Evolutionary and Ecological Consequences of Multiscale Variation in Pollen Receipt for Seed Production

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Abstract: Variation in resource availability can select for traits that reduce the negative impacts of this variability on mean fitness. Such selection may be particularly potent for seed production in flowering plants, as they often experience variation in pollen receipt among individuals and among flowers within individuals. Using analytically tractable models, we examine the optimal allocations for producing ovules, attracting pollen, and maturing seeds in deterministic and stochastic pollen environments. In deterministic environments, the optimal strategy attracts sufficient pollen to fertilize every ovule and mature every zygote into a seed. Stochastic environments select for allocations proportional to the risk of seed production being limited by zygotes or seed maturation. When producing an ovule is cheap and maturing a seed is expensive, among-plant variation selects for attracting more pollen at the expense of producing fewer ovules and having fewer resources for seed maturation. Despite this increased allocation, such populations are likely to be pollen limited. In contrast, within-plant variation generally selects for an overproduction of ovules and, to a lesser extent, pollen attraction. Such populations are likely to be resource limited and exhibit low seed-to-ovule ratios. These results highlight the importance of multiscale variation in the evolution and ecology of resource allocations.

Keywords: evolution of reproductive allocations, pollen limitation, resource limitation, stochastic environments.

Introduction

In natural environments, individuals within populations experience variation in the availability of the resources required for reproductive success. When reproductive success increases at a diminishing rate with resource availability, resources above the average availability increase reproductive success less than it is reduced by below-average availability, lowering average reproductive success compared with that expected for the average resource availability (Jensen’s [1906] inequality). Because of this effect, selection favors bet-hedging when this variation is spread across generations and favors risk-averse traits when this variation occurs within generations (Frank and Slatkin 1990; Real and Ellner 1992; Childs et al. 2010; Frank 2011).

Such selection could be particularly potent for plants because of two essential plant characteristics. Because of their immobility, individual plants must contend with the availabilities of light, nutrients, water, and pollen where they are rooted, so that environmental heterogeneity imposes among-individual variation in resources. Plants also grow by the addition of modules such as roots, leaves, and flowers (White 1979; Preston and Ackerly 2004), enabling within-individual variation if modules experience heterogeneous availability of nutrients, light, or pollen (Jackson and Caldwell 1993a, 1993b; Coley 1983; Alonso and Herrera 1996; Herrera 2009). These two scales of resource variation could affect trait selection differently. In particular, among-individual variation weakens the covariance between the fitnesses and traits of individuals on which selection depends, whereas within-individual variation reduces individual fitness via Jensen’s equality. Variation at either scale can select for risk-averse traits that impact fruit-to-flower ratios, susceptibility to pollen limitation, and seed production (Cohen and Dukas 1990; Burd 1995, 2008; Farrior et al. 2013). However, the ecological and evolutionary implications of simultaneous variation at both scales are poorly understood (Burd et al. 2009).

Seed production by flowering plants should be particularly susceptible to the magnitude and structure of variation because pollen receipt by stigmas differs extensively among flowers within and among plants (Burd 1995; Herrera 2002, 2004), owing to heterogeneity in both the number of pollinator visits (Waites and Agren 2004; Ghazoul 2005) and pollen deposition by individual pollinators (Waser and Price 1984; Thomson 1986; Pettersson 1991; Richards et al. 2009). Because received pollen cannot be...
surplus of pollen typically mature
produce more ovules per flower (Burd et al. 2009). However, experiences greater variation in pollen availability pro-
ing occur within individual flowers, whereas seed resources can be redistributed among a plant’s flowers (Zimmerman and Pyke 1988; Wesselingh 2007).

Some of the ecological and evolutionary implications of stochastic pollen receipt have been examined in previous theoretical studies. These models considered the consequences of dichotomous trade-offs between attracting pollen and either producing ovules (Burd 1995) or maturing seeds (Burd 2008; Rosenheim et al. 2010). Under the assumption that resources for seed maturation are not limiting and producing an ovule is cheap relative to attracting sufficient pollen to fertilize one ovule, Burd (1995) found that within-plant variation in pollen receipt selects for production of more ovules than can be fertilized on average, a finding that applies generally to offspring production functions: fraction \(a_{p}\) of ovules or greater allocations to attracting pollinators? Burd et al. (2009) emphasized the importance of this latter question when stating that “[t]he metameric hierarchy of reproductive modules in flowering plants may have important effects on fitness, such that random disparity among modules that make partial contributions to whole-plant female fitness is not adequately modeled by random variation at the whole-plant level. If ... random mating success at the floral level is important, it would be interesting to see how including this feature in future models affects predictions for the evolutionary stability of excess ovule production” (p. 1165). Second, our analysis addresses the question, are populations adapted to within-plant or among-plant variation more likely to be pollen limited or resource limited? Finally, plants exhibit a continuum of reproductive costs from producing inexpensive seeds, as in the case of orchids, to producing large, expensive seeds. How does the evolutionary response to stochastic pollen receipt vary among species with different reproduction costs?

### Model and Methods

#### The Multiscale Model

Consider a population of semelparous plants that are identical except for their pollen receipt. Plants start each season with \(R\) resources, which are allocated to three reproductive functions: fraction \(a_{o}\) is used to produce ovules, fraction \(a_{p}\) is used to produce floral components to attract pollen, and the remaining fraction, \(a_{c}\), is used to develop and disperse seeds (see table 1 for a list of terms). These allocations are summarized by the allocation vector \(a = (a_{o}, a_{p}, a_{c})\). Because all reproductive resources are used, these fractions sum to 1 \((a_{o} + a_{p} + a_{c} = 1)\). Resources for ovules and pollen attraction are allocated equally among a plant’s \(k\) flowers. Each ovule costs \(c_{o}\) resources, so a flower produces \(a_{o}R/kc_{o}\) ovules. Similarly, attraction of enough pollen to ensure fertilization of one ovule, on average, costs \(c_{p}\) resources, so \(a_{p}R/kc_{p}\) is the number ovules that can be fertilized in the average flower. Finally, each seed costs \(c_{s}\) resources, so a plant can maximally produce \(a_{c}R/kc_{s}\) seeds per flower.

Spatial and within-season temporal variation in pollen deposition by abiotic or biotic vectors creates differences among plants and among flowers within plants in pollen receipt, ovule fertilization, and seed production (e.g., fig. 1). To account for stochasticity among plants, we introduce

\[
S = \frac{a_{o}}{H_{1001}} \quad a_{p} \quad R \quad c_{o} \quad k \\
\]

...
Table 1: Key terms of the multiscale model

<table>
<thead>
<tr>
<th>Term</th>
<th>Meaning</th>
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<tbody>
<tr>
<td>( R )</td>
<td>Total resources available for reproduction</td>
</tr>
<tr>
<td>( c_o, c_p, c_s )</td>
<td>Resources required to produce one ovule, attract enough pollen to fertilize one ovule, and mature one seed</td>
</tr>
<tr>
<td>( a_o, a_p, a_s )</td>
<td>Fractions of resources allocated for producing ovules, attracting pollen, and maturing seeds ((a_o + a_p + a_s = 1))</td>
</tr>
<tr>
<td>( k )</td>
<td>Number of flowers per plant</td>
</tr>
<tr>
<td>( P )</td>
<td>Mean pollen receipt per flower for a random plant</td>
</tr>
<tr>
<td>( P_i )</td>
<td>Pollen receipt for the ( i )th flower on a plant, measured in the number of ovules that could be fertilized</td>
</tr>
<tr>
<td>( F_i )</td>
<td>Number of fertilized ovules on flower ( i )</td>
</tr>
<tr>
<td>( s )</td>
<td>Fraction of seeds successfully germinating</td>
</tr>
<tr>
<td>( CV_{ovu}, CV_{plant} )</td>
<td>Coefficients of variation for pollen availability within and among plants</td>
</tr>
<tr>
<td>( f(a) )</td>
<td>Plant fitness as a function of ( a = (a_o, a_p, a_s) )</td>
</tr>
</tbody>
</table>

A positive random variable, \( Y \), with mean 1 and variance \( \sigma^2 \), such that

\[
P = Y a_p R/c_p k
\]

(fig. 1A) is the expected pollen receipt per flower on a randomly chosen plant. For a plant with (normalized) mean pollen availability \( Y \), pollen receipt among this plant’s \( k \) flowers is determined by \( k \) random variables, \( Z_1^i, \ldots, Z_k^i \), each with mean \( Y \). The \( i \)th flower on this plant receives sufficient pollen to fertilize

\[
P_i = a_p R Z_i^i / k c_p
\]

ovules (fig. 1B). Pollen cannot be redistributed between flowers, which imposes Liebig’s law of the minimum (Hooker 1917; Brock 2002). Therefore, the number of fertilized ovules (zygotes) for a plant’s \( i \)th flower is

\[
F_i = \min\{a_o R/k c_o, P_i\}
\]

zygotes (fig. 1C), which can have an upper bound when pollen receipt exceeds ovule number. Summation of the zygote number \( F_i \) over all \( k \) flowers yields the total number \( \sum_{i=1}^{k} F_i \) of zygotes on a plant (fig. 1D). Although pollen receipt is assumed to be proportional to pollen availability, Liebig’s law and stochastic variation in pollen receipt cause the average number of zygotes across multiple flowers to increase at a diminishing rate with increasing pollen availability (fig. B1; figs. B1, C1–C4 are available online).

If resources for seed maturation distribute freely among flowers in proportion to zygote numbers, then a plant’s seed production is

\[
S = \min\left\{a_i R / c_s, \sum_{i=1}^{k} F_i\right\}
\]  

(1)

seeds (fig. 1E), which has an upper bound when the number of fertilized ovules exceeds the resources available for seed maturation. Depending on a population’s average pollen receipt and the extent of pollination stochasticity, the seed production of individuals within the population could be primarily zygote limited (not illustrated in fig. 1), could be primarily resource limited (fig. 1E, blue example), or could involve a mixture of zygote- and resource-limited individuals (fig. 1E, green example). Individual plants with zygote-limited fecundity may have some ovule-limited fruit and others that are pollen limited. Thus, ovule, pollen, and resource limitation may limit seed production in some plant populations. Finally, if fraction \( s \) of seeds survive to germinate, a plant’s expected lifetime fitness is

\[
f(a) = s E \left[ \min\left\{a_i R/c_s, \sum_{i=1}^{k} F_i\right\} \right].
\]  

(2)

For populations experiencing any form of within-generation variation in demographic rates, the results of Gillespie (1974) and Frank and Slatkin (1990) suggest that natural selection favors genotypes with larger values of \( \mu - \sigma^2 / N \), where \( \mu \) is the expected fitness of an individual, \( \sigma^2 \) is the variance of the fitness, and \( N \) is the population size. For sufficiently large populations, the variance term is negligible, and evolution selects for genotypes maximizing the expected fitness of an individual. Hence, consistent with Burd (1995, 2008) and Rosenheim et al. (2010), our analysis focuses on maximizing the expected fitness \( f \) with respect to the allocation strategy \( a \). The case of small populations will be considered elsewhere.

Analytical and Numerical Methods

We investigated the optimal allocation, \( a^* = (a^*_o, a^*_p, a^*_s) \), and its implications using analytic and numerical approaches. To derive analytic results, the distributions of \( Y \) and \( Z_i^k \) need to be continuous, such as the gamma distribution. The mathematical analyses, which are presented...
Figure 1: Model of seed production response to multiscale stochastic variation in pollen receipt. Mean pollen receipt per flower varies among individual plants according to the distribution shown in A. The green and the light blue bars represent two “draws” from the distribution of the mean pollen availability $P_i$. In one case (light blue), the plant hits the jackpot—it flowers in a location or period with high pollen availability. In the other case (green), the plant is in a pollen-poor location or period. A plant’s flowers receive random numbers of pollen grains $P_i$ (in units of fertilized ovules) whose distribution (B) is centered around the plant’s mean pollen receipt. Because each flower has a fixed number of ovules, some flowers receive an excess of pollen (in dark green and dark blue), which truncates the distribution of fertilized ovules, or zygotes (C). The total number of zygotes per plant (D) sums over all flowers, which smooths the distribution for each plant. Because there are fixed resources for provisioning seeds, some plants have an excess of zygotes (in dark green and dark blue in D), which truncates the distribution of a plant’s seed production (E). Parameters: $k = 5$ flowers, $c_1 : c_2 : c_3 = 1 : 10 : 100$, $CV_{plan} = 0.3$, $CV_{flower} = 0.45$. 

in appendixes A–C (available online), use standard methods in probability theory and multivariate calculus to characterize the optimal allocation in terms of the frequency and fitness contributions of pollen- or ovule-limited fertilization in flowers and zygote- or resource-limited seed development by plants. Following Harder et al. (2008), a flower’s zygote formation is pollen limited if ovules remain unfertilized and is ovule limited otherwise. Similarly, a plant’s seed production is zygote limited if the available zygotes do not consume all resources available for seed maturation and is seed resource limited otherwise. Poor pollen receipt constrains seed production only when ovule fertilization in some of a plant’s flowers is pollen limited and its seed development is zygote limited. A notable subtlety in the mathematical analysis stems from the model being piecewise differentiable. Hence, the marginal advantage theorem (Lloyd 1988), which states that the marginal gains from increasing each allocation (the partial derivative with respect to an allocation) are equal at the optimal allocation strategy, need not always apply.

We used numerical simulations to explore the effects of flower number and within- and among-plant variation in pollen receipt on the optimal allocation, the frequencies of pollen-limited flowers and zygote-limited plants, the expected fitnesses of zygote- and resource-limited plants, and the fitness gains expected from experimental supple-
Supplementation of ovules, pollen receipt, and resources for seed development. In these simulations, the random variable characterizing among-plant variability, Y, is gamma distributed with mean 1 and coefficient of variation CVplant. The random variables characterizing variability among flowers on a plant, Z_{i}^{Y}, \ldots, Z_{n}^{Y}, are gamma distributed with mean Y and coefficient of variation CVflower.

To explore key regions of the continuum of cost ratios observed in plants, we consider three cost-ratio scenarios: \( c_{O} : c_{P} : c_{S} = 1 : 10 : 100 \) (baseline), \( 1 : 10 : 10 \) (expensive flowers), and \( 1 : 3 : 1 \) (orchid-like). Our presentation focuses on the baseline scenario in which attracting enough pollen to fertilize one ovule costs an average of 10 times more than producing one ovule and maturing one seed costs 100 times more than producing one ovule. Similar cost ratios are likely common in some angiosperm clades. In particular, \( c_{O} : c_{S} = 1 : 100 \) is consistent with the observation of Greenway and Harder (2007) that individual seeds grew a median 93-fold larger in volume than individual ovules for 45 species of eudicots. Furthermore, a literature survey of 80 angiosperm species found that a \( 1 : 10 \) ratio of flower costs to seed costs is common, with few cases showing more expensive flowers, with flower-to-seed cost ratios up to \( 1 : 1 \) (Rosenheim et al. 2014). The relatively extreme case of \( c_{O} : c_{S} = 1 : 1 \), for which producing a single ovule is as costly as maturing one seed, is consistent with orchids, which produce many tiny seeds that comprise only an embryo in a testa, with no storage tissue, and so are scarcely larger than the ovules from which they develop (Arditti and Ghani 2000). The ratio of \( c_{O} : c_{P} = 1 : 3 \) is consistent with estimates of daily floral maintenance costs (42.5% of floral biomass per day) for 29 species of orchids (Hobbhahn 2012) and with the average ratio (1 : 2.24) of ovary mass to floral mass associated with pollen attraction for seven species of the orchid genus Disa (N. Hobbhahn, unpublished data). The results for the \( 1 : 10 : 10 \) and \( 1 : 3 : 1 \) cost-ratio scenarios are presented in appendixes A–C.

We also used numerical analysis to examine the effects of supplementation of ovules, pollen, and seed resources on the fitness of plants with the optimal allocation. Ovule supplementation ensured sufficient ovules for fertilization by all received pollen, so that the percent increase in expected fitness is

\[
s \min\left\{ \frac{a_{o}^{*} R(c_{o})}, \frac{s \min\{a_{o}^{*} R(c_{o}), \sum_{i=1}^{k} a_{o}^{*} R Z_{i}^{Y}(c_{o}, k)\} - f(a^{*})}{f(a^{*})} \right\} \times 100.
\]

Pollen supplementation ensured enough pollen that seed production was resource limited, so that the percent increase in expected fitness is

\[
s \frac{s \min\{a_{o}^{*} R(c_{o}), \sum_{i=1}^{k} a_{o}^{*} R Z_{i}^{Y}(c_{o}, k)\} - f(a^{*})}{f(a^{*})} \times 100.
\]

Supplementation of seed resources ensured that all zygotes mature into seeds, so that the percent increase in expected fitness is

\[
s \frac{s \min\{a_{o}^{*} R(c_{o}), \sum_{i=1}^{k} a_{o}^{*} R Z_{i}^{Y}(c_{o}, k)\} - f(a^{*})}{f(a^{*})} \times 100.
\]

We also consider simultaneous supplementation of pollen and seed resources, in which case the percent increase in expected fitness is

\[
s a_{o}^{*} R(c_{o}) - f(a^{*}) \times 100.
\]

In contrast to the assumption that seed resources distribute as needed among a plant’s flowers, plants commonly comprise multiple independently integrated physiological units (IPUs; Wesselingh 2007). This situation can be addressed by considering three levels of heterogeneity in pollen receipt: among flowers within an IPU, among IPUs within a single plant, and among plants. Our analysis concludes by examining the effect of this modularity on optimal resource allocation.

### Results

**Expectations under Deterministic Pollination**

To set a baseline for the stochastic results, we describe the deterministic case whereby a given allocation to pollen attraction results in equal pollen receipt by all flowers on all plants (i.e., \( CV_{\text{inner}} = CV_{\text{plant}} = 0 \)). In this case, the optimal allocation causes colimitation of seed production by ovules, pollen attraction, and seed resources (fig. 2A).

Specifically,

\[
a_{o}^{*} R(c_{o}) = a_{p}^{*} R(c_{p}) = a_{s}^{*} R(c_{s}),
\]

and allocation to each reproductive component is proportional to its production cost:

\[
a_{i}^{*} = \frac{c_{i}}{c_{o} + c_{p} + c_{s}} \quad \text{for } i = O, P, S.
\]

The maternal fitness for individuals implementing this allocation is

\[
f^{*} = \frac{s R}{c_{o} + c_{p} + c_{s}}.
\]

Quite simply, \( f^{*} / s \) is the number of seeds that can be produced with \( R \) resources when no resources are wasted: at the optimum, no excess ovules are produced, no excess pollen is received, and no resources remain after all the
Figure 2: Optimal allocations in environments with no variation (A), only among-plant variation (B), only within-plant variation (C), and both among- and within-plant variation (D) in pollen receipt. In each panel, fitness contours at $f = 0, 1, \ldots, 10$ viable seeds per plant are plotted as functions of allocations to pollen attraction $a_p$ and ovule production $a_o$. Allocation to seed maturation is $a_s = 1 - a_p - a_o$. In deterministic environments, differing allocations result in seed production being ovule limited, pollen limited, seed resource limited, and colimited by two factors (dashed lines) or colimited by all three factors (red circle in A). In stochastic environments, differing allocations result in seed production being predominately ($>$50% of cases) seed resource limited (cream region) or zygote limited (blue region). Optimal allocations correspond to the red circle in all panels (eq. [3] in A, eq. [5] in B, eq. [7] in C and D); the deterministic optimum is shown in white in B–D. White regions correspond to nonrealizable allocation strategies, where $a_p + a_o > 1$. Parameters: $c_o : c_p : c_s = 1 : 10 : 100$; $CV_{ovule} = CV_{plant} = 0$ in A; $CV_{ovule} = 0$, $CV_{plant} = 1.6$ in B; $CV_{ovule} = 2.4$, $CV_{plant} = 0$ in C; $CV_{ovule} = 2.4$, $CV_{plant} = 1.6$ in D.

Figure 2: Optimal allocations in environments with no variation (A), only among-plant variation (B), only within-plant variation (C), and both among- and within-plant variation (D) in pollen receipt. In each panel, fitness contours at $f = 0, 1, \ldots, 10$ viable seeds per plant are plotted as functions of allocations to pollen attraction $a_p$ and ovule production $a_o$. Allocation to seed maturation is $a_s = 1 - a_p - a_o$. In deterministic environments, differing allocations result in seed production being ovule limited, pollen limited, seed resource limited, and colimited by two factors (dashed lines) or colimited by all three factors (red circle in A). In stochastic environments, differing allocations result in seed production being predominately ($>$50% of cases) seed resource limited (cream region) or zygote limited (blue region). Optimal allocations correspond to the red circle in all panels (eq. [3] in A, eq. [5] in B, eq. [7] in C and D); the deterministic optimum is shown in white in B–D. White regions correspond to nonrealizable allocation strategies, where $a_p + a_o > 1$. Parameters: $c_o : c_p : c_s = 1 : 10 : 100$; $CV_{ovule} = CV_{plant} = 0$ in A; $CV_{ovule} = 0$, $CV_{plant} = 1.6$ in B; $CV_{ovule} = 2.4$, $CV_{plant} = 0$ in C; $CV_{ovule} = 2.4$, $CV_{plant} = 1.6$ in D.

Expectations in Stochastic Pollination Environments

Stochastic variation in pollen receipt reduces an individual’s expected fitness regardless of its allocation strategy. As with other aspects of stochastic demography (Lewontin and Cohen 1969; Gillespie 1973; Tuljapurkar 1990; Boyce et al. 2006), this reduction occurs because fitness is a decelerating function of input (pollen receipt; Jensen 1906; Roberts and Varber, 1973).

The consequences of stochastic pollination depend on the filtering of variation during zygote formation and seed development caused by the upper bounds on both processes (fig. 1). In particular, for well-pollinated flowers, the fixed number of ovules reduces variation in zygote number, and the fixed seed resources per plant reduces variation in seed production. The extent of this variance reduction depends positively on both the mean and the variance of pollen receipt per plant. For example, plants with mean pollen receipt illustrated by the blue bar in figure 1A have higher within-plant pollen variance ($[P \times CV_{ovule}]^2$) but lower zygote variance (fig. 1C) and especially seed variance (fig. 1E) than plants, illustrated by the green bar. This winnowing of variation and its dependence on the distribution of pollen receipt determine the consequences of stochastic pollination for the optimal partitioning of resources among the steps that govern female success.

Among-Plant Variation in Pollen Receipt

Suppose that pollen receipt varies only among plants because plants are single flowered. In this case, the fitness function (eq. [2]) simplifies to

$$f(a) = s \mathbb{E} \left[ \min(a_o R/c_o, a_p R/c_p, a_s Y R/c_s) \right],$$

with pollen, ovule, and seed terms equally coupled. As in
the deterministic case, this fitness expression and our nu-
merical simulations indicate that the optimal allocation
tends to invest more resources in the more costly repro-
ductive functions (e.g., greatest allocation to seeds fol-
lowed by pollen attraction for the baseline cost ratio
c_o : c_p : c_z = 1 : 10 : 100 in fig. 2B). Therefore, our sto-
chastic analysis focuses on how pollen variation selects for
overinvestment in some reproductive functions relative to
the optimal deterministic allocations (i.e., \( a_i^* > c_i/(c_o +
\)
\( c_p + c_z \)) for some \( i = O, P, S \) and underinvestment in the
remaining reproductive functions (i.e., \( a_i^* < c_i/(c_o +
\)
\( c_p + c_z \)) for the other \( i \).

In the absence of within-plant variation in pollination,
extected maternal fitness depends only on the lesser of
pollen receipt or ovule number per flower rather than on
the combined incidence of pollen and ovule limitation
among a plant’s flowers. As a result, the optimal allocation
strategy always matches the number of seeds produced with
the number of seeds that can be matured (i.e.,
\( a_o^* c_o = a_o c_o \)). This match is optimal when pollen
receipt is abundant, as it ensures no waste or excess ovules or
seed resources (both will be used in their entirety). This
match is also optimal when pollen receipt is scarce because
although there will be both excess ovules and seed re-
sources, no reallocation between ovules and seed resource
can augment fitness (only increased allocation to pollen
attraction would increase fitness). Such ovule-seed pack-
aging reduces the stochastic optimization from three to
two reproductive functions, seed-ovule units (SO) and
pollen attraction (P). Consequently, the optimal allocation
to reproductive function \( i \) (SO or P) equals the product
of the probability of being limited by that function (\( p_i \))
and the relative fitness of individuals limited by the same
function (\( w_i \); Rosenheim et al. 2010). Mathematically,

\[
\begin{align*}
\hat{a}_o + \hat{a}_o^* &= p_ow_{SO}, \\
\hat{a}_p &= p_bw_p.
\end{align*}
\]

(5)

Intuitively, as plants experience more uncertainty in pollen
availability (i.e., \( p_i \) increases), they lower their risk of pol-
len limitation by increasing investment in attracting pol-
linators at the expense of reducing investment in seed-
ovule packages (fig. 3A, 3B). When the risks of pollen
limitation or seed-ovule limitation are equal, equation (5)
implies that the optimal allocation invests collectively more
into seed-ovule units than attracting pollinators, as plants
limited by successful seed-ovule units are much fitter than
pollen-limited individuals (\( w_{SO} \gg w_p \); see fig. 3C). Inter-
estingly, unlike the deterministic case, stochasticity in pol-
len receipt “smooths” out the fitness function with respect
to \( a_o \) and the joint allocation \( a_{SO} = a_o + a_o^* \). Thus, the
marginal advantage theorem applies (Lloyd 1988): for
plants allocating optimally, the marginal gain from in-
creasing allocations to seed-ovule units equals the marginal
gain from increasing allocations to pollen attraction.

Plants experiencing among-plant variation in pollen
availability should overinvest in pollen attraction, relative
to the deterministic case, whenever

\[
E[Y|Y < 1](c_o + c_o) > c_p
\]

(6)

and underinvest whenever inequality (6) is reversed. The
expectation \( E[Y|Y < 1] \) represents the expected (normal-
ized) pollen receipt by a plant receiving less than the av-
average amount of pollen, and this expectation is always \(<1\).
Consequently, the optimal strategy overinvests in pollen
attraction unless attracting enough pollen to fertilize an
ovule is nearly as costly as producing one ovule and
maturating it into a seed. For our baseline cost ratios
\( c_o : c_p : c_z = 1 : 10 : 100, \) overinvestment in pollen attrac-
tion is always optimal, as seed development is the most
expensive reproductive function (figs. 2C, 3A). Overin-
vesting in pollen attraction substantially increases pollen
receipt and seed production for plants that occupy loca-
tions with below-average pollen availability but only
slightly decreases seed production for plants that occupy
locations with above-average pollen availability.

Within-Plant Variation in Pollen Receipt

With only within-plant variation in pollen receipt, the op-
timal allocations depend on the probability of a plant’s
seed production being limited by zygote formation (\( p_z \))
or seed resources (\( p_o \)). Our mathematical analysis (see app.
A) reveals that the optimal allocations to ovules or pollen
attraction are proportional to \( p_z \) and that the optimal
allocation to maturing seeds is proportional to \( p_o \). More
precisely,

\[
\begin{align*}
\hat{a}_o &= p_o w_o, \\
\hat{a}_p &= p_z w_p, \\
\hat{a}_o^* &= p_o w_o^*,
\end{align*}
\]

(7)

where \( w_o \) and \( w_p \) are the collective contributions of all
ovule-limited or pollen-limited flowers to fitness, respec-
tively, and \( w_p \) is the relative fitness of seed-resource-limited
plants. In contrast to among-plant variation, for which the
risks of pollen limitation and seed-resource limitation gov-
ern the evolution of resource allocations, equation (7) im-
plies that the risks of zygote limitation and seed-resource
limitation govern these evolutionary dynamics in the pres-
ence of within-plant variability.

Unlike among-plant variation in pollen availability,
within-plant variation selects for overinvestment in ovule
production in addition to overinvestment in pollen attrac-
tion (figs. 2C, 3D). Production of many cheap ovules
provides an easy solution to within-plant variation, as it increases the number of fertilized ovules in flowers winning the pollen lottery, with little cost for less lucky flowers. This solution is more feasible when plants produce many flowers (compare 25-flowered plants with 2-flowered plants in fig. 3D).

With within-plant variation in pollen receipt, the fraction of pollen-limited flowers in a population with \( a = a^* \) always exceeds the fraction of zygote-limited plants (fig. 3E). In contrast, seed production by few-flowered plants is more likely to be zygote limited when all flowers are pollen limited. Indeed, for single-flowered plants, having a pollen-limited flower and being a zygote-limited plant are one and the same event.

Plants that produce more—and hence smaller—flowers have higher fitness (in the absence of a fixed cost of flower production) than few-flowered plants (fig. 3F) because they have more fertilization opportunities, despite predominant pollen limitation. However, increased flower number solves only the problem of within-plant variability...
in pollen. The fitness difference between plants with opti-
mal allocations given few versus many flowers is greatest
for zygote-limited plants (fig. 3F). Intuitively, seed-
resource-limited plants have won the lottery of pollen
receipt, so few-flowered plants produce almost as many
seeds as many-flowered plants.

**Combined Among- and Within-Plant
Variation in Pollen Receipt**

The optimal allocation in the presence of pollen variability
at both scales also satisfies equation (7). For the baseline
cost ratios, among- and within-plant variation in pollen
receipt primarily have additive effects on the optimal al-
locations (fig. 4A–4C). However, these effects saturate rela-
tively quickly with among-plant variation, whereas there
is little of sign of saturation with within-plant variation.
Within-plant variation affects allocation to ovules much
more than among-plant variation (fig. 4B), whereas the
opposite is true for allocation to pollen attraction (fig. 4A).
Both within- and among-plant variation select for reduc-
tions in seed-development resources (fig. 4C), with
among-plant variation causing the larger reduction due to
resources being diverged to the more expensive of the other
reproductive functions, pollen attraction (fig. 4A).

**Effects of Supplemental Allocations on Seed Production**

Given the baseline cost ratios, responses of plants with
optimal allocations to supplementation of pollen, ovules,
and seed resources depend on the magnitudes of within-
and among-plant variation in pollination. Seed production
increases most with pollen supplementation (as much as
200% in fig. 4D), especially for plants experiencing exten-
sive among-plant variation; within-plant variation con-
tributes only weakly to this response. In contrast to pollen
supplementation, supplementing ovules yields almost no
gain in seed production (<3% in fig. 4E) because plants
subject to within-plant variability optimally overinvest in
ovules (fig. 4A). The effect of supplementing seed resources
also varies with the scale of variation in pollen availability.
As plants subject to only among-plant variation are co-
limited by ovules and seeds, supplementation of their seed
resources has no effect. However, for plants experiencing
within-plant variation, supplementing seed resources
causes intermediate improvement in seed production
(about 80% in fig. 4F). The greatest response to resource
supplementation occurs for plants experiencing high
among-plant variation and intermediate within-plant var-
iation in pollen availability.

Pollen supplementation greatly increases the number of
unmatured zygotes (as much as 89.2% in fig. 5A) for plants
experiencing within-plant variation but not for those sub-
ject to among-plant variation. This reproductive shortfall
results from within-plant variation selects for overpro-
duction of ovules at the expense of resources for seed
maturation. As a result, supplementing these plants si-
multaneously with pollen and seed resources increases seed
production more than predicted from additive effects
alone (fig. 5B). This interactive effect is strongest (as much
as 2,000% in fig. 5B) for plant populations experiencing
multiscale variation, as within-plant variation selects for
resource limitation through ovule overproduction and
among-plant variation generates pollen limitation.

**Effects of Modularity**

Instead of free redistribution of seed resources among a
plant’s flowers, suppose that plants have n IPUs each with
k flowers and that seed resources cannot be redistributed
among modules. If reproductive resources partition
equally among IPUs, so each receives R/n resources, a plant’s
expected maternal fitness is

\[
f(a) = \sum_{j=1}^{n} \min \left( \frac{1}{k} \sum_{i=1}^{k} F_i, \frac{1}{n} \sum_{j=1}^{n} Z_j \right),
\]

where

\[ F_i = \min \{ a_i R(kn c_i), a_i Z_i R(kn c_i) \}, \]

and \( Z_j \) are random variables accounting for variation in
pollen receipt with mean 1. If the random vectors
\((Z_1, \ldots, Z_j, \ldots, Z_n)\) have the same distribution,
then equation (8) simplifies to the base model in
equation (2), for which among-plant variation corre-
sponds to among-IPU variation and within-plant variation
corresponds to within-IPU variation. This condition is
met, for instance, when the plant mean \( Y \) is determined
by a fixed distribution, the IPU means \( I_1, \ldots, I_n \) are
independent draws from a fixed distribution determined by
the plant mean, and \( Z_1, \ldots, Z_n \) within the \( j \)th IPU
are independent draws from a fixed distribution determined
by the IPU mean \( I_j \). Under this condition, our core results
apply to plants with multiple IPUs, with among-plant var-
iation reinterpreted as among-IPU variation.

**Discussion**

Several orders of magnitude of variation in pollen receipt
among flowers is common in plant populations (Burd
1994; Burd et al. 2009). For 13 animal-pollinated species,
50.4% to 100% of this variation was attributed to variation
among flowers within individuals, whereas the remaining
variation occurred among individuals (Herrera 2004,
2009). In contrast, for wind-pollinated plants, among-
plant variation likely plays a more dominant role than
Figure 5: Resource limitation following pollen supplementation and the interactive effect of joint supplementation of pollen and seed resources on fitness. Following pollen supplementation, the fraction of unmatured zygotes increases with within-plant variation in pollen availability (A). The interactive effect of joint pollen- and seed-resource supplementation on seed production (% increase due to supplementing both − % increase due supplementing pollen − % increase due to supplementing seed resources) is always positive (B). Parameters: $c_0 : c_1 : c_2 = 1 : 10 : 100$, $k = 25$ flowers.

Within-plant variation (Friedman and Barrett 2011). Here, we show that stochastic pollination within and among plants should pervasively influence the optimal allocation of reproductive resources to the three components of female function: ovule production, pollen attraction, and seed development. Compared with deterministic environments, in which the optimal allocations are proportional to per capita costs (Haig and Westoby 1988), stochastic pollination environments should favor allocation of more resources to some female functions at the expense of other functions (Burd 1995, 2008; figs. 3A, 3D, 4A–4C, C1, C3). By partitioning pollination variation into among- and within-plant components and examining various cost structures for female function, our models reveal conditions that promote diverse evolutionary outcomes. In general, within-plant variation selects for the overproduction of ovules to minimize the risk of fitness being limited by the reproductive function with the lowest per capita cost. When the cost of developing a seed equals or exceeds the cost of attracting enough pollen to fertilize an ovule, allocation to ovules is insensitive to among-plant variation, generating a dichotomous trade-off between attracting pollen and allocations to the remaining reproductive functions. In this situation, the increased cost of developing a seed shifts the optimal allocation from overinvesting only in seeds (fig. C1) to overinvesting only in pollen attraction (fig. 4A–4C), with among-plant variation having a stronger effect than within-plant variation. In contrast, when pollen attraction is relatively expensive compared with both producing an ovule and maturing a seed (fig. C3), among-plant pollination variation favors simultaneous overinvestment in ovules and seed maturation. As within- and among-plant variation in pollination do not generally influence optimal allocation in an additive fashion, their effects must be considered jointly to appreciate fully the evolutionary consequences of stochastic pollination.

Before discussing the implications of these basic principles for the evolution of allocation to ovules, pollen attraction, and seed development, we identify the specific variance conditions to which Burd’s models of stochastic pollination apply. Burd (1995) assumed a dichotomous resource trade-off between ovule production and pollen attraction, with all fertilized ovules maturing into seeds. This corresponds largely to our model with low maturation costs per seed and only within-plant variability in pollen availability (fig. C3, along the CVflower axis), which favors increased ovule production at the expense of pollen attraction compared with the deterministic case. In contrast, Burd (2008) assumed a dichotomous trade-off between attracting pollen and maturing seeds. This corresponds to our model with relatively expensive seeds and only among-plant variation in pollen receipt (fig. 4A–4C along the CVplant axis), which favors increased pollen attraction at the expense of seed development. Thus, Burd addressed two special cases of the...
broader diversity of evolutionary influences of stochastic pollination environments.

**Ovule Production**

Increased investment in reproductive capacity (ovules per flower in plants, offspring per clutch in animals) in less predictable environments is a long-standing expectation (Levin and Turner 1977; May 1978; Burd 1995). Correspondingly, increased ovule production in response to within-plant variation in pollination is the most consistent prediction (figs. 4B, C1B, C3B), and among-plant variation accentuates this effect when seeds are inexpensive (fig. C3B). That variable pollination promotes copious ovule production is supported by a phylogenetically informed comparative analysis of 187 angiosperm species (Burd et al. 2009) that detected a strong positive association between ovule number per flower and variability in pollen receipt. Although this meta-analysis did not assess the relative extent of among- versus within-plant variation in pollination, studies of animal-pollinated plants indicate that within-plant variation predominates (Herrera 2009).

Production of many inexpensive ovules increases the number of zygotes on the lucky flowers that receive abundant pollen and invokes little cost for the less lucky flowers. This means of combating within-plant variation will result in optimal plants with maximal seed production having failed ovules (either unfertilized or aborted) because more ovules will have been fertilized than could be developed into seeds, given the available seed resources. The common incidence of seed-to-ovule ratios <1 following abundant cross-fertilization (Harder and Routley 2006) is consistent with this expectation. Similarly, because of copious ovule production, experimental addition of ovules to flowers (if it were possible) should generally have limited impact on seed production.

Enhanced ovule production combats variable pollination within individuals most effectively when plants produce many flowers, as some flowers are then almost certain to receive abundant pollen (compare 25-flowered plants with 2-flowered plants in fig. 3D). In contrast, plants with fewer flowers (e.g., 2 flowers per plant) should overinvest more heavily in pollen attraction than in ovules to increase the chance of full pollination for at least some flowers. Hence, plants having multiple flowers exhibit the within-generational analog of bet-hedging theory’s “putting one’s eggs in different baskets” (Frank and Slatkin 1990). However, instead of individuals producing offspring with partially correlated fates to reduce variation in the number of surviving offspring, producing multiple flowers reduces the net variation in pollen receipt experienced by an individual. These associations suggest that flower number and ovule number per flower are optimized jointly, which warrants analysis by both an expanded allocation model and comparative studies.

Among-plant pollination variation affects optimal ovule production only when ovules and seeds are inexpensive compared with pollen attraction (fig. C3B). Orchids exemplify this condition, as their seeds lack nutritive tissue and instead rely on association with fungal mutualists to establish seedlings (Arditti and Ghani 2000), and in many orchid species ovules do not develop unless a flower is pollinated (Wirth and Withner 1959). In addition, orchids likely experience extremely variable pollination within and among plants because pollen of most species disperses as discrete aggregated units, precluding the continuous variation in pollen receipt typical of species with granular pollen (Harder and Johnson 2008). Furthermore, most orchids rely on specialist pollinators whose abundance varies spatially (Micheneau et al. 2009), and they commonly experience annual reproductive failure (Neiland and Wilcock 1998; Tremblay et al. 2005), in part because a third of species provide no pollinator reward (Dressler 1981). In association with this unique combination of traits, orchids exhibit prodigious ovule production (Burd et al. 2009).

Wind-pollinated (anemophilous) species typically produce few ovules per flower, including many species with uniovulate flowers (Stebbins 1974; Friedman and Barrett 2011). A comparison of 19 anemophilous species from Friedman and Barrett (2011) and 187 angiosperm species from Burd et al. (2009; of which all but three species are animal-pollinated) reveals that anemophilous species experience 67% less variation in pollen receipt (CV = 0.4) than animal-pollinated species (CV = 1.2). Friedman and Barrett (2011) proposed that pollination of “anemophilous species may be more predictable because of the higher synchrony of anthesis and the possibility that all stigmas on a plant will have approximately the same probability of pollen capture” (p. 254). Our model and Burd’s (1995) model both predict that such low variability (especially within-plant variability) in pollen receipt selects for reduced ovule number. Because we did not consider either absolute ovule number or trade-offs between flower number and size, ovule production, pollen attraction, and seed maturation, our model cannot completely explain why anemophilous species often produce many inexpensive flowers with few ovules. However, models accounting for the aerodynamics of pollen capture and the trade-off in flower size and number predicted that plants benefit from producing many small, inexpensive flowers, despite some flowers capturing too few pollen grains to fertilize their ovules (Friedman and Barrett 2011).

**Pollen Attraction**

Variable pollination affects allocation to pollen attraction under all cost structures that we considered, favoring in-
creased allocation when individual seeds are relatively expensive (fig. 4A) and reduced allocation when pollen attraction per zygote is at least as expensive as maturation of a seed (figs. C1A, C3A). Among-plant variation had a consistently strong effect, whereas within-plant variation had limited influence, except when pollen attraction was the most expensive per capita component of female function. When seeds are expensive, the risk of zygote limitation places a premium on floral and inflorescence traits that promote adequate pollination of at least some of a plant’s flowers because the associated copious ovule production and free distribution of seed resources among fruits ameliorate the effect of within-plant variation in pollen receipt on total seed production. In contrast, when pollen attraction is expensive, overinvestment in seed resources rather than pollen attraction results in larger gains for individuals receiving an excess of pollen than the losses incurred when receiving too little pollen.

Despite these optimal adjustments of allocation to pollen attraction, among-plant variation in pollination should always select for allocations that predispose plants to pollen-limited seed production (figs. 4D, C2A, C4A). According to this expectation, pollen limitation should be manifest as the proportion of plants that do not maximize seed production, given the available resources, regardless of the distribution of those seeds among flowers. In contrast, within-plant variation has little effect on the incidence of pollen limitation in our models because it is mitigated by the increased ovule production that such variation favors and the redistribution of seed resources. For instance, using Burd et al.’s (2009) estimate of a mean CV of 1.2 for pollen receipt, our baseline model predicts a 33% increase in seed production when variability is completely among plants but only a 2% increase when variability is completely within plants. For monocarpic species, which our model addresses most directly, Knight et al. (2006) found that pollen supplementation of all flowers increased seed production, on average, by 13%. According to our model, this response would occur if 60% of the variation in pollen receipt occurs within plants, an estimate consistent with several naturally pollinated plant populations (Herrera 2002, 2004, 2009).

Although many studies have demonstrated pollen limitation, most have focused on seed production by individual flowers rather than by the entire plant (Knight et al. 2006). Studies at the flower level can overestimate pollen limitation (i.e., result in false positives) as “enhanced seed set in some flowers on a plant may occur at the expense of reduced seed set in other blossoms on the same plant” (Zimmerman and Pyke 1988, p. 725). Our basic model allows for such resource redistribution and predicts the greatest overestimation of pollen limitation when pollen receipt varies extensively within plants (fig. 3B, 3E). For example, if the overall CV of pollen receipt is 1.2 (Burd et al. 2009) and 60% of this variation comes from within-plant variation (Herrera 2009), our baseline model predicts that pollen supplementation of a small subset of flowers increases seed production of treated flowers by 30%, on average, compared with only a 13% increase following supplemental pollination of all flowers. These back-of-the-envelope calculations largely agree with Knight et al.’s (2006) meta-analysis, which found a 35.3% effect size on seed set with partial supplementation and only a 17.8% effect size with supplementation of all of a plant’s flowers.

Seed Development

The distinct consequences of within- and among-plant pollination variation are particularly evident in the allocation to seed development. Increased costs per seed reduce the optimal seed allocation under high variation of either type, intensifying the negative relation between seed allocation and within-plant variation and causing a shift from a strongly positive relation to a negative relation for among-plant variation (compare figs. 4C, C1C, C3C). Given the copious ovule production that characterizes all optimal allocations, the number of zygotes should commonly exceed the number of seeds that can be matured, especially when per capita seed maturation costs are high.

Unlike pollen limitation, our model predicts resource limitation of seed production only for plants adapted to within-plant variation in pollen receipt, although among-plant variation can magnify this effect. When seeds are expensive these gains are modest (as much as 80% in fig. 4F), but they are negligible otherwise (always <4% in fig. C4C). However, for populations adapted to within-plant variation, jointly supplementing plants with seed resources and pollen should substantially increase seed production beyond the additive effects of supplementing resources and pollen separately (as much as 2,000% in fig. 5B). Among-plant variation magnifies this interactive effect.

Only a few empirical studies have simultaneously assessed resource and pollen limitation (Vaughton 1991; Campbell and Halama 1993; Mattila and Kuitunen 2000; Suzuki 2000; Yang et al. 2005; Brookes et al. 2008). Many of these studies demonstrated complex interactive effects between resource and pollen limitation of seed and fruit production, several of which are consistent with our model predictions. Notably, fruit production in Banksia spinulosa increased by 65% and 114% following separate additions of resources and pollen, respectively, and by 298% following the addition of both (Vaughton 1991). A more extreme interactive effect was observed in a 2-year study of Styliodium armeria (Brookes et al. 2008). Treatments with separate additions of pollen and resources led to 3% and 21% increases in seed production, respectively, whereas joint...
additions led to a 110% increase. Brookes et al. (2008) stated that “[t]hese results match the direction of effects predicted by the [deterministic] Haig-Westoby model” (p. 557), which predicts no response to individual additions. Alternatively, our model predicts similar responses to individual additions and an extreme interactive effect when populations primarily experience within-plant variation in pollen receipt, which is likely given that *S. armeria* had, on average, 56 flowers per plant in this study.

Empirical and Theoretical Challenges

Multiscale variation in pollen receipt and variation in per capita pollen attraction, ovule, and seed costs pose diverse empirical challenges. To test the predictions that within-plant variation and low per capita seed maturation costs select for overproduction of ovules, more studies that estimate ovule number per plant (Burd et al. 2009), partition the sources of variation in pollen receipt (Burd et al. 2009), and estimate relative per capita costs of female functions are needed. In addition to the latter two data requirements, testing the predictions that (1) each percent of among-plant variation in pollen receipt leads to more pollen limitation than each percent of within-plant variation and (2) pollen limitation should be greater for species with lower per capita seed maturation cost requires pollen supplementation experiments on entire plants, not subsamples of flowers, as noted previously (Zimmerman and Pyke 1988; Knight et al. 2006). Alternatively, testing the resource limitation predictions (e.g., within-plant variation selecting for seed-resource limitation in plants with expensive seeds) is likely to be experimentally challenging, as it requires supplementing resources only for seed maturation (e.g., performing resource additions or flower removals shortly after pollination is largely complete).

Although our analysis contends with more biological complexities than prior studies (Haig and Westoby 1988; Burd 1995, 2008; Rosenheim et al. 2010), several additional complexities likely influence the evolution of reproductive allocations. Like prior studies, we assumed that male function does not deflect selection significantly from the optimal allocation for female function, which applies formally only to female plants of dioecious or gynodioecious species. Also like earlier studies, we assumed fixed reproductive investment during a reproductive season, so our model does not account for adjustments during a reproductive season or more generally during the lifetime of an individual (Harder and Johnson 2005; Knight et al. 2005; Nepi and Stpiczyska 2007). For example, plants may adjust flower longevity (Harder and Johnson 2005), modulate the number of future flowers produced (Avila-Sakar et al. 2001), and abort fruits and flowers (Stephenson 1981). These phenotypically plastic responses may reduce the impacts of stochastic pollination on seed production and, consequently, select for reproductive allocations closer to the deterministic optimum. Finally, we considered variation in only pollen receipt and assumed that all zygotes develop into seeds and that all seeds have equivalent potential for seedling establishment. However, pollen varies considerably in siring ability (Lau and Stephenson 1993, 1994), and relatedness of parents affects offspring quality (Charlesworth and Charlesworth 1987; Husband and Schenske 1996). How these additional within- and among-season complexities modulate allocation to the components of seed production for all sexual systems presents a diversity of challenges for future studies.

Conclusions

Variation in pollen receipt selects for resource allocations to reproductive functions proportional to their risk in limiting seed production. Whether increased allocations to ovule production, pollen attraction, or seed maturation can minimize these risks generally depends on a subtle interplay between the partitioning of variation across multiple scales and the relative per capita costs of these reproduction functions. Nevertheless, our results expose several testable predictions about macroevolutionary and macroecological patterns. We predict more ovules per flower for species experiencing high within-plant variation in pollen receipt, such as multiflowered plants in habitats where pollen receipt is uncertain. This overproduction of ovules should be greatest when per capita seed maturation costs are low and when floral traits minimize pollen transport among flowers within an individual (e.g., pollinia in milkweeds or some orchid species with almost binary deposition patterns or inflorescences in which pollinators visit female[-phase] flowers before male[-phase] flowers). Indeed, reduced pollen transport decouples pollen receipt among flowers and thereby is likely to increase within-plant variability in pollen receipt. Alternatively, we predict that plants adapted to landscapes with spatial variation in pollinator densities are more prone to pollen limitation, as this spatial variation is likely to generate greater among-plant variability in pollen receipt. More generally, our results illustrate that multiscale resource variability can select for diverse strategies to minimize its impacts on reproductive success.

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Appendix A from S. J. Schreiber et al., “Evolutionary and Ecological
Consequences of Multiscale Variation in Pollen Receipt for Seed
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(Am. Nat., vol. 185, no. 1, p. E14)

The Optimal Allocation Strategy
In this appendix, we derive the analytical results presented in the main text. Let \( \rho(x_1, \ldots, x_k) = \rho(x) \) be the joint density function for the continuous random variables \( Z_1, \ldots, Z_k \). Let \( \mathbb{R}^k_+ = \{ x = (x_1, \ldots, x_k) : x_i \geq 0 \text{ for all } i \} \) be the nonnegative orthant of \( \mathbb{R}^k \). We first characterize of the optimal allocation strategy and then derive results about over- and underinvestment.

Define the following events (depending on \( a \)).

Seed production is seed resource limited:

\[
S(a) = \{ x \in \mathbb{R}^k_+ : a_S/c_S < \frac{1}{k} \sum_{i=1}^k \min\{a_O/c_O, a_p x_i/c_p\} \}.
\]

Seed production is zygote limited:

\[
Z(a) = \{ x \in \mathbb{R}^k_+ : a_S/c_S > \frac{1}{k} \sum_{i=1}^k \min\{a_O/c_O, a_p x_i/c_p\} \}.
\]

Seed production of the set \( I \subset \{1, \ldots, k\} \) of flowers is ovule limited:

\[
O_I(a) = \{ x \in \mathbb{R}^k_+ : a_p x_i/c_p > a_O/c_O \text{ for } i \in I, \text{ otherwise } a_p x_i/c_p < a_O/c_O \}.
\]

The set \( \mathbb{R}^k_+ \setminus \bigcup_{I \subset \{1, \ldots, k\}} O_I(a) \) has Lebesgue measure 0 for any choice of \( a \), that is, a flower’s seed production being jointly pollen and ovule limited occurs with probability 0. In contrast, a plant’s seed production can be jointly zygote and seed resource limited with positive probability. This occurs only when seed production of all flowers is ovule limited (i.e., in the event \( O_{\{1, \ldots, m\}}(a) \)) and when \( a \) satisfies \( a_S/c_S = a_O/c_O \).

Define

\[
g(a, x) = \min\{a_S R/c_S, \frac{1}{k} \sum_{i=1}^k \min\{a_O R/c_O, a_p x_i R/c_p\} \}.
\]

For \( x \in S(a) \),

\[
\frac{\partial g}{\partial a_S}(a, x) = \frac{R}{c_S},
\]

\[
\frac{\partial g}{\partial a_p}(a, x) = \frac{\partial g}{\partial a_O}(a, x) = 0.
\]

For \( x \in Z(a) \cap O_I(a) \) with \( I \subset \{1, \ldots, k\} \),

\[
\frac{\partial g}{\partial a_S}(a, x) = 0,
\]

\[
\frac{\partial g}{\partial a_O}(a, x) = \frac{|I|}{k} \frac{R}{c_O},
\]

\[
\frac{\partial g}{\partial a_p}(a, x) = \frac{1}{k} \sum_{i \in I} \frac{R x_i}{c_p},
\]

where \( |I| \) denotes the cardinality of the set \( I \).
Define the quantities

\[ p_z = \int_{Z(a)} \rho(x) \, dx \]

= probability of a plant’s seed production being zygote limited,

\[ p_s = \int_{S(a)} \rho(x) \, dx \]

= probability of a plant’s seed production being seed resource limited,

\[ N_s = \frac{a_s R}{c_s} \]

= number of seeds produced by a seed-resource-limited plant,

\[ N_o = \frac{a_o R}{k c_o} \sum_{i \in \{1, \ldots, k\}} \int_{Z(a) \cap \Omega(a)} |I| \rho(x) \, dx \]

= expected seed production by ovule-limited flowers on a zygote-limited plant,

\[ N_p = \frac{a_p R}{k c_p} \sum_{i \in \{1, \ldots, k\}} \sum_{i \neq j} x_i \rho(x) \, dx \]

= expected seed production by pollen-limited flowers on a zygote-limited plant.

Because \( g(a, x) \) has well-defined derivatives for a set of full Lebesgue measure provided that \( a_s / c_s \neq a_o / c_o \), our objective function \( f(a) = \int g(a, x) \rho(x) \, dx \), where \( dx = dx_1 \, dx_2 \ldots dx_a \), is differentiable except when \( a_s / c_s = a_o / c_o \). In particular, the partial derivatives are given by

\[ \frac{\partial f}{\partial a_s}(a^*) = \frac{p_s N_s}{a_s}, \]

\[ \frac{\partial f}{\partial a_o}(a^*) = \frac{p_z N_o}{a_o}, \]

\[ \frac{\partial f}{\partial a_v}(a^*) = \frac{p_z N_p}{a_v}, \]

whenever \( a_s / c_s \neq a_o / c_o \). By the method of Lagrange multipliers, if the optimal allocation strategy satisfies \( a_s / c_s \neq a_o / c_o \), then there exists a real number \( \lambda \) such that

\[ \lambda = \frac{\partial f}{\partial a_s}(a^*) = \frac{\partial f}{\partial a_o}(a^*) = \frac{\partial f}{\partial a_v}(a^*) = \frac{p_s N_s}{a_s} = \frac{p_z N_o}{a_o} = \frac{p_z N_p}{a_v}. \]

Since \( \lambda \) corresponds to the marginal increase in fitness when marginally increasing the constraint \( 1 = a_s + a_o + a_v \) and \( f(\alpha a) = \alpha f(a) \) for all \( \alpha \geq 0 \), \( \lambda = f(a^*) = p_s N_s + p_o(N_o + N_p) \). Hence,

\[ a_s^* = \frac{N_s}{p_s N_s + p_o(N_o + N_p)}, \]

\[ a_o^* = \frac{N_o}{p_s N_s + p_o(N_o + N_p)}, \]

\[ a_v^* = \frac{N_p}{p_s N_s + p_o(N_o + N_p)}. \]  

(A1)
Alternatively, when the optimal strategy satisfies $a_p/c_s = a_p/c_o$, the optimization problem simplifies to maximizing

$$h(a_p) = \mathbb{E}\left[(1 - a_p)(c_s + c_o), \frac{1}{k} \sum_i \min((1 - a_p)(c_s + c_o), a_p x_i/c_p)\right]$$

with respect to $a_p$, where $a_s = (1 - a_p)c/(c_s + c_o)$ and $a_o = (1 - a_p)c/(c_s + c_o)$. Unlike $g(a)$, $h$ is differentiable for all $a_p \in (0, 1)$. Specifically, its derivative is given by

$$h'(a_p) = -\frac{R}{c_s + c_o} \left[ \int_{z \in \mathbb{R}} \rho(x) \, dx + \sum_{j \in \{1, \ldots, k\}} \int_{z \in \mathbb{R}} \frac{|I|}{c_s + c_o} + \sum_{i \in \{1, \ldots, k\}} \rho(x) \, dx \right]$$

$$+ \frac{R}{kc_p} \sum_{j \in \{1, \ldots, k\}} \int_{z \in \mathbb{R}} \sum_{i \in \{1, \ldots, k\}} x_i \rho(x) \, dx - \frac{p_s N_s + p_o N_o}{1 - a_p} + \frac{p_z N_p}{a_p} = \lambda,

$$

where $p_s = \mathbb{E}_{z \in \mathbb{R}}[\rho(x) \, dx]$ is the probability of a plant’s seed production being purely seed resource limited, $p_{so}$ is the probability of zygote limitation with some flowers being ovule limited (possibly colimited by seeds when all flowers are ovule limited), $p_z$ is the probability of seed production being purely colimited by zygotes, $N_s$ is the fitness of a seed-limited plant, $N_o$ is the expected number of seeds produced by ovule-limited flowers on a zygote-limited plant (possibly colimited by seed resources), and $N_p$ is the expected number of seeds produced by pollen-limited flowers on a pollen-limited plant (possibly colimited by seed resources). Because $h(0) = h(1)$, at the optimal $a_p$, $h'(a_p) = 0$. Equivalently,

$$\lambda = \frac{p_s N_s + p_o N_o}{1 - a_p} + \frac{p_z N_p}{a_p},

$$

where $\lambda$ (as argued above) must equal a plant’s expected fitness $p_s N_s + p_z (N_o + N_p)$.

In the absence of within-plant variation in pollen receipt (e.g., single-flowered plants), $Z_1 = Z_2 = \cdots = Z_s$ and

$$f(a) = \mathbb{E}[\min(a_s R/c_s, a_o R/c_o, a_p R z_i/c_p)].$$

Notice that $\min(a_s R/c_s, a_o R/c_o, a_p R z_i/c_p) = \min(a_s R/c_s, a_o R/c_o, a_p R z_i/c_p)$. Furthermore, for any $a_p < 1,

$$\min(a_s R/c_s, a_o R/c_o)$$

is maximized when $a_s = c_s/(1 - a_p)/(c_o + c_s)$ and $a_o = c_o/(1 - a_p)/(c_s + c_o)$. Equivalently, this maximization occurs when $a_s R/c_s = a_o R/c_o$. Therefore, in the absence of within-plant variation in pollen receipt, equation (A2) is satisfied when $p_s = 0$, as a plant’s seed production can never be purely seed resource limited in this case.

**Overinvestment and Underinvestment**

First, consider the problem of between-plant variability but no within-plant variability (e.g., a single-flowered plant). In this case, the optimization problem reduces to maximizing $h(a_p) = \mathbb{E}[\min((1 - a_p)(c_s + c_o), a_p Z_i/c_p)]$. When the environment is deterministic, that is, $Z_1 = 1$ with probability 1, the optimal strategy is $a_p = c_p/(c_s + c_o + c_p)$. Now assume that $Z_1$ has a continuous, symmetric distribution about 1. Then

$$h'(a_p) = p_p \mathbb{E}[Z_1 | Z_1 < 1] R/c_p - p_{so} R/c_s + c_o$$

$$= \frac{R}{2} \mathbb{E}[Z_1 | Z_1 < 1] - \frac{1}{c_s + c_o},$$

Appendix A from S. J. Schreiber et al., Multiscale Variation in Pollen Receipt
where the second line follows from \( p_{so} = p_{p} = 1/2 \), as seed production by a plant implementing the deterministic strategy is equally likely to be limited by pollen or seed-ovule packets owing to symmetric variation in \( Z_{i} \). It follows that \( a'_{p} \) with symmetric, stochastic variation in \( Z_{i} \) is greater than the deterministic optimum \( a_{p} \) whenever

\[
\mathbb{E}[Z_{i}|Z_{i} < 1](c_{s} + c_{o}) > c_{p}.
\] (A3)

Because \( \mathbb{E}[Z_{i}|Z_{i} < 1] < 1 \), equation (A3) may not hold when \( c_{s} + c_{o} > c_{p} \). However, if the variation in \( Z_{i} \) is sufficiently small, it will. On the other hand, \( a'_{p} \) with symmetric stochastic variation is less than the deterministic optimum whenever inequality (A3) is reversed. Because \( \mathbb{E}[Z_{i}|Z_{i} < 1] < 1 \), the reverse of inequality (A3) always holds when \( c_{p} > c_{s} + c_{o} \).

Next, consider the case of pure within-plant variability. Given \( \alpha = a_{s} \) and \( \beta = a_{o}/(1 - a) \), the fitness function is

\[
h(\alpha, \beta) = \mathbb{E} \left[ \min \{\alpha/c_{s}, \frac{1 - \alpha}{k} \sum_{i} \min \{\beta/c_{o}, (1 - \beta)Z_{i}/c_{p}\} \} \right].
\]

Therefore,

\[
\frac{\partial h}{\partial \beta}(\alpha, \beta) = \sum_{i} \frac{R}{k} \int_{x < 0} \left( \frac{|I|}{c_{o}} - \sum_{i} \frac{x_{i}}{c_{o}} \right) \rho(x) \, dx.
\]

Assume \( \alpha = c_{s}(c_{s} + c_{o} + c_{p}) \) and \( \beta = c_{o}(c_{o} + c_{p}) \), which correspond to the optimal allocation strategy for the deterministic environment. If the \( Z_{i} \) are symmetric about 1 and independent, then \( p_{z} = (1 - 0.5^{k}) \), which is approximately 1 for \( k \) large. Because \( \sum_{x < 0}(|I|/k) \rho(x) \, dx \approx 1/2 \) and \( \sum_{x < 0}(1/k) \sum_{x > 0} x_{i} \rho(x) \, dx \approx (1/2)\mathbb{E}[Z_{i}|Z_{i} < 1] \),

\[
\frac{\partial h}{\partial \beta}(\alpha, \beta) \approx \frac{R}{2} \left( 1/c_{o} - \mathbb{E}[Z_{i}|Z_{i} < 1]/c_{p} \right)
\]

for \( k \) large. Hence, stochasticity promotes larger investment in ovules than seeds whenever \( c_{p}/c_{o} > \mathbb{E}[Z_{i}|Z_{i} < 1] \).
Appendix B from S. J. Schreiber et al., “Evolutionary and Ecological Consequences of Multiscale Variation in Pollen Receipt for Seed Production”  
(Am. Nat., vol. 185, no. 1, p. E14)

Expected Number of Zygotes with Increasing Pollen Availability

In this appendix, we describe how the expected number of zygotes on a plant increases with pollen availability. Even though our model incorporates linear responses of pollen attraction and ovule production to increased resource allocations, the application of Liebig’s law and stochasticity in pollen receipt results in an emergent nonlinear saturating relation between the expected number of zygotes per flower and the mean pollen availability (fig. B1). Intuitively, the maximal variation in number of zygotes per flower occurs at intermediate pollen availability, as at low pollen availability most flowers have few zygotes and at high pollen availability nearly all ovules are fertilized on all flowers.

Figure B1: Mean number (± SD) of zygotes $E[F]$ produced per flower as a function of mean pollen availability. Parameters: $c_0 : c_p : c_s = 1 : 10 : 100$, $k = 25$ flowers, $CVP_{plant} = CV_{flower} = 0.5$. 

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Numerical Results for Alternative Allocation Cost Ratios

In this appendix, we provide numerical results for alternative cost ratios. If attraction of sufficient pollen to fertilize one ovule and development of one seed are equally expensive and individual ovules are inexpensive (e.g., $c_o : c_p : c_s = 1 : 10 : 10$), then selection favors modest overinvestment in seeds (up to 20%; fig. C1A) but a modest underinvestment in pollen (up to 25% in fig. C1A) when among-plant variability is high and within-plant variability is low. This result shows that the bundling of pollen attraction with ovule production creates unequal investments in equally “priced” commodities, which can be understood in terms of equation (7). When pollen attraction and seed development are approximately equally costly per seed, the optimal strategy is to overinvest in the resource that limits seed production for plants with the highest fitness, namely, those with high pollen receipt. These plants’ seed production is limited by seed resources, promoting overinvestment in seed resources, with the trade-off imposing reduced investment in pollen attraction.

Despite this reversal of over- and underinvestment for seeds and pollen attraction compared with the baseline parameters, overinvestment in ovules remains substantial, although not as extreme (up to 400% in fig. C1C instead of 700% in fig. 4A). Furthermore, the effects of pollination supplementation on enhanced seed production are similar to the baseline case, although with greater impact of pollen supplementation (up to 400% in fig. C2A as opposed to 200% in fig. 4E). Increased investments in developing seeds result in weaker effects of seed-resource supplementation (up to 20% in fig. C2C as opposed to 80% in fig. 4F). Reduced investments in ovules result in greater responses to ovule supplementation (up to 10% in fig. C2B as opposed to 3% in fig. 4D).

When seeds and ovules are individually inexpensive and pollen attraction is expensive (i.e., $c_o : c_p : c_s = 1 : 3 : 1$), variability in pollen availability selects for strong underinvestment in pollen attraction (up to 30% in fig. C3A), continued overinvestment in ovule production (up to 120% in fig. C3B), and over- or underinvestment in seed maturation depending on the scale of variation (from −40% to 40% in fig. C3C). Unlike our baseline case, both among- and within-plant variability contribute substantially to overinvestment in ovule production. As in the other scenarios, pollen supplementation greatly enhances seed production of plants with optimal allocations for extensive among-plant variation (up to 425% in fig. C4A). However, supplementing seed resources has virtually no effect on seed production (only up to 4% in fig. C4C), and supplementing resources for ovule production creates greater increases in seed production (up to 35% in fig. C4B) than for the other cost ratios.
Figure C1: Percent overinvestment in pollen (A), ovules (B), and seeds (C) relative to the deterministic optimal allocations in response to within- and among-plant variation in pollination. Values less than 0 correspond to underinvestment. Parameters: $c_{o} : c_{p} : c_{s} = 1 : 10 : 10$, $k = 25$ flowers.
Figure C2: Percent fitness gains due to addition of pollen (A), ovules (B), and resources for seed provisioning (C) for plants with optimal allocations given the identified within and among variability in pollination. Parameters: $c_O : c_F : c_S = 1 : 10 : 10$, $k = 25$ flowers.
Figure C3: Percent overinvestment in pollen (A), ovules (B), and seeds (C) relative to the deterministic optimal allocation. Values less than 0 correspond to underinvestment. Parameters: $c_o : c_p : c_s = 1 : 3 : 1$, $k = 25$ flowers.
Figure C4: Percent fitness gains due to addition of pollen (A), ovules (B), and resources for seed provisioning (C). Parameters: $c_o : c_p : c_s = 1 : 3 : 1$, $k = 25$ flowers.