms exhibit parental optimism, producing more of the initial stages of offspring (e.g., eggs, embryos) than they can usually mature. For plants, parental optimism may be linked to the risk of seed production being limited by pollen receipt (pollen limitation). Here we elaborate a stochastic model of pollen limitation developed by Haig and Westoby (1988) and Burd (2008) and link it with published data on the magnitudes of prepollination costs versus postpollination costs of seed production in 80 plant species. We demonstrate that parental optimism should be expected when prepollination costs of seed production are small relative to postpollination costs. This was observed for most (62 of 80) of the plant taxa surveyed. Under parental optimism, plants overinvest in securing fertilized ovules, and consequently pollen limitation is predicted to be uncommon. However, for a sizable minority of plant species (18 of 80), prepollination costs approach or exceed postpollination costs. For these species, parental pessimism is instead optimal. Parents initiate fewer zygotes than they can usually mature, and pollen limitation is predicted to be severe. Because the relative magnitudes of prepollination and postpollination costs vary by more than 1,000-fold across plant taxa, parental outlook (optimism vs. pessimism) and levels of pollen limitation are predicted to vary widely.

Keywords: parental optimism, parental pessimism, pollen limitation, limiting factors, Liebig's law of the minimum.

Introduction

For many organisms, parental investment in a particular offspring is made over an extended period of time, either relatively continuously or in a progressive series of discrete staged allotments. For example, many animals (e.g., insects, birds) first invest in a nutrient-provisioned egg and subsequently in feeding or protecting the resulting offspring, and many plants first invest in generating fertilized ovules (= zygotes), incurring the costs of the ovules themselves plus those of the floral structures used to attract pollinators, and sub-

sequently in provisioning the zygotes to produce mature seeds. These successive installments of parental investment represent essential, nonsubstitutable components of reproductive effort; without each separate allocation, reproduction fails. Such allocation problems can be analyzed with an evolutionary application of Liebig's law of the minimum (Cohen and Dukas 1990; Ehrlén 1991; Burd 1995, 2008; Ellers et al. 2000; Rosenheim et al. 2010; Rosenheim 2011), which states that fitness is defined by the minimum of a series of quantities.

Three predictions emerge from these analyses. First, in an environment that is predictable, the optimal allocation to each of the essential stages of parental investment is that which produces the perfect balance, such that the number of offspring provisioned at each stage is equal and that no resources are left over or wasted (see also van der Berg et al. 2002). We call this the deterministic optimal allocation strategy. Second, in the more realistic case where the environment is unpredictable, such that the future availability of resources for later stages of reproductive investment is uncertain at the time of initial investment, organisms should generally overinvest, relative to the deterministic optimum, in the allocation stage for which the per-offspring cost is small relative to the other essential stage(s). Thus, the stochastic optimum includes this characteristic overinvestment in the cheaper allocation stage. Third, in spatially heterogeneous environments, the optimal strategy also increases the allocation to the stage of parental investment that limits the most highly reproductive members of the population. These highly reproductive individuals make disproportionately large contributions to the next generation, and thus allocations that further enhance their reproduction are favored. This second deviation from the deterministic optimum can act to either reinforce or oppose the tendency to overinvest in the cheaper allocation stage (Rosenheim et al. 2010; S. J. Schreiber, J. A. Rosenheim, N. M. Williams, and L. D. Harder, unpublished data).

For many organisms, the early stages of parental investment in a particular offspring are generally considered to be

inexpensive relative to subsequent stages (Lloyd 1980; Kozlowski and Stearns 1989; Mock and Forbes 1995). This empirical generalization means that parents are often expected to overproduce the early stages of offspring (eggs, embryos, fertilized ovules) relative to their anticipated ability to provision those offspring to maturity—a phenomenon termed "parental optimism" (Mock and Forbes 1995). Ecologists continue to study the scope, causes, and consequences of parental optimism in diverse taxa in nature (e.g., birds: Forbes et al. 2002; Muller and Groothuis 2013; plants: Holland and Chamberlain 2007; mammals: Andersen et al. 2011; insects: Segoli and Rosenheim 2013). One central question is, how often does a shortfall in allocation to a particular stage of reproduction emerge as a limit to fitness (e.g., Burd 2008; Rosenheim et al. 2008)? For example, were an organism to adopt the deterministic optimal allocation in an unpredictable environment, we might expect it to experience an equal chance of overproducing or underproducing the initial stage(s) of offspring (e.g., eggs). In contrast, mathematical models predict that for organisms that have two sequential stages of reproductive allocations, the optimal overinvestment in the less expensive of the two stages should reduce the likelihood that reproductive success is limited by the less expensive allocation. The overinvestment is a form of insurance against a less expensive component of reproductive investment emerging as the limit of total reproductive output (Mock and Forbes 1995).

Perhaps nowhere has the question of reproductive deficit due to a shortfall in the initial stages of offspring production received more recent attention than in plants, whose reproduction may be placed at risk by insufficient pollination (Burd 1994; Larson and Barrett 2000; Ashman et al. 2004; Knight et al. 2005). Plants may face substantial uncertainty regarding the availability of both pollen and pollen vectors (Wilcock and Neiland 2002). Plants can expand their investment in securing pollen by producing more or larger flowers but generally at the expense of reducing their subsequent ability to provision seeds. Pollen limitation, the degree to which a plant's production of seeds is constrained by a shortfall in the quality or quantity of pollen received, may have important influences on plant population dynamics and conservation as well as on the evolution of floral morphology, plant life histories, and mating systems (Ashman et al. 2004; Knight et al. 2005; Vamosi et al. 2006, 2013; Aizen and Harder 2007; Burd et al. 2009; Richards et al. 2009; Alonso et al. 2010, 2012; Harder and Aizen 2010; Anderson et al. 2011).

Ecologists have expressed diverse and changing views regarding the likely prevalence of pollen limitation in undisturbed plant populations (reviewed by Wilson et al. 1994). Seminal treatments of sexual selection acting on plant populations included the suggestion that seed production should rarely (Willson 1979; Willson and Burley 1983) or perhaps never (Janzen 1977) be limited by pollen receipt. Haig and Westoby (1988) used a graphical model to argue cogently that plant allocations to pollen attraction (i.e., investment in all floral attributes that attract pollinators or, for abiotically pollinated plants, floral attributes that enhance pollen capture directly from the environment) versus seed provisioning should evolve to balance the expected number of ovules fertilized with the expected number of seeds that can be provisioned. Thus, at the optimum in an environment with predictable availability of pollen, female fitness should be limited simultaneously by both the availability of pollen and the resources for provisioning seeds (the deterministic optimum). As a result, pollen supplementation cannot increase seed production. Haig and Westoby (1988) recognized, however, that unpredictable heterogeneity in pollen or resource availability would make it unlikely that plants could attain the perfect balance. They discussed scenarios in which a plant might find itself with either too little pollen (resulting in pollen limitation) or with excess pollen (in which case resources become limiting), but they did not address the relative likelihoods of these two types of imbalances. Nevertheless, they suggested that most plant populations should fail to exhibit major increases in seed production under experimental pollen supplementation.

Two details of the graphical model presented by Haig and Westoby (1988) are critical to the analysis that we present below. First, they considered pollen attraction effort to include the costs of both producing ovules and attracting pollen. Despite lumping these two costs, they interpreted any shortfall in fertilized ovules as resulting from insufficient pollen receipt. This may be a reasonable approximation for the many plants that produce inexpensive ovules and that are therefore expected to produce a sufficiently large number of ovules that ovules are unlikely to constrain seed production. We retain this simplifying assumption in the model we develop below; elsewhere we will present a detailed treatment of pollen limitation with separate allocations to ovules and pollen attraction (S. J. Schreiber, J. A. Rosenheim, N. M. Williams, and L. D. Harder, unpublished data). Second, Haig and Westoby (1988) considered a plant that experiences high costs of pollen attraction: the number of ovule fertilizations that could be obtained if the plant were to invest 100% of its resources in pollen attraction is smaller than the number of seeds that could be provisioned if instead the plant were to invest 100% of its resources in seed maturation (fig. 1A). Thus, in this sense, Haig and Westoby (1988) considered the case where prepollination costs of female reproduction (the cost of the ovule and the cost of securing its fertilization) exceed postpollination costs (the costs of maturing each seed).

The Haig and Westoby (1988) model has been interpreted
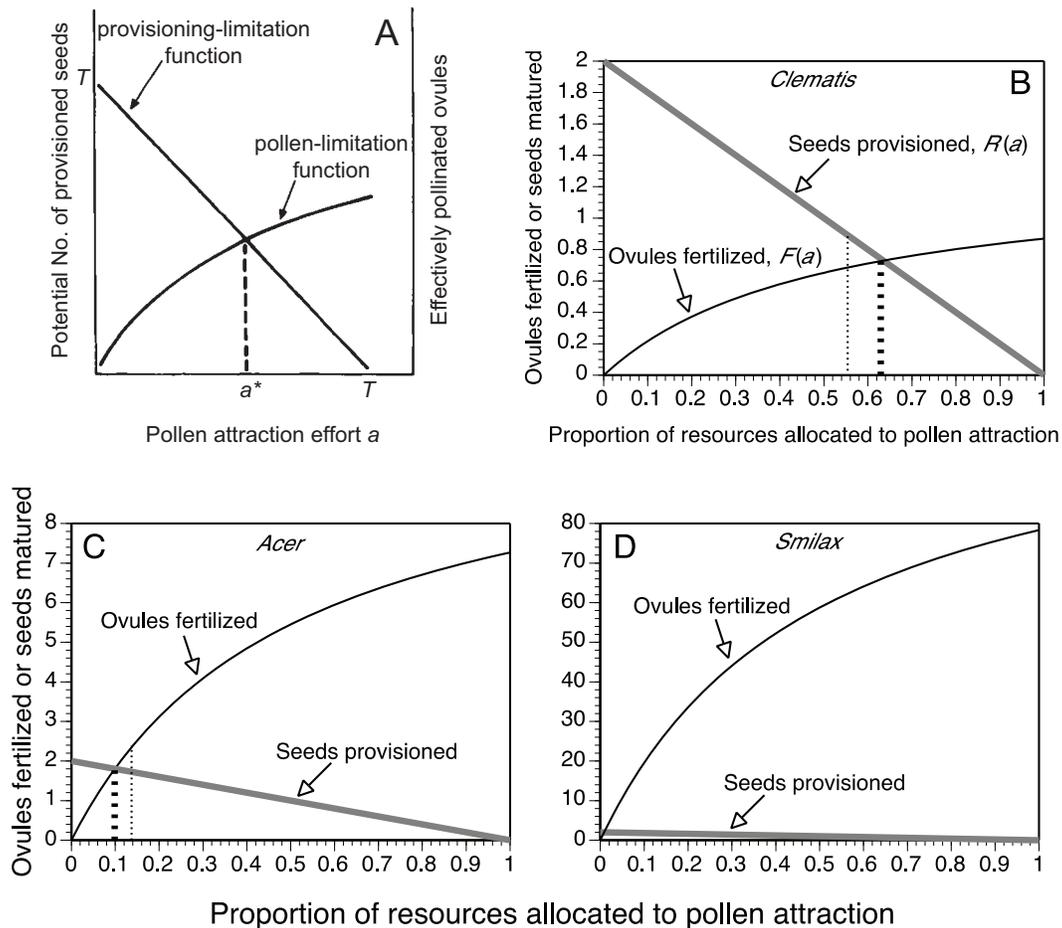
Figure 1: Influence of plant allocation to pollen attraction on the ability to secure ovule fertilizations and provision seeds for plant species with widely varying pre- and postpollination costs of seed production. *A*, Haig and Westoby's (1988) original figure 1. Note that the maximum value of the pollen-limitation function is less than the maximum value of the provisioning-limitation function. Ovule-fertilization functions, $F(a)$, and seed-provisioning functions, $R(a)$, parameterized for *Clematis microphylla* (*B*), a plant with high prepollination costs; *Acer japonicum* (*C*), a plant whose prepollination costs were near the median value; and *Smilax glycophylla* (*D*), a plant with low prepollination costs. The optimal allocation to pollen attraction in a deterministic environment (thick dotted line) occurs where the two functions intersect. The optimal allocation in a stochastic environment (thin dotted line) includes an overinvestment in the less expensive component of reproductive effort. Changes in the functions describing the costs of ovule fertilization and seed maturation alter the predictions for optimal allocations to pollen attraction and the resulting importance of pollen limitation.

to mean that individual plants are equally likely to have a deficit or an excess of pollen (i.e., a 50% incidence of pollen limitation and a 50% incidence of resource limitation; e.g., Thomson 2001; Burd 2008). Burd (2008) extended Haig and Westoby's (1988) model by incorporating the effects of spatial environmental heterogeneity. Again, Burd (2008) focused on the case where the cost of fertilizing an ovule exceeds the cost of maturing a seed. Burd's (2008) analysis showed that spatial heterogeneity generally favors less investment in pollen attraction compared to the case for a deterministic environment, resulting in pollen limitation being expressed more commonly and zygote production often falling below the ability of the plant to mature seeds

(i.e., parental pessimism). Thus, Burd (2008) concluded that natural selection acting to maximize plant fitness might result in the average plant being pollen limited.

Here we integrate measurements of the relative magnitudes of prepollination costs versus postpollination costs of seed production (i.e., the costs of a zygote vs. the costs of a mature seed) with Burd's (2008) model of the evolution of pollen limitation. First, we surveyed the literature to obtain a sample of plant taxa for which we could calculate the pre- and postpollination costs of seed production in a common currency. We then use these cost estimates to parameterize a simple extension of Burd's (2008) model, with which we calculate the expected levels

of pollen limitation. Our overarching question is, what is the relationship between prepollination costs versus postpollination costs of seed production, optimal plant allocation strategies (parental optimism vs. parental pessimism), and the incidence of pollen limitation? More specifically, for undisturbed plant populations expressing optimal life histories, we ask three questions. (1) Should we generally expect some risk of pollen limitation to be present? This question focuses on the incidence of pollen limitation, that is, what proportion of individuals within the population do not receive enough pollen to fertilize at least the number of ovules that will exhaust all resources available for seed maturation. (2) If a risk of pollen limitation is present, how big of a shortfall in seed production should we expect it to generate? This question focuses on the consequences of pollen limitation for plant reproduction. (3) Should we expect to see similar impacts of pollen limitation across different plant species, or should we instead expect to see substantial between-species variation? If plants exhibit substantial variation in the relative costs of pollen attraction versus those of seed provisioning, we might expect correspondingly strong variation in the importance of pollen limitation.

Methods

Pre- and Postpollination Costs of Seed Production

We surveyed the literature to compile estimates for the prepollination costs versus postpollination costs of female reproduction. We searched the Web of Science using keywords "sex allocation" and "flower" and supplemented the search results ($N = 455$ publications through 2012) with our own less systematic reading, but we did not attempt to cover the literature exhaustively. We also included our unpublished data for male-sterile morphs of *Limnanthes douglasii* (appendix A; appendixes A–H are available online).

How best to measure the cost of reproduction in plants is a challenging question (Charlesworth and Morgan 1991; Ashman 1994b; Obeso 2002). Nearly all of the surveyed studies generated cost estimates using the dry mass of plant structures as at least one of the currencies. A minority also reported costs in one or more alternate currencies, including nitrogen, phosphorus, potassium, or carbon content; energy content; wet weight; or use of experimental methods. It became clear that if we wished to obtain an ample set of observations that could be compared in a single common currency, the only viable option was to utilize dry weight data. However, to address the important possibility that other currencies might generate substantially different cost estimates, we also extracted cost estimates reported in any alternate currency. Cost estimates were compared by calculating ln[(proportional contribu-

tion from prepollination costs based on alternate currency)/(proportional contribution from prepollination costs based on dry weight)]. Data were obtained from tables and text and extracted from graphs using ImageJ software, version 1.42. Authors were contacted as needed to clarify aspects of study design or taxon biology to ensure appropriate cost estimates.

The minimum data requirements for inclusion of a study were that it report dry weight cost estimates for (i) a flower (or inflorescence), f; (ii) a mature fruit, including the seeds and any associated protective or dispersal structures, s; and (iii) an estimate of fruit set (i.e., the proportion of flowers that result in mature fruit), p, for openpollinated flowers in nature. We included studies that used hand-pollination treatments only for comparisons of different cost currencies. In some cases, an estimate for one of these metrics was obtained from a companion study. Whenever possible, we followed the decisions of the original authors regarding whether flower costs should be subtracted from fruit costs when estimating postpollination costs (sometimes floral structures are retained in fruiting structures; other times they are largely shed); our default in cases where the authors did not specify this detail was not to subtract floral costs. We excluded cases that involved domesticated crop plants and plants that practice autogamous self-fertilization exclusively (e.g., cleistogamous flowers of *Impatiens* spp.; Schemske 1978) or nearly exclusively (e.g., *Arabidopsis thaliana*; Baker et al. 2005). We also recorded the pollination system (wind pollinated vs. animal pollinated) and the sexual function of the flower/inflorescence (bisexual vs. female).

The entire weight of the flower was included in prepollination costs of seed production for plants reproducing strictly as females in dioecious or gynodioecious populations or for female flowers of diclinous species (whose reproductive structures are either functionally male or functionally female but not both). In all of these cases, we could isolate unambiguously the costs of reproducing as a female from the costs of reproducing as a male. For plants producing bisexual flowers, we were faced with the often-noted quandary of how to partition the costs of structures that potentially contribute to both male and female functions (e.g., Schoen 1982; Morgan and Barrett 1989; Belaoussoff and Shore 1995). For studies that reported the dry weights of different substructures within the flower, we excluded the weight of the androecium (i.e., filaments and anthers) and retained the weight of the gynoecium (i.e., ovary, style, and stigma). As perhaps the simplest working hypothesis, we assigned 50% of the cost of the remaining attractive structures (sepals and petals, nectar) and structural elements (e.g., the flower pedicel) to the prepollination costs of seed production. The full cost of nectar production over the lifetime of the flower

was included in the floral cost estimate when available, as these costs can be substantial (Pyke 1991; Ashman and Schoen 1994). Likewise, the cost of young, aborted fruits were included in the postpollination costs when data were available, following the method of Haig and Westoby (1991) and Lord and Westoby (2006, 2012). The proportion of the costs of seed production that occurs prepollination, a, was calculated as: $a = f/(f + ps)$. We included only a single estimate for each plant species but included separate estimates for female flowers and bisexual flowers or for other types of discrete floral morphs when present (e.g., Sato and Yahara 1999). When multiple populations or seasons were reported in a single publication, cost estimates were averaged. Our final data set included prepollination cost estimates versus postpollination cost estimates for gymnosperms (all wind pollinated; 13 records; app. B); wind-pollinated angiosperms producing female flowers (12 records) and bisexual flowers (2 records; app. C); and animal-pollinated angiosperms producing female flowers (31 records) and bisexual flowers (22 records; app. D); data are also deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.5459n (Rosenheim et al. 2014). In many cases, limits to the data available constrained our ability to capture the full suite of factors shaping floral costs. In appendix E, we consider the most important sources of error in our cost estimates and the likely influences of these errors on our projections of the incidence of pollen limitation.

Parameterizing Burd's (2008) Model to Estimate Expected Levels of Pollen Limitation

We incorporated empirical estimates of pre- and postpollination costs of seed production into Burd's (2008) model of pollen limitation, when pollen receipt—but not total resource availability—varies unpredictably in space. Burd's (2008) model is directly applicable to plants that rely on exogenous delivery of pollen (either self or nonself) to the stigma to produce seed. We have chosen to work with Burd's (2008) model because we believe that its simplicity provides a transparent demonstration of the effects of variable pre- and postpollination costs, the impacts of which can be clouded by more complex models. In the "Discussion" section, we address additional features of plant reproductive biology not considered in Burd's (2008) model that may impinge on pollen limitation.

The essential features of the model are as follows. Function F, which relates the expected number of ovules fertilized to a, the proportion of a plant's resources available for reproduction that is devoted to ovule production and pollen attraction (the prepollination costs; henceforth, "pollen attraction") is described with a Michaelis-Menten equation,

$$F(a) = ka/(\beta + a), \qquad (1)$$

where k is the asymptote (which controls the overall cost of securing a fertilized ovule), and β, the half-saturation constant, was set equal to 0.5 following Burd (2008). Equation (1) implies diminishing returns on continuing investment in pollen attraction. To incorporate unpredictability in pollen availability, the realized number of ovules fertilized, x, given investment a was described as a probability density function $p(x|a)$. Following Burd (2008), we use a normal distribution with mean $F(a)$ and standard deviation equal to $F(a)/3$. Although the distribution of pollen receipt per flower may often be highly variable and nonnormal (Burd 1995; Richards et al. 2009), here our focus is on total pollen receipt per individual plant. If plants have a reasonably large number of flowers, and if the numbers of pollen grains received per flower are independent and identically distributed random variables, then the central limit theorem implies that pollen receipt across plants should be approximately normally distributed (but see app. F for a nonnormal case). The number of seeds that can be matured with the resources remaining after the expenditure for pollen attraction and given the level of resource availability in the environment, b, was described as

$$R(a) = b - ba. \qquad (2)$$

Following Burd (2008), we set b equal to 2. Haig and Westoby's (1988) solution for optimal allocation to pollen attraction in a deterministic environment, a_{det}^*, can be obtained by equating the right-hand sides of equations (1) and (2) and solving the resulting quadratic equation for a.

We can write the realized mean seed set, $S(a)$, as the sum of two terms:

$$S(a) = \int_0^{R(a)} xp(x|a)dx + \int_{R(a)}^{\infty} R(a)p(x|a)dx. \qquad (3)$$

The first term on the right-hand side of equation (3) represents fitness returns from pollen-limited individuals (i.e., the number of ovules fertilized is less than the number of seeds that can be matured, $x < R(a)$). For these individuals, fitness is equal to x; note that by setting the lower limit of integration at zero, we imply that seed set fails entirely for $x \leq 0$. The second term on the right-hand side of equation (3) represents fitness returns from individuals whose fitness is limited by the availability of resources for maturing seeds (i.e., $x > R(a)$); for these individuals, fitness is equal to $R(a)$. For both terms, fitness returns from plants that receive x ovule fertilizations are weighted by the likelihood of observing that value of x given the allocation strategy adopted, $p(x|a)$. Given values for k and b, equation (3) can be solved numerically using the optimize

package in R (R Core Team 2012) for the allocation strategy that maximizes expected seed production, a^*. Note that a^* controls both the optimal allocation to pollen attraction (a^*) and seed maturation ($b - ba^*$), since the model assumes that no reproductive resources remain after the single reproductive event.

By setting $k = b = 2$, Burd (2008) considered the case where securing an ovule fertilization is more expensive than maturing a seed. Here we retain Burd's (2008) choice of $b = 2$ (sensitivity analysis shows that model predictions are almost completely insensitive to this choice), but we numerically fit a value for k such that the predicted optimal investment in pollen attraction, a^*, is equal to the prepollination resource allocation cost that was observed in nature for each of the surveyed species. This is the key step that integrates the empirical measurements of actual plant life histories into Burd's (2008) model, as it is the value of k relative to b (and not their absolute values) that determines the relative importance of prepollination costs versus postpollination costs. Finally, we can extend Burd's (2008) model to calculate the expected proportion of individuals in the population that are pollen limited, $P_{\text{pol-lim}}$, under the optimal allocation strategy as

$$P_{\text{pol-lim}} = \int_{-\infty}^{R(a^*)} p(x|a^*)dx \qquad (4)$$

and the associated loss of seed production, expressed relative to realized seed production, as

$$\omega = \frac{R(a^*) - S(a^*)}{S(a^*)}, \qquad (5)$$

where $R(a^*)$ and $S(a^*)$ are defined by equations (2) and (3), with $a = a^*$.

Results

Pre- and Postpollination Costs of Seed Production

We first address the possibility that our estimates of prepollination costs versus postpollination costs might be consistently biased due to our use of the dry weight currency. Across our sample of plant taxa, cost estimates based on alternate currencies ($N = 27$) proved to be relatively well centered on the dry weight currency estimate (16 estimates fell below, 11 above; fig. 2). Across all alternate currencies, mean prepollination costs were just 5.9% greater than cost estimates based on dry weight. Of 27 alternate currency estimates of prepollination costs, 24 fell between 0.5 and 2.0 times the same-species dry weight cost estimate, and we did not detect any severe outliers (fig. 2). The largest deviations from the dry weight cost

estimates (0.35–3.02 times the dry weight estimate) produced an 8.6-fold range of variation, which was modest in comparison to the interspecific variation in cost estimates using the dry weight currency (>1,000-fold; see below). Thus, although cost estimates are clearly sensitive to the choice of currency, mandating care in choosing an appropriate currency for each study system, our primary conclusions focusing on broad trends of interspecific variation appear unlikely to be strongly influenced by our use of the dry weight cost currency.

Our survey suggests that prepollination costs of seed production are usually smaller than costs incurred postpollination, representing on average 20.0% (median 13.3%) of the total cost of seed production across all sampled plant taxa. This result was consistent across gymnosperms (mean = 4.7%, median = 0.5%; table 1), wind-pollinated angiosperms (mean = 23.1%, median = 17.5%; table 2), and animal-pollinated angiosperms (mean = 22.9%, median = 14.4%; table 3). Thus, as has been observed for many animal taxa, the initial stage of offspring production by plants appears to be relatively inexpensive, and we might expect substantial scope for the expression of parental optimism in the initiation of zygotes. Importantly, however, strong interspecific variation was also evident: across all surveyed taxa, prepollination costs represent 0.08%–91.0% of the total cost of seed production, values spanning more than three orders of magnitude. Substantial variability was observed within gymnosperms and within wind- and animal-pollinated angiosperms (tables 1–3). Notably, for 9 of our 80 records, prepollination costs of seed production actually exceeded postpollination costs, suggesting that parental optimism may not be a universal expectation for plants and that there may be some scope for parental pessimism, in which the number of zygotes initiated routinely undershoots the subsequent ability to provision seeds.

Predicted Incidence of Pollen Limitation

Our extension of Burd's (2008) model predicts a nonzero risk of pollen limitation for each of the plant species considered (tables 1–3). Given the broad range of parameter values represented in the surveyed taxa, this result is consistent with the hypothesis that some risk of pollen limitation is a universal feature of optimal plant life histories for nonautogamous species in unpredictable environments.

Our model predicts that spatial heterogeneity favors overinvestment in attracting pollen, relative to the deterministic case, for 77.5% (62 of 80) of the surveyed taxa (tables 1–3); for these species, the prepollination costs of seed production are substantially smaller than postpollination costs. This overinvestment in securing pollen results in <50% of individuals within the population being pollen limited. For example, a population of the plant *Dodonaea*
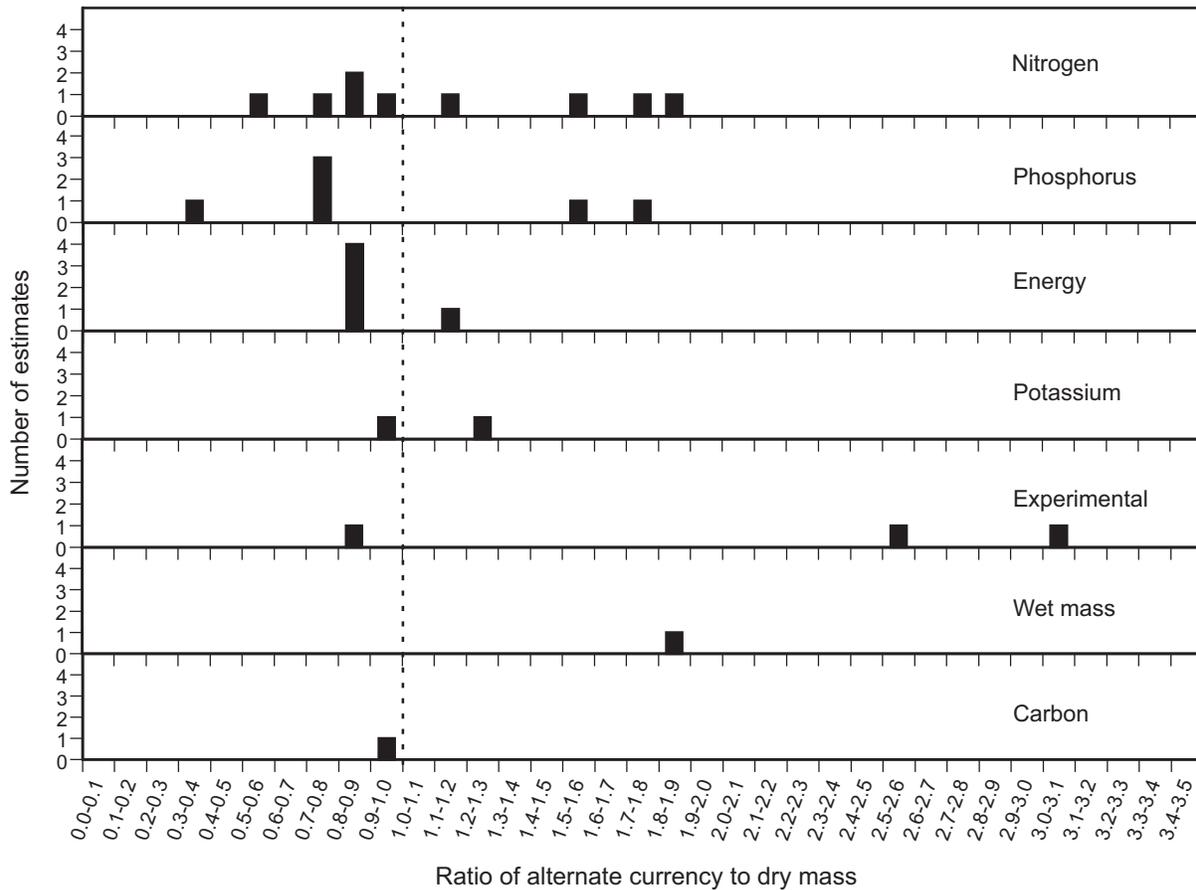
Figure 2: Influence of different measurement currencies (nitrogen, phosphorus, potassium, carbon, or energy content; wet mass; or use of experimental methods) on estimates of the proportional contribution of prepollination costs to the total costs (prepollination plus post-pollination) of seed production. Shown are the ratios of cost estimates relative to the estimate based on dry weight; a ratio of 1.0 indicates perfect agreement between an alternate currency and dry weight, whereas ratios >1.0 (or <1.0) indicate that alternate currencies support a larger (or smaller) proportional contribution of prepollination costs to the total costs of seed production. Estimates derived from a survey of the published literature (see app. H, available online, for a list of the taxa and literature citations).

triquetra would optimally invest 3.6% of its resources in pollen attraction in a predictable environment to achieve the deterministic optimum (this would result in the fertilization of the number of ovules exactly equal to the number of seeds that the plant can successfully mature). If a *Dodonaea* population were to adopt this deterministic optimum in an environment in which pollen availability varied symmetrically about the mean, then 50% of individuals would be pollen limited. But spatial heterogeneity increases the optimal investment to 6.5%. This 1.8-fold overinvestment in pollen attraction is an expression of parental optimism; it insures against pollen shortfall and drives down the expected incidence of pollen limitation to just 9.8% ($P_{pol-lim} = .098$). As a result, a pollen supplementation experiment performed with *D. triquetra* is predicted to increase population-wide seed production by

just 2.8% ($\omega = 0.028$; the 9.8% of the plant population that is pollen limited must be increasing their seed production by $0.028/0.098 = 28.6\%$ on average to push population-wide seed production up by 2.8%). In general, the cheaper it is to secure pollen relative to maturing seeds, the stronger the overinvestment in pollen attraction (i.e., the wilder the optimism of the parent plant) and the smaller the expected incidence of pollen limitation (tables 1–3). On average, across the 62 taxa expressing parental optimism, only 16.6% of individual plants are expected to be pollen limited. Consequently, pollen supplementation is mostly expected to produce modest increases in seed production, boosting plant fitness by 4.8% on average.

Our model also predicts, however, that for 22.5% (18 of 80) of the surveyed taxa, spatial heterogeneity in the availability of pollen favors underinvestment in attracting pollen

Table 1: Wind-pollinated gymnosperm taxa: optimal investment in pollen attraction and resulting expected incidence of pollen limitation and increase in seed production in response to pollen supplementation as predicted by Burd's (2008) model of pollen limitation when parameterized with empirically observed pre- and postpollination costs of seed production

Species	Observed prepollination costs, a_{obs}	Fitted k, the asymptote in ovule fertilization function	Deterministic solution: prepollination costs, a_{det}^*	Stochastic solution: prepollination costs, a_{sto}^*	Proportional over- or underinvestment in pollen attraction, a_{sto}^*/a_{det}^*	Expected proportion of pollen-limited individuals, $P_{pol\text{-}lim}$	Expected increase in seed production following pollen supplementation, ω
Callitris muelleri	.0008	16,193.6	.000062	.0008	12.9541	.0015	.0020
Araucaria bidwillii	.0010	11,296.9	.000089	.0010	11.2959	.0018	.0021
Cedrus deodara	.0013	7,401.1	.000135	.0013	9.6202	.0022	.0023
Ginkgo biloba	.0015	5,898.7	.000170	.0015	8.8466	.0026	.0024
Actinostrobus arenarius	.0023	2,989.0	.000335	.0023	6.8724	.0038	.0029
Sequoia sempervirens	.0044	1,121.6	.000892	.0044	4.9309	.0071	.0040
Cupressus sp.	.0052	882.1	.00113	.0052	4.5818	.0082	.0044
Juniperus thurifera	.0078	492.6	.00203	.0078	3.8405	.0121	.0055
Taxus baccata	.0124	258.7	.00388	.0124	3.1959	.0187	.0074
Chamaecyparis lawsoniana	.0212	124.9	.00807	.0212	2.6281	.0312	.0108
Podocarpus spinulosus	.0344	65.6	.0155	.0344	2.2248	.0503	.0158
Pinus halepensis	.0478	42.7	.0240	.0478	1.9945	.0700	.0208
Macrozamia communis	.4702	1.8	.526	.4702	.8937	.7070	.2596
Mean	.0469	3,597.6	.0448	.0469	5.6830	.0705	.0262

Note: Value k was fitted so that the optimal solution for a stochastic environment would equal the observed proportional allocation to prepollination costs.

Table 2: Wind-pollinated angiosperm taxa: optimal investment in pollen attraction and resulting expected incidence of pollen limitation and increase in seed production in response to pollen supplementation

Species	Flower sexual function	Observed prepollination costs, a_{obs}	Fitted k	Deterministic solution: prepollination costs, a^*_{det}	Stochastic solution: prepollination costs, a^*_{sto}	a^*_{sto}/a^*_{det}	Expected proportion of pollen-limited individuals, $P_{pol\text{-}lim}$	Expected increase in seed production following pollen supplementation, ω
Casuarina distyla	Female	.0050	935.6	.00107	.0050	4.6733	.0079	.0042
Pistacia lentiscus	Female	.0500	40.2	.0255	.0500	1.9639	.0734	.0217
Spinifex hirsutus	Female	.0570	33.9	.0303	.0570	1.8787	.0842	.0244
Platanus racemosa	Female	.0610	31.1	.0332	.0610	1.8373	.0902	.0259
Dodonaea triquetra	Female	.0650	28.6	.0361	.0650	1.7987	.0963	.0275
Corema album	Female	.0780	22.6	.0461	.0780	1.6915	.1165	.0327
Schiedea salicaria	Bisexual	.1457	10.1	.108	.1457	1.3527	.2271	.0622
Caustis recurvata	Female	.2040	6.5	.172	.2040	1.1844	.3254	.0914
Schiedea salicaria	Female	.2289	5.5	.202	.2289	1.1299	.3670	.1048
Rumex acetosella	Female	.2305	5.5	.205	.2305	1.1267	.3696	.1057
Rumex acetosa	Female	.2320	5.4	.206	.2320	1.1239	.3720	.1065
Schiedea adamantis	Bisexual	.4243	2.2	.466	.4243	.9105	.6537	.2272
S. adamantis	Female	.5490	1.4	.622	.5490	.8823	.7851	.3179
Carex picta	Female	.9102	.17	.946	.9102	.9622	.9786	.6881
Mean		.2315	80.6	.221	.2315	1.6083	.3248	.1314

relative to the deterministic case—that is, parental pessimism. This group of pessimists includes not only taxa for which the prepollination costs of seed production exceed the postpollination costs (9 of 80 records) but also another group of taxa (9 of 80 records) for which prepollination costs are moderately smaller than postpollination costs. These "surprising pessimists" occur because of selection favoring the more highly reproductive individuals in the population. Plants that win the pollen-receipt lottery and become resource limited are expected, on average, to have higher fitness than plants that lose the pollen-receipt lottery and become pollen limited. Thus, selection favors a stronger allocation to seed maturation (which will augment the fitness of the more successful, resource-limited individuals) rather than enhance allocation to pollen attraction (which would instead augment the fitness of the less successful, pollen-limited individuals).

Among the plant taxa predicted to express parental pessimism, the incidence of pollen limitation is predicted to be substantially more common, occurring in 73.5% of individuals on average (tables 1–3). As the predicted incidence of pollen limitation increases, so does the predicted magnitude of foregone seed production (tables 1–3); across all plant taxa expressing parental pessimism, experimental pollen supplementation is predicted to increase average seed production by 30.6%.

Haig and Westoby's (1988) graphical analysis shows why a change in the relative costliness of securing ovule fertilizations versus maturing seeds leads to changes in the expected importance of pollen limitation. As noted above, Haig and Westoby (1988) and Burd (2008) focused on the

case where maturing a seed is less expensive than securing an ovule fertilization (fig. 1A). This case is exemplified by species such as *Clematis microphylla*, which produces expensive flowers (1.75 mg dry weight per ovule) but relatively small seeds (1.20 mg dry weight; Lord and Westoby 2006; fig. 1B). Overinvesting in the cheaper component of reproduction (seed maturation) implies underinvestment in pollen attraction, and thus pollen limitation is predicted to be common (79.5% of individuals). In contrast, the apparently more typical situation is found in species such as *Acer japonicum*, which produces flowers that are inexpensive (5.3 mg dry weight) relative to the cost of the fruit (33.1 mg; Sato 2002; fig. 1C). The optimal life history is then to overinvest in the attraction of pollen, resulting in a low predicted incidence of pollen limitation (21.4% of individuals). For species with still lower prepollination costs, such as *Smilax glycophylla*, the expected incidence of pollen limitation will be very small (3.2% of individuals; fig. 1D; table 3). As the costs of ovule fertilization and seed maturation change, so do the predictions for parental outlook (optimism vs. pessimism) and the importance of pollen limitation.

Discussion

Our study shows that for plants, unlike for animals, it is not safe to assume that parents will be optimistic about their reproductive prospects, initiating more offspring than they expect to be able to mature. Parental optimism is expected only when the early stages of reproductive allocation are inexpensive relative to subsequent stages; we

Table 3: Animal-pollinated angiosperm taxa: optimal investment in pollen attraction and resulting expected incidence of pollen limitation and increase in seed production in response to pollen supplementation

Species	Flower sexual function	Observed prepollination costs, a_{obs}	Fitted k	Deterministic solution: prepollination costs, a^*_{det}	Stochastic solution: prepollination costs, a^*_{sto}	a^*_{sto}/a^*_{det}	Expected proportion of pollen-limited individuals, $P_{pol\text{-}lim}$	Expected increase in seed production following pollen supplementation, ω
Smilax glycophylla	Female	.0220	118.8	.00849	.0220	2.5916	.0324	.0111
Solanum dulcamara	Bisexual	.0230	111.9	.00902	.0230	2.5532	.0338	.0115
Borderea pyrenaica	Female	.0275	88.3	.0115	.0275	2.4002	.0403	.0132
Micrantheum ericoides	Female	.0290	82.2	.0123	.0290	2.3565	.0425	.0138
Stephania japonica	Female	.0310	75.4	.0134	.0310	2.3067	.0452	.0145
Ilex aquifolium	Female	.0419	50.7	.0201	.0419	2.0828	.0613	.0186
Oemleria cerasiformis	Female	.0450	46.1	.0221	.0450	2.0329	.0660	.0198
Cucurbita foetidissima	Female	.0505	39.7	.0258	.0505	1.9575	.0741	.0219
Phyllanthus thymoides	Female	.0680	27.0	.0384	.0680	1.7723	.1009	.0287
Dioscorea japonica	Female	.0778	22.7	.0460	.0778	1.6928	.1163	.0326
Nyssa sylvatica	Female	.0799	21.9	.0476	.0799	1.6775	.1196	.0334
Aucuba japonica	Female	.0808	21.6	.0483	.0808	1.6713	.1210	.0338
Hesperis matronalis	Bisexual	.0866	19.7	.0531	.0866	1.6318	.1302	.0362
Wurmbea dioica	Female	.0869	19.6	.0533	.0869	1.6297	.1307	.0363
Gilia achilleifolia	Bisexual	.1024	15.9	.0665	.1024	1.5391	.1556	.0428
Diospyros australis	Female	.1050	15.4	.0688	.1050	1.5260	.1597	.0439
Smyrnium olusatrum	Bisexual	.1101	14.5	.0734	.1101	1.4996	.1683	.0462
Ilex leucoclada	Female	.1113	14.3	.0745	.1113	1.4942	.1701	.0467
Aconitum gymnadrum	Bisexual	.1129	14.0	.0760	.1129	1.4864	.1728	.0474
Rubus chamaemorus	Female	.1234	12.5	.0857	.1234	1.4393	.1900	.0520
Lathyrus vernus	Bisexual	.1250	12.3	.0873	.1250	1.4325	.1927	.0527
Oxalis violacea	Bisexual	.1318	11.5	.0938	.1318	1.4046	.2040	.0558
Clutia pulchella	Female	.1338	11.2	.0958	.1338	1.3966	.2074	.0567
Sisyrinchium campestre	Bisexual	.1370	10.9	.0989	.1370	1.3844	.2127	.0582
Acer japonicum	Female	.1375	10.9	.0994	.1375	1.3825	.2135	.0584
Hepatica nobilis	Bisexual	.1385	10.8	.100	.1385	1.3789	.2151	.0589

Stylidium armeria	Bisexual	.1443	10.2	.106	.1443	1.3580	.2246	.0615
Silene alba	Female	.1497	9.7	.112	.1497	1.3387	.2339	.0641
Siparuna grandiflora	Female	.1527	9.5	.115	.1527	1.3286	.2389	.0656
Geranium maculatum	Bisexual	.1568	9.1	.119	.1568	1.3151	.2458	.0675
Rhus trichocarpa	Female	.1827	7.5	.148	.1827	1.2384	.2894	.0803
Rhus javanica	Female	.1950	6.9	.162	.1950	1.2061	.3103	.0867
Hebe subalpina	Female	.2227	5.7	.195	.2227	1.1427	.3567	.1014
Gynatrix pulchella	Female	.2438	5.1	.221	.2438	1.1013	.3915	.1131
Asclepias quadrifolia	Bisexual	.2512	4.9	.231	.2512	1.0880	.4035	.1173
Leucopogon melaleucoides	Female	.2797	4.2	.268	.2797	1.0421	.4494	.1339
Narthecium asiaticum	Bisexual	.2895	4.0	.282	.2895	1.0282	.4647	.1398
Zanthoxylum ailanthoides	Female	.3101	3.6	.310	.3101	1.0017	.4965	.1523
L. melaleucoides	Bisexual	.3112	3.6	.311	.3112	1.0005	.4980	.1530
Limnanthes douglasii	Female	.3130	3.6	.314	.3130	.9983	.5009	.1541
Cirsium arvense	Female	.3160	3.5	.318	.3160	.9948	.5055	.1560
Ligularia virgaurea	Bisexual	.3708	2.8	.393	.3708	.9429	.5844	.1912
Aciphylla simplicifolia	Female	.3878	2.6	.417	.3878	.9309	.6072	.2024
Blandfordia grandiflora	Bisexual	.4220	2.2	.463	.4220	.9116	.6508	.2256
Impatiens hypophylla var. *microhypophylla*	Bisexual	.4708	1.8	.527	.4708	.8935	.7076	.2600
Impatiens biflora	Bisexual	.4758	1.8	.533	.4758	.8922	.7131	.2637
Ipomopsis aggregata	Bisexual	.5510	1.4	.625	.5510	.8823	.7869	.3195
Clematis microphylla	Female	.5600	1.3	.635	.5600	.8821	.7947	.3263
Phacelia linearis	Bisexual	.6025	1.1	.682	.6025	.8837	.8294	.3598
I. hypophylla var. *hypophylla*	Bisexual	.6113	1.1	.691	.6113	.8844	.8359	.3668
Impatiens pallida	Bisexual	.6179	1.0	.698	.6179	.8851	.8407	.3720
Lomandra longifolia	Female	.6260	1.0	.707	.6260	.8860	.8467	.3788
Phacelia linearis	Female	.7065	.70	.785	.7065	.9000	.8972	.4475
Mean		.2290	19.1	.223	.2290	1.3902	.3411	.1190

find that whereas this is true for most plants, there are many exceptions. Prepollination costs represent 0.08%–91.0% of the total costs of seed production. Consequently, our optimality model predicts that whereas 77.5% of the plants studied should express parental optimism by over-producing fertilized ovules, 22.5% should instead express parental pessimism by producing fewer fertilized ovules than they expect to be able to mature as seeds. Thus, we should expect to find both optimists and pessimists in a taxonomically diverse plant community.

These observations have immediate consequences for the expected expression of pollen limitation. We draw three primary conclusions. First, in stochastic environments, some risk of pollen limitation is predicted to be present for all plant taxa, parental optimists and pessimists alike. What varies is the magnitude of the risk. This conclusion flows immediately from Burd's (2008) model. Plants evolve a risk of pollen limitation in response to universal features of their reproduction: unpredictability in pollen availability and trade-offs between investment in prepollination stages versus postpollination stages of female reproduction. Thus, we should not expect evolution to eliminate all risk of pollen limitation, and persistent pollen limitation should not be viewed as being enigmatic. These conclusions are entirely consistent with previous models of pollen limitation (Haig and Westoby 1988; Ashman et al. 2004; Burd 2008; see also Cohen and Dukas 1990; Ehrlén 1991) and with theory suggesting that organisms should evolve to balance the risks imposed by different fitness-limiting factors when these represent essential, nonsubstitutable components of reproduction (Rosenheim et al. 2010). Whether this risk of pollen limitation is realized for any particular plant, however, may depend on both local environmental conditions and the ability of the plant to adjust dynamically its reproductive allocations within or across breeding seasons through phenotypic plasticity (Lloyd 1980; Wesselingh 2007).

Second, pollen limitation is, on average, predicted to be a minority condition within plant populations. This is because pollen attraction appears to be inexpensive relative to provisioning seeds on average (Lloyd 1980); because, in an unpredictable environment, selection favors overinvestment in securing the less expensive of two essential resources; and because this overinvestment buffers the plant against fluctuations in pollen availability, depressing the expected incidence of pollen limitation substantially below 50%.

Third, the substantial among-species variation in the relative costs of ovule fertilization and seed maturation translates to the equally substantial variation in the predicted incidence of pollen limitation. Thus, even if pollen limitation is generally rare, there will be important exceptions. Those plants that produce expensive flowers will frequently act as parental pessimists, underproducing fertilized ovules. For these parental pessimists, pollen limitation may act as a major constraint on fitness. Strong and persistent pollen limitation is observed in some plant populations (e.g., in many orchids, although it is difficult to measure fitness effects of pollen limitation in perennials; Tremblay et al. 2005; Wesselingh 2007); our model predicts that these taxa will be found to have high prepollination costs of seed production.

The prediction that plants with high investment in pollen attraction will nevertheless experience high risks of pollen limitation may seem counterintuitive—should not high investment solve the problem of pollen limitation? Life-history models suggest otherwise (Rosenheim et al. 2010), instead predicting that organisms should invest their reproductive resources in direct proportion to the likelihood that a shortfall in a particular factor will constrain fitness. Thus, factors that rarely emerge as fitness constraints should command only modest investments, whereas factors that frequently emerge as fitness constraints should command heavy investments (Rosenheim et al. 2010). Thus, theory suggests that we should expect a strong positive relationship between pollen limitation and the magnitude of investment in pollen attraction.

Observed declines in pollinator communities have fueled concerns that pollination shortfalls could depress the yield of world crop plants (Garibaldi et al. 2013) and threaten the viability of some natural plant populations (Wilcock and Leiland 2002; Ashman et al. 2004; Knight et al. 2005; Biesmeijer et al. 2006; Pauw 2007; Anderson et al. 2011; Pauw and Hawkins 2011). Chronically pollen-limited plant populations may be particularly vulnerable to pollinator declines in those cases where plant population growth rates are also seed limited (Clark et al. 2007). Our model suggests that when considering pollinator declines, conservation biologists should pay particular attention to those plant taxa (the parental pessimists) that are likely to be more sensitive to disruptions in pollen availability.

How to Test Predictions for Pollen Limitation

Our analysis predicts highly variable levels of pollen limitation across plant taxa with different prepollination costs versus postpollination costs of seed production. Although a test of these predictions is beyond the scope of this article, we here address some key requirements for generating such a test.

First, an empirical test would rely on the assumptions that (i) our extension of Burd's (2008) model and our approach to parameter estimation capture the essential features of the evolution of pollen limitation and that (ii) plant traits observed in nature approach their optimal values. Below we address the potential influence of several features of plant reproduction that are omitted from our

model. Whereas we expect that the qualitative trends of our predictions should be relatively robust (i.e., plant species with lower prepollination costs of seed production should have lower incidences of pollen limitation), the quantitative predictions are associated with considerable uncertainty. In appendix F, we present a sensitivity analysis that suggests that for animal-pollinated angiosperms, the incidence of pollen limitation, $P_{\text{pol-lim}}$, could range from .3142 to .4257 and that the expected proportional increase in seed production following pollen supplementation, ω, could range from 0.0492 to 0.4886. The interspecific rank ordering of the incidence of pollen limitation is, nevertheless, invariant across the scenarios explored.

Second, our model generates predictions for both (i) the fraction of plant individuals whose fitness is constrained by a shortfall in pollen receipt, $P_{\text{pol-lim}}$, and (ii) the expected proportional increase in seed production following pollen supplementation, ω. However, it is not generally possible to measure the fraction of individuals within a population that are pollen limited, $P_{\text{pol-lim}}$, directly, because a given plant can be observed in only one condition (either open pollinated or with pollen supplemented) but not both. Thus, it is not generally possible to ask if an individual plant's fitness would have increased under pollen supplementation. Instead, pollen limitation is typically measured at the population level and in terms of its primary consequence, foregone seed production. The empirical literature is usually interpreted as indicating that pollen limitation is widespread. For example, Burd (1994) reported that 62% of 258 plant species receiving experimental pollen supplementation exhibited a statistically significant increase in some metric related to seed production at some times or in some sites. Similarly, Knight et al. (2005) reported that 63% of 482 experimental pollen supplementation data records showed significant pollen limitation. However, scoring an experiment for whether seed production increased significantly may not produce the most useful metric of pollen limitation. As noted above, all plant taxa are predicted to express a nonzero incidence of pollen limitation. Thus, as researchers increase the statistical power of their experiments, the fraction of species exhibiting statistically significant increases in seed production at some times or in some places should approach 100%. Thus, we support Knight et al.'s (2006) suggestion that a preferable index of pollen limitation is the magnitude of the proportional increase in seed production elicited by a pollen supplementation treatment.

Our model predicts the influence of pollen supplementation on lifetime seed production by a plant. As emphasized by Knight et al. (2006), to measure effects of pollen limitation on lifetime seed production requires an exacting experimental protocol, in which supplemental pollen is delivered to all flowers produced during a plant's lifetime and total seed output is summed. Only in this way can one isolate responses to pollen supplementation that truly reflect lost female fitness, as opposed to reallocation of resources between reproductive structures within or between breeding seasons (Willson and Burley 1983; Knight et al. 2006; Wesselingh 2007; Harder and Aizen 2010). As noted by Wesselingh (2007), the requirement that pollen be supplemented for all flowers may restrict the sample of tractable study species to monocarpic species—or, perhaps, species with a small number of reproductive seasons—that produce a modest number of relatively large flowers.

Elaborating Models of Pollen Limitation

Although our simplest-case model has the advantage of facile interpretation, it has the disadvantage of omitting several potentially important features of plant reproductive ecology:

A finite supply of ovules. We have followed Haig and Westoby (1988) and Burd (2008) in combining the costs of ovule production and pollen attraction into a single allocation (a). However, as noted by Richards et al. (2009), pollen cannot be reallocated from stigmas that receive excess pollen to those that have a pollen shortfall. Consequently, plants may respond to variation in pollen harvest across flowers by overproducing ovules (ovule packaging; Burd 1995; Ashman et al. 2004; Burd et al. 2009; Friedman and Barrett 2011). In appendix G, we briefly describe a more realistic stochastic model of pollen limitation that includes separate allocations to ovules, pollen attraction, and seed maturation (S. J. Schreiber, J. A. Rosenheim, N. M. Williams, and L. D. Harder, unpublished data). Importantly, this model still predicts a strong positive correlation between prepollination costs of seed production and the intensity of pollen limitation.

Plasticity in resource allocation. Our model assumes that total resource availability is known perfectly when a single, irreversible allocation is made to pollen attraction. More realistically, plants may continually adjust allocations to ovules, pollen attraction, and seed and fruit maturation in response to fluctuating resource and pollen availability (Lloyd 1980; Harder and Johnson 2005; Wesselingh 2007). Plastic allocations may be further complicated by the partial physiological independence of different plant modules (Casper and Niesenbaum 1993; Wesselingh 2007). Plasticity, which may be most developed in perennials and in annuals with sequential and indeterminate flowering, may increase the ability of plants to achieve a perfectly balanced allocation to ovules, pollen attraction, and seed maturation (Wesselingh 2007; see also Rosenheim et al. 2010).

Bisexual flowers. As noted above, bisexual flowers introduce two challenging questions: (i) how might optimal allocation to pollinator attraction change when flowers

function both to secure ovule fertilizations and to export pollen, and (ii) which flower costs can be ascribed to female function and which to male? Burd (2008) has argued that, at least for animal-pollinated plants, fitness accrual through pollen donation (male function) might favor greater investment in attracting and rewarding pollinators than predicted by a model that considers female function only, reducing expected levels of pollen limitation. Until this hypothesis is explored formally, we must be cautious in applying our model predictions to bisexual flowers.

Self-compatibility. Self-compatible plants raise the important issue of variation in pollen quality (Aizen and Harder 2007; Alonso et al. 2012) and the possibility that plants may conditionally seek reproductive assurance through selfing, despite the costs of inbreeding (Harder and Aizen 2010). Our model does not allow plants to autonomously self-fertilize whenever outcross or geitonogamous pollen is unavailable and thus is likely to overstate the impact of pollen limitation for autonomously selfing species. Indeed, pollen limitation appears to be less severe in selfing species (Larson and Barrett 2000; Knight et al. 2005; Alonso et al. 2010).

Spatial heterogeneity versus temporal heterogeneity. We have interpreted our model in terms of spatial variation in pollen availability. In some cases, temporal stochasticity may favor bet-hedging strategies that differ from those that are optimal under spatial stochasticity (Roff 2002; Rosenheim 2011). An important area for future work is to examine bet-hedging strategies for pollen attraction and how they might interact with other forms of bet-hedging, including seed dormancy.

Conclusion

Our analysis suggests that the relative costs of producing a zygote versus provisioning that zygote to mature a seed are central to plant reproductive ecology. For most plants, as for most animals, the early stages of allocation to reproduction as a female are relatively inexpensive. In this case, in an unpredictable environment, selection favors parental optimism: plants should overinvest, relative to the deterministic case, in producing ovules and securing their fertilization. This overproduction buffers plants against spatial variation in pollen availability. As a result, few individual plants receive insufficient pollen, and at the population level the resulting shortfall in seed production is modest. However, for nearly one-quarter of the surveyed plant taxa, the story is different. The earlier stages of allocation to female reproduction are more similar in cost to the later stages. This weakens or removes the incentive to overproduce zygotes. The most highly reproductive individuals in the plant population are those that win the pollen-receipt lottery; the fitness of these individuals is

constrained by the availability of resources for maturing seeds. Selection in a spatially heterogeneous environment favors allocations that alleviate the fitness constraint acting on the most reproductive individuals; thus, the optimal strategy shifts to overallocating to seed maturation, even at the expense of underproducing zygotes. This is parental pessimism. It is among these pessimistic parents that pollen limitation exerts a major impact on plant reproduction. Most individuals in these populations will face a shortfall in pollen, and at the population level the predicted loss of seed production is substantial. The substantial interspecific variation in the relative costs of zygotes versus those of mature seeds, which spans three orders of magnitude, means that optimal plant life histories can be either optimistic or pessimistic, and the importance of pollen limitation is consequently highly variable.

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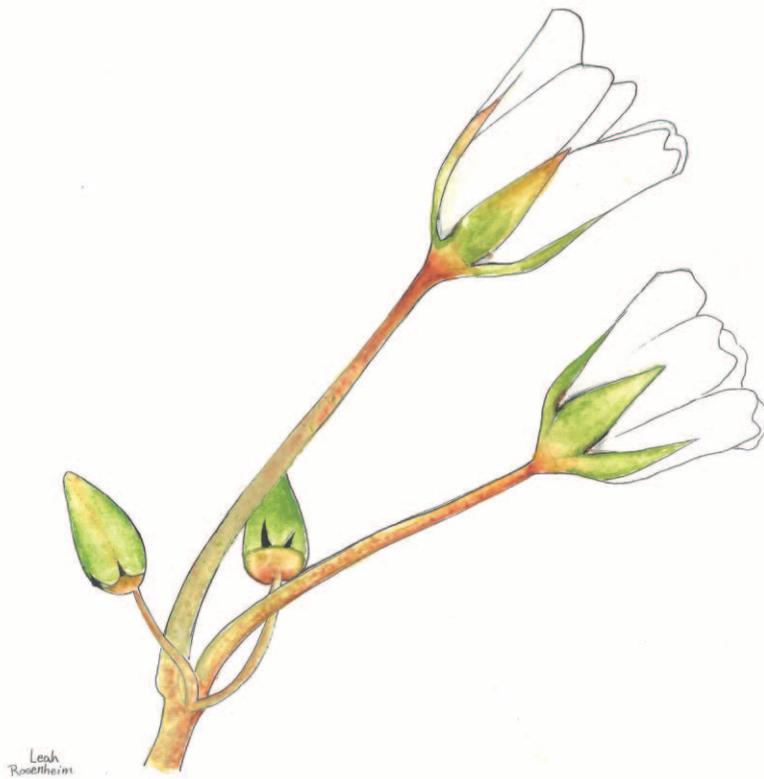
Limnanthes douglasii ssp. *rosea* male-sterile morph. Illustration by Leah Rosenheim.