

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

Sebastian J. Schreiber,^{1,*} Jay A. Rosenheim,² Neal W. Williams,² and Lawrence D. Harder³

1. Department of Evolution and Ecology, University of California, Davis, California, 95616; 2. Department of Entomology, University of California, Davis, California, 95616; 3. Department of Biological Sciences, University of Calgary, Calgary, Alberta T2L 0M5, Canada

Submitted July 26, 2013; Accepted May 2, 2014; Electronically published December 12, 2014

Online enhancements: appendices.

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 1993*a*, 1993*b*; 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

* Corresponding author; e-mail: sschreiber@ucdavis.edu.

Am. Nat. 2015. Vol. 185, pp. E14–E29. © 2014 by The University of Chicago. 0003-0147/2015/18501-54859\$15.00. All rights reserved.

DOI: 10.1086/678982

redistributed among a plant's flowers, variable pollination should select for floral and inflorescence traits with variance-reducing properties (Waser and Price 1984; Thomson 1986; Pettersson 1991; Richards et al. 2009) as well as specific resource allocations to pollen attraction, ovule production, and seed maturation (Burd 1995, 2008; Rosenheim et al. 2010). However, the details of these allocations are not straightforward because pollen receipt and ovule fertilization 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 (Kozłowski and Stearns 1989). Such overproduction of ovules allows flowers winning the pollen lottery to cash in, returning fitness gains that exceed the fitness costs associated with flowers that lose the pollen lottery. This expectation is supported by observations that plant species experiencing greater variation in pollen availability produce more ovules per flower (Burd et al. 2009). However, this model fails to explain why plants pollinated with a surplus of pollen typically mature <70% of ovules into seeds (Harder and Routley 2006), an observation indicating that resources for seed maturation ultimately limit seed production capacity (Stephenson 1981; Ehrlén 1992; Griffin and Barrett 2002; Shi et al. 2005). Alternatively, studies of a dichotomous trade-off between the allocations of resources to maturing seeds and attracting pollen (Burd 2008; Rosenheim et al. 2010) found that among-plant variation in pollen receipt selects for risk-averse strategies, with the optimal allocation to pollen attraction proportional to the risk of seed production being limited by pollen receipt. Paradoxically, this implies that plants selected to be more attractive to pollinators should exhibit greater pollen limitation of their seed production.

These earlier studies do not account for the modular structure of plants or the trichotomous trade-off among producing ovules, attracting pollen to fertilize ovules, and maturing fertilized ovules to seeds. To understand the ecological and evolutionary implications of these additional complexities, we introduce and analyze a model for semelparous plants accounting for multiscale variation in pollen receipt. We use this model to address three questions.

First, how do among- and within-plant variation in pollination affect optimal reproductive allocations to producing ovules, attracting pollen, and seed maturation? In particular, what scale of variation selects for overproduction 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_s , is used to develop and disperse seeds (see table 1 for a list of terms). These allocations are summarized by the allocation vector $\mathbf{a} = (a_o, a_p, a_s)$. Because all reproductive resources are used, these fractions sum to 1 ($a_o + a_p + a_s = 1$). 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 $a_o R / k c_o$ ovules. Similarly, attraction of enough pollen to ensure fertilization of one ovule, on average, costs c_p resources, so $a_p R / k c_p$ 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 $a_s R / k c_s$ 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

Table 1: Key terms of the multiscale model

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

a positive random variable, Y , with mean 1 and variance σ_Y^2 , such that

$$\bar{P} = Ya_p R/c_p k$$

(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^Y, \dots, Z_k^Y , each with mean Y . The i th flower on this plant receives sufficient pollen to fertilize

$$P_i = a_p R Z_i^Y / k c_p$$

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

$$S = \min\left\{a_s R / c_s, \sum_{i=1}^k F_i\right\} \quad (1)$$

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

$$f(\mathbf{a}) = s \mathbb{E}\left[\min\left\{a_s R / c_s, \sum_{i=1}^k F_i\right\}\right]. \quad (2)$$

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 μ is the expected fitness of an individual, σ^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 \mathbf{a} . The case of small populations will be considered elsewhere.

Analytical and Numerical Methods

We investigated the optimal allocation, $\mathbf{a}^* = (a_o^*, a_p^*, a_s^*)$, and its implications using analytic and numerical approaches. To derive analytic results, the distributions of Y and Z_i^Y need to be continuous, such as the gamma distribution. The mathematical analyses, which are presented

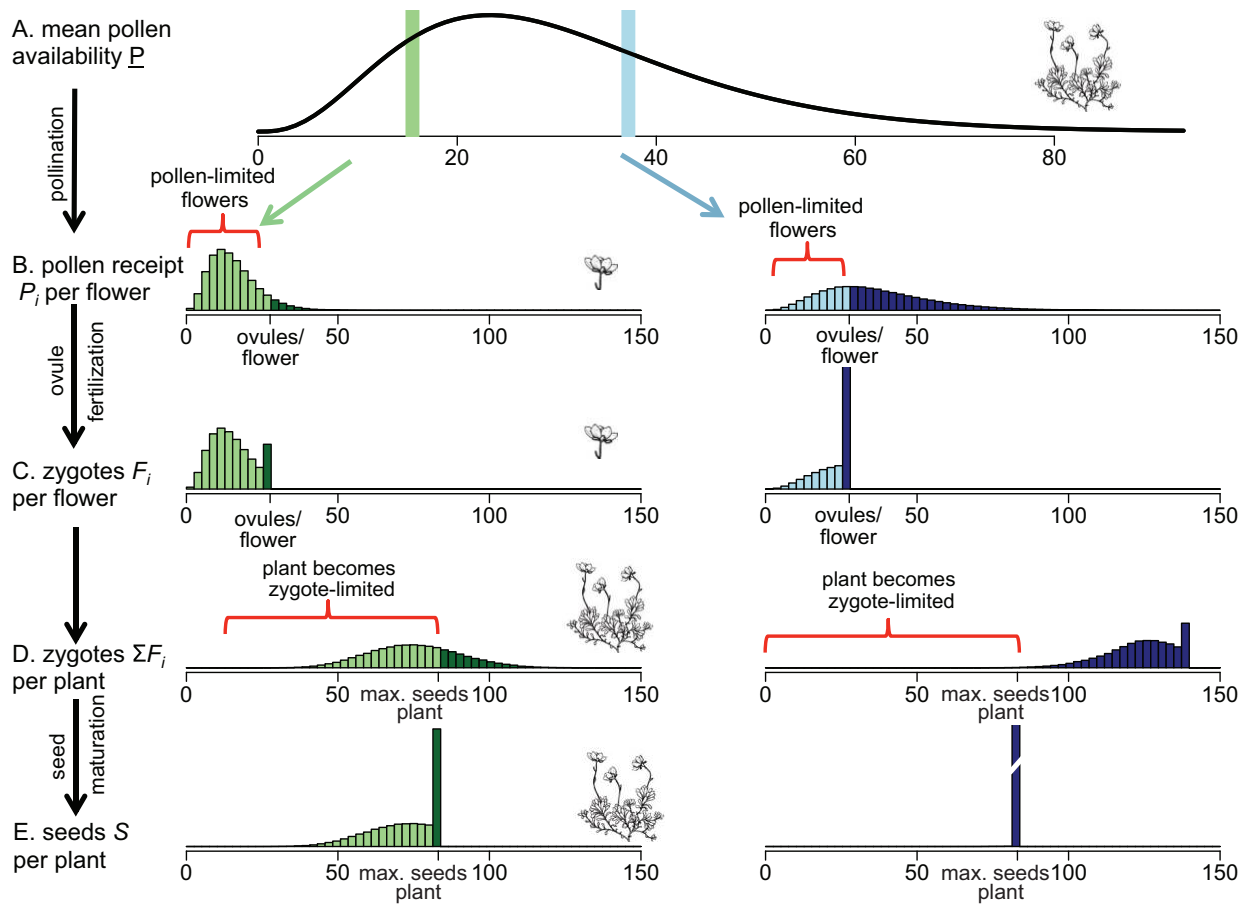


Figure 1: Model of seed production response to multiscale stochastic variation in pollen receipt. Mean pollen receipt per flower varies among individual plants according to the distribution shown in A. The green and the light blue bars represent two “draws” from the distribution of the mean pollen availability \bar{P} . 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, $c_0 : c_p : c_s = 1 : 10 : 100$, $CV_{\text{plant}} = 0.3$, $CV_{\text{flower}} = 0.45$.

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-

mentation 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 CV_{plant} . The random variables characterizing variability among flowers on a plant, Z_1^Y, \dots, Z_k^Y , are gamma distributed with mean Y and coefficient of variation CV_{flower} .

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

$$\frac{s \mathbb{E}[\min\{a_S^* R/c_S, \sum_{i=1}^k a_P^* R Z_i^Y / (c_P k)\}] - f(\mathbf{a}^*)}{f(\mathbf{a}^*)} \times 100.$$

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

$$\frac{s \min\{a_S^* R/c_S, a_O^* R/c_O\} - f(\mathbf{a}^*)}{f(\mathbf{a}^*)} \times 100.$$

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

$$\frac{s \mathbb{E}[\min\{a_O^* R/c_O, \sum_{i=1}^k a_P^* R Z_i^Y / (c_P k)\}] - f(\mathbf{a}^*)}{f(\mathbf{a}^*)} \times 100.$$

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

$$\frac{s a_O^* R/c_O - f(\mathbf{a}^*)}{f(\mathbf{a}^*)} \times 100.$$

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., $CV_{\text{flower}} = CV_{\text{plant}} = 0$). In this case, the optimal allocation causes colimitation of seed production by ovules, pollen attraction, and seed resources (fig. 2A). Specifically,

$$a_O^* R/c_O = a_P^* R/c_P = a_S^* R/c_S, \quad (3)$$

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

$$f^* = s \frac{R}{c_O + c_P + c_S}.$$

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

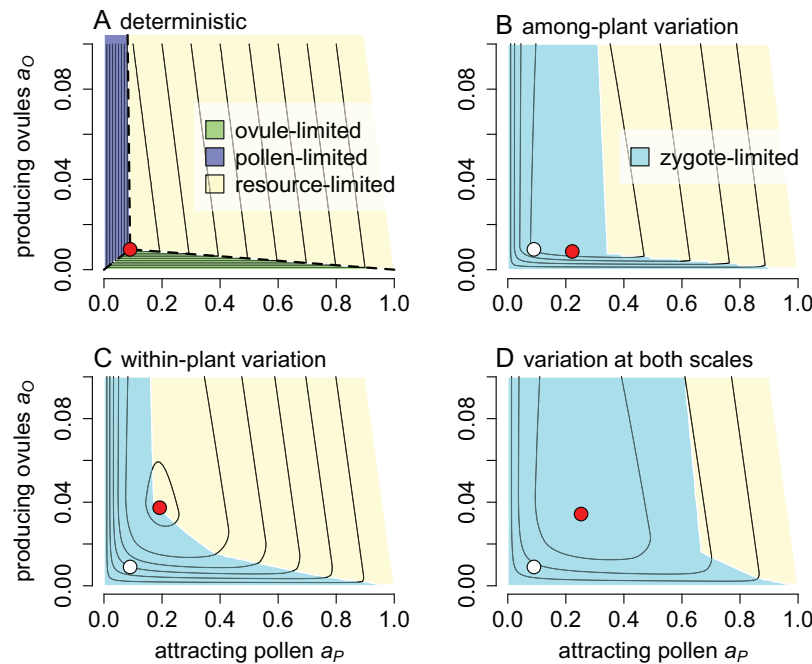


Figure 2: Optimal allocations in environments with no variation (A), only among-plant variation (B), only within-plant variation (C), and both among- and within-plant variation (D) in pollen receipt. In each panel, fitness contours at $f = 0, 1, \dots, 10$ viable seeds per plant are plotted as functions of allocations to pollen attraction a_p and ovule production a_o ; allocation to seed maturation is $a_s = 1 - a_o - a_p$. 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: $c_o : c_p : c_s = 1 : 10 : 100$; $CV_{\text{flower}} = CV_{\text{plant}} = 0$ in A; $CV_{\text{flower}} = 0, CV_{\text{plant}} = 1.6$ in B; $CV_{\text{flower}} = 2.4, CV_{\text{plant}} = 0$ in C; $CV_{\text{flower}} = 2.4, CV_{\text{plant}} = 1.6$ in D.

seeds have matured. We note that as the partial derivatives of f with respect to a_i do not exist at the optimal allocation strategy, the marginal advantage theorem (Lloyd 1988) does not apply to the deterministic case.

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 Varberg 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 ($[P \times CV_{\text{flower}}]^2$) 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

$$f(\mathbf{a}) = s \mathbb{E}[\min\{a_s R/c_s, a_o R/c_o, a_p YR/c_p\}], \quad (4)$$

with pollen, ovule, and seed terms equally coupled. As in

the deterministic case, this fitness expression and our numerical simulations indicate that the optimal allocation tends to invest more resources in the more costly reproductive functions (e.g., greatest allocation to seeds followed by pollen attraction for the baseline cost ratio $c_O : c_P : c_S = 1 : 10 : 100$ in fig. 2B). Therefore, our stochastic analysis focuses on how pollen variation selects for overinvestment in some reproductive functions relative to the optimal deterministic allocations (i.e., $a_i^* > c_i/(c_O + c_P + c_S)$ for some $i = O, P, S$) and underinvestment in the remaining reproductive functions (i.e., $a_i^* < c_i/(c_O + c_P + c_S)$ for the other i).

In the absence of within-plant variation in pollination, expected 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 ovules produced with the number of seeds that can be matured (i.e., $a_S^*/c_S = a_O^*/c_O$). 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 resources, no reallocation between ovules and seed resource can augment fitness (only increased allocation to pollen attraction would increase fitness). Such ovule-seed packaging 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,

$$\begin{aligned} a_S^* + a_O^* &= p_{SO}w_{SO}, \\ a_P^* &= p_Pw_P. \end{aligned} \quad (5)$$

Intuitively, as plants experience more uncertainty in pollen availability (i.e., p_P increases), they lower their risk of pollen limitation by increasing investment in attracting pollinators 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). Interestingly, unlike the deterministic case, stochasticity in pollen receipt "smooths" out the fitness function with respect to a_P and the joint allocation $a_{SO} = a_S + a_O$. 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

$$\mathbb{E}[Y|Y < 1](c_S + c_O) > c_P \quad (6)$$

and underinvest whenever inequality (6) is reversed. The expectation $\mathbb{E}[Y|Y < 1]$ represents the expected (normalized) pollen receipt by a plant receiving less than the 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 maturing it into a seed. For our baseline cost ratios $c_O : c_P : c_S = 1 : 10 : 100$, overinvestment in pollen attraction is always optimal, as seed development is the most expensive reproductive function (figs. 2C, 3A). Overinvesting in pollen attraction substantially increases pollen receipt and seed production for plants that occupy locations 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 optimal allocations depend on the probability of a plant's seed production being limited by zygote formation (p_Z) or seed resources (p_S). 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_S . More precisely,

$$\begin{aligned} a_O^* &= p_Zw_O, \\ a_P^* &= p_Zw_P, \\ a_S^* &= p_Sw_S, \end{aligned} \quad (7)$$

where w_O and w_P are the collective contributions of all ovule-limited or pollen-limited flowers to fitness, respectively, and w_S 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 govern the evolution of resource allocations, equation (7) implies that the risks of zygote limitation and seed-resource limitation govern these evolutionary dynamics in the presence 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 attraction (figs. 2C, 3D). Production of many cheap ovules

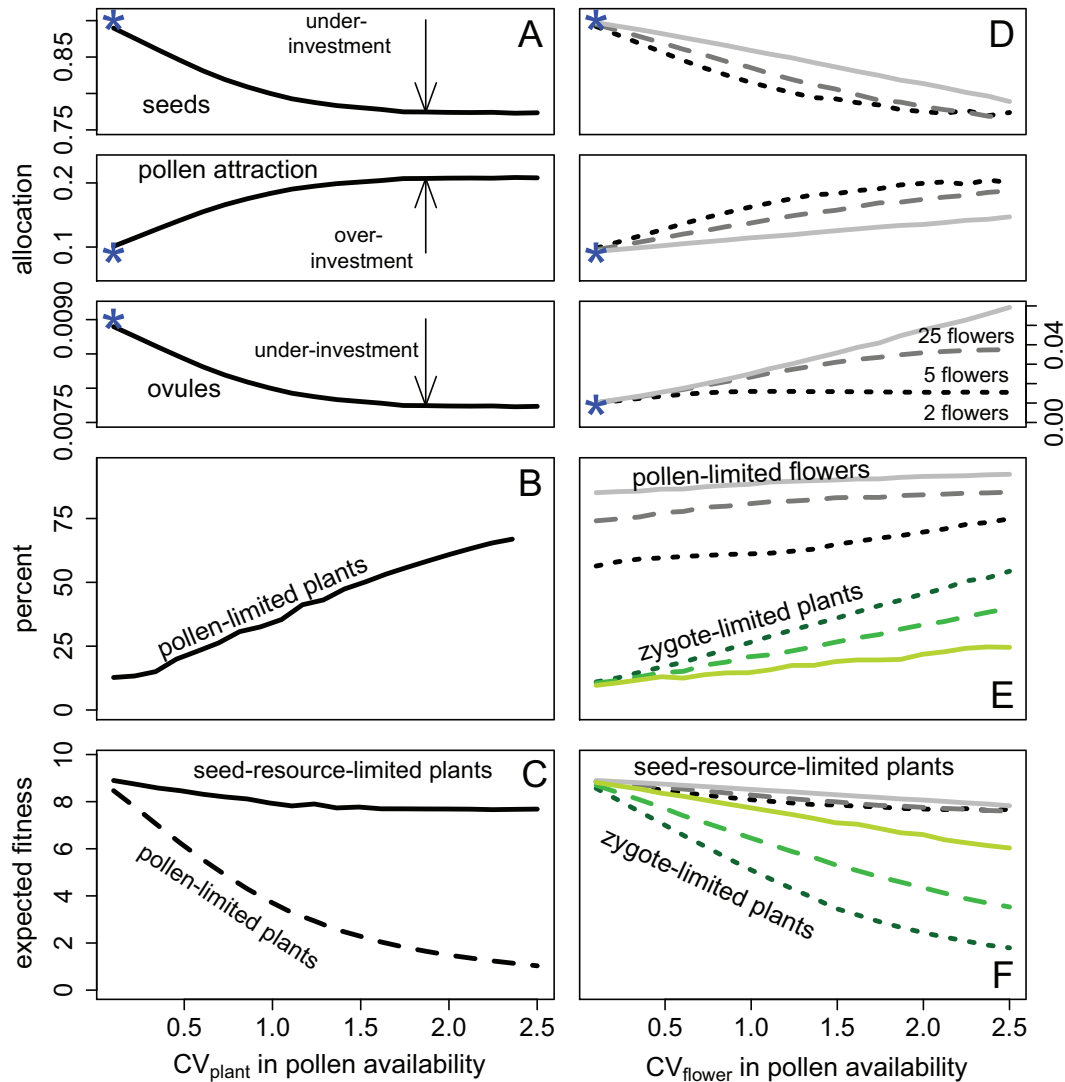


Figure 3: Impacts of among-plant variation (A–C) and within plant-variation (D–F) in pollen receipt on optimal reproductive allocations (A and D), frequencies of pollen/zygote limitation (B and E), and expected female fitness of plants conditioned on seed production being limited by either seed resources or pollen receipt (C and F). The blue asterisks in A and D correspond to the optimal allocations for the deterministic environment. In C, solid and dashed lines correspond to expected fitness conditioned on plants being limited by seed resources or pollen receipt, respectively. In D–F, solid, long-dashed, and short-dashed curves correspond to plants with 25, 5, and 2 flowers, respectively. Vertical scales on the left- and right-hand side panels are the same, except for ovules in A and D. Parameters: $c_o : c_p : c_s = 1 : 10 : 100$, $CV_{flower} = 0$ for A–C; $CV_{plant} = 0$ for D–F.

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 optimal 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 allocations (fig. 4A–4C). However, these effects saturate relatively quickly with among-plant variation, whereas there is little 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 reductions in seed-development resources (fig. 4C), with among-plant variation causing the larger reduction due to resources being diverted 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 extensive among-plant variation; within-plant variation contributes 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 variation in pollen availability.

Pollen supplementation greatly increases the number of unmaturing 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 arises because within-plant variation selects for overproduction of ovules at the expense of resources for seed maturation. As a result, supplementing these plants simultaneously 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

$$f(\mathbf{a}) = s \sum_{j=1}^n \mathbb{E} \left[\min \left\{ (a_s R/n)/c_s, \sum_{i=1}^k F_i^j \right\} \right], \quad (8)$$

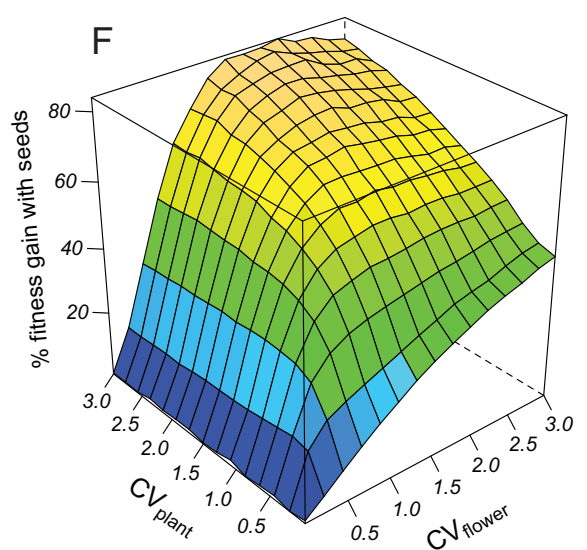
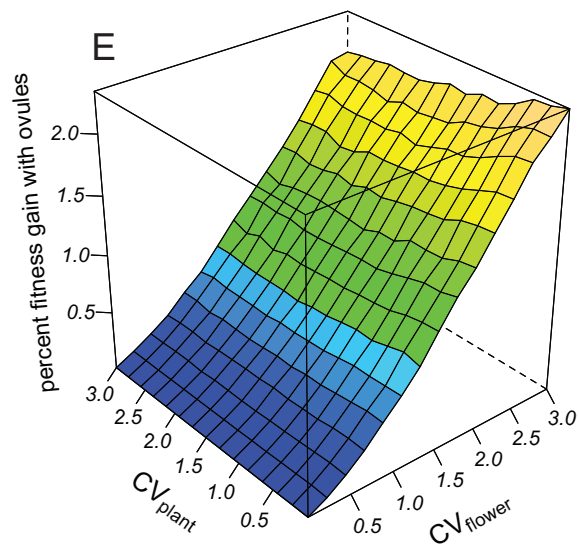
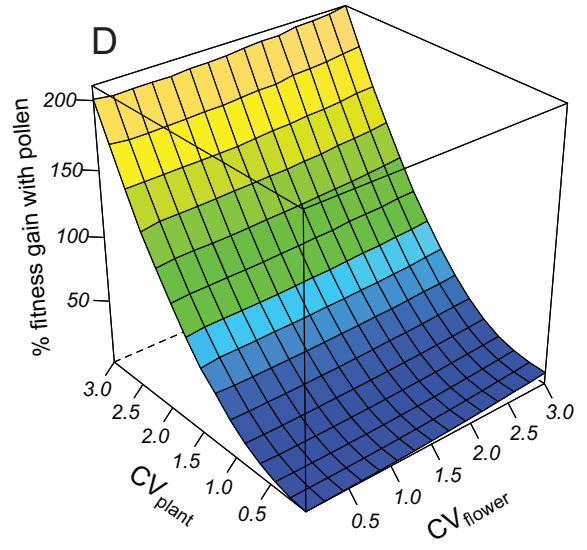
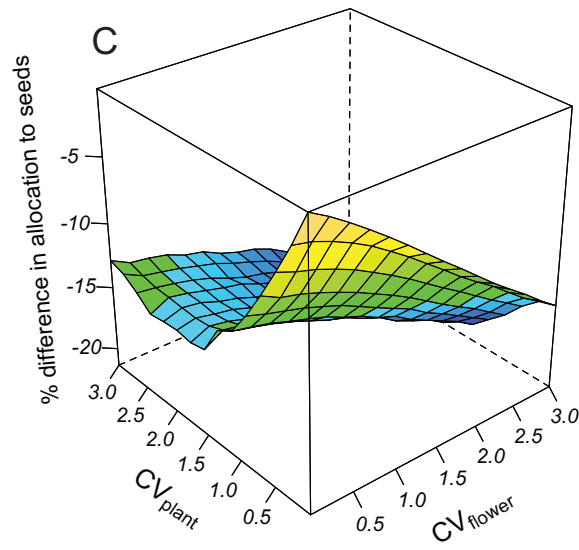
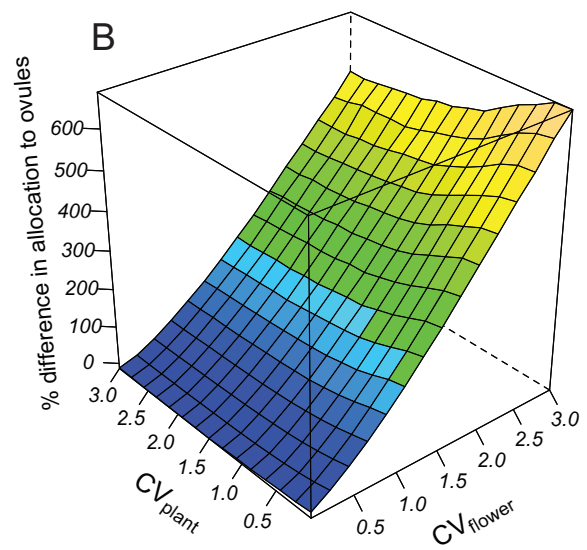
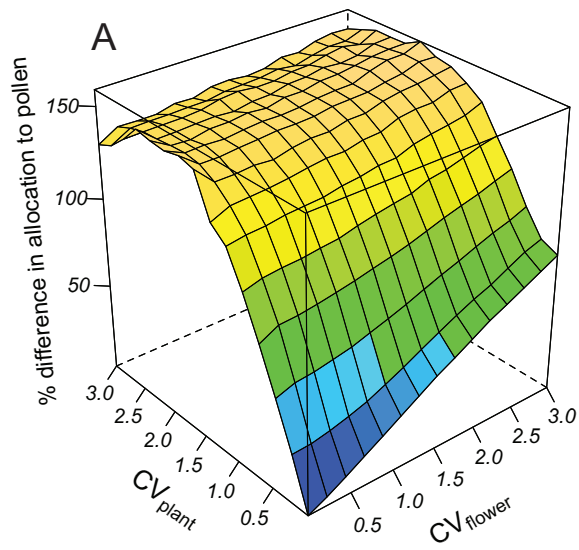
where

$$F_i^j = \min \{ a_o R/(knc_o), a_p Z_i^j R/(knc_p) \},$$

and Z_i^j are random variables accounting for variation in pollen receipt with mean 1. If the random vectors $(Z_1^1, \dots, Z_k^1), \dots, (Z_1^n, \dots, Z_k^n)$ have the same distribution, then equation (8) simplifies to the base model in equation (2), for which among-plant variation corresponds 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, \dots, I_n are independent draws from a fixed distribution determined by the plant mean, and Z_i^j, \dots, Z_k^j 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 variation 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



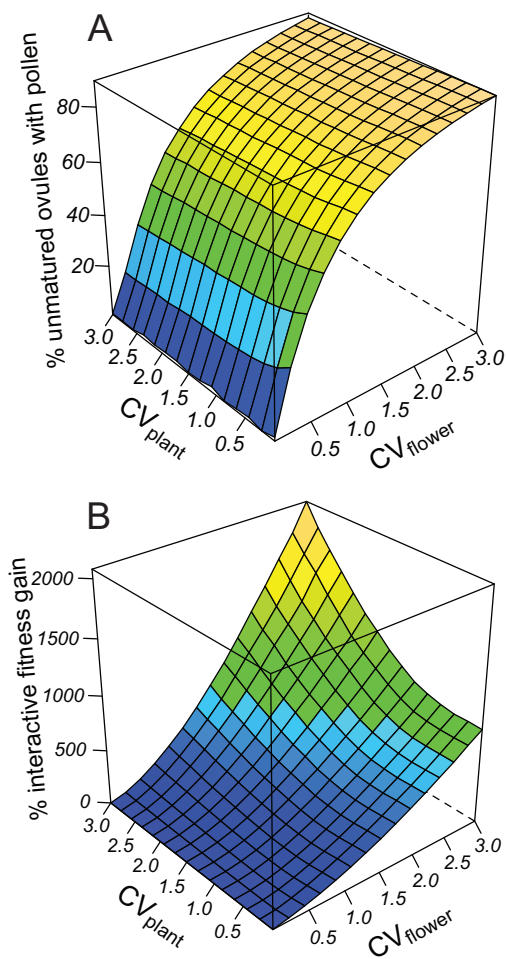


Figure 5: Resource limitation following pollen supplementation and the interactive effect of joint supplementation of pollen and seed resources on fitness. Following pollen supplementation, the fraction of unmatured zygotes increases with within-plant variation in pollen availability (A). The interactive 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: $c_o : c_p : c_s = 1 : 10 : 100$, $k = 25$ 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 CV_{flower} 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 CV_{plant} axis), which favors increased pollen attraction at the expense of seed development. Thus, Burd addressed two special cases of the

Figure 4: Comparisons of the optimal allocations to pollen attraction (A), ovule production (B), and seed development (C) for within- and among-plant variation in pollination to the deterministic expectation and the responses of optimal plants to supplementation of pollen (D), ovules (E), and seed resources (F). Parameters: $c_o : c_p : c_s = 1 : 10 : 100$, $k = 25$ flowers.

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 *Stylidium 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 Stpczyska 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 Schemske 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.

Acknowledgments

We thank two anonymous reviewers, N. Fabina, and J. Maron for many useful comments that greatly improved the quality of this work. S.J.S., N.W.W., and J.A.R. were supported in part by US National Science Foundation grant DMS-1022639. L.D.H. was supported in part by a

Discovery Grant from the Natural Sciences and Engineering Research Council of Canada.

Literature Cited

- Alonso, C., and C. M. Herrera. 1996. Variation in herbivory within and among plants of *Daphne laureola* (Thymelaeaceae): correlation with plant size and architecture. *Journal of Ecology* 84:495–502.
- Arditti, J., and A. K. A. Ghani. 2000. Numerical and physical properties of orchid seeds and their biological implications. *New Phytologist* 145:367–421.
- Avila-Sakar, G., G. A. Krupnick, and A. G. Stephenson. 2001. Growth and resource allocation in *Cucurbita pepo* ssp. *texana*: effects of fruit removal. *International Journal of Plant Sciences* 162:1089–1095.
- Boyce, M. S., C. V. Haridas, C. T. Lee, and the NCEAS Stochastic Demography Working Group. 2006. Demography in an increasingly variable world. *Trends in Ecology and Evolution* 21:141–148.
- Brock, W. H. 2002. *Justus von Liebig: the chemical gatekeeper*. Cambridge University Press, Cambridge.
- Brookes, R. H., L. K. Jesson, and M. Burd. 2008. A test of simultaneous resource and pollen limitation in *Stylidium armeria*. *New Phytologist* 179:557–565.
- Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. *Botanical Review* 60:83–139.
- . 1995. Ovule packaging in stochastic pollination and fertilization environments. *Evolution* 49:100–109.
- . 2008. The Haig-Westoby model revisited. *American Naturalist* 171:400–404.
- Burd, M., T. L. Ashman, D. R. Campbell, M. R. Dudash, M. O. Johnston, T. M. Knight, S. J. Mazer, R. J. Mitchell, J. A. Steets, and J. C. Vamosi. 2009. Ovule number per flower in a world of unpredictable pollination. *American Journal of Botany* 96:1159–1167.
- Campbell, D. R., and K. J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. *Ecology* 74:1043–1051.
- Charlesworth, D., and B. Charlesworth. 1987. Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology and Systematics* 18:237–268.
- Childs, D. Z., C. J. E. Metcalf, and M. Rees. 2010. Evolutionary bet-hedging in the real world: empirical evidence and challenges revealed by plants. *Proceedings of the Royal Society B: Biological Sciences* 277:3055–3064.
- Cohen, D., and R. Dukas. 1990. The optimal number of female flowers and the fruits-to-flowers ratio in plants under pollination and resources limitation. *American Naturalist* 135:218–241.
- Coley, P. D. 1983. Herbivory and defensive characteristics of tree species in a lowland tropical forest. *Ecological Monographs* 53:209–234.
- Dressler, R. L. 1981. *The orchids: natural history and classification*. Harvard University Press, Cambridge, MA.
- Ehrlén, J. 1992. Proximate limits to seed production in a herbaceous perennial legume, *Lathyrus vernus*. *Ecology* 73:1820–1831.
- Farrior, C. E., G. D. Tilman, R. Dybzinski, P. B. Reich, S. A. Levin, and S. W. Pacala. 2013. Resource limitation in a competitive context determines complex plant responses to experimental resource additions. *Ecology* 94:2505–2517.
- Frank, S. A. 2011. Natural selection. I. Variable environments and uncertain returns on investment. *Journal of Evolutionary Biology* 24:2299–2309.
- Frank, S. A., and M. Slatkin. 1990. Evolution in a variable environment. *American Naturalist* 136:244–260.
- Friedman, J., and S. C. H. Barrett. 2011. The evolution of ovule number and flower size in wind-pollinated plants. *American Naturalist* 177:246–257.
- Ghazoul, J. 2005. Pollen and seed dispersal among dispersed plants. *Biological Reviews* 80:413–443.
- Gillespie, J. 1973. Polymorphism in random environments. *Theoretical Population Biology* 195:193–195.
- . 1974. Natural selection for within-generation variance in offspring number. *Genetics* 76:601–606.
- Greenway, C. A., and L. D. Harder. 2007. Variation in ovule and seed size and associated size-number trade-offs in angiosperms. *American Journal of Botany* 94:840–846.
- Griffin, S. R., and S. C. H. Barrett. 2002. Factors affecting low seed : ovule ratios in a spring woodland herb, *Trillium grandiflorum*. *International Journal of Plant Sciences* 163:581–590.
- Haig, D., and M. Westoby. 1988. On limits to seed production. *American Naturalist* 131:757–759.
- Harder, L. D., and S. D. Johnson. 2005. Adaptive plasticity of floral display size in animal-pollinated plants. *Proceedings of the Royal Society B: Biological Sciences* 272:2651–2657.
- . 2008. Function and evolution of aggregated pollen in angiosperms. *International Journal of Plant Sciences* 169:59–78.
- Harder, L. D., S. A. Richards, and M. B. Routley. 2008. Effects of reproductive compensation, gamete discounting and reproductive assurance on mating-system diversity in hermaphrodites. *Evolution* 62:157–172.
- Harder, L. D., and M. B. Routley. 2006. Pollen and ovule fates and reproductive performance by flowering plants. Pages 61–80 in L. D. Harder and S. C. H. Barrett, eds. *Ecology and evolution of flowers*. Oxford University Press, Oxford.
- Herrera, C. M. 2002. Censusing natural microgametophyte populations: variable spatial mosaics and extreme fine-graininess in winter-flowering *Helleborus floetidus* (Ranunculaceae). *American Journal of Botany* 89:1570–1578.
- . 2009. *Multiplicity in unity: plant subindividual variation and interactions with animals*. University of Chicago Press, Chicago.
- Herrera, M. 2004. Distribution ecology of pollen tubes: fine-grained, labile spatial mosaics in southern Spanish Lamiaceae. *New Phytologist* 161:473–484.
- Hobbhahn, N. 2012. Correlates and consequences of repeated nectar evolution in the ancestrally rewardless orchid genus *Disa*. PhD thesis. University of Calgary.
- Hooker, H. D. 1917. Liebig's law of the minimum in relation to general biological problems. *Science* 46:197–204.
- Husband, B. C., and D. W. Schemske. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50:54–70.
- Jackson, R. B., and M. M. Caldwell. 1993a. Geostatistical patterns of soil heterogeneity around individual perennial plants. *Journal of Ecology* 81:683–692.
- . 1993b. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* 74:612–614.

- Jensen, J. L. W. V. 1906. Sur les fonctions convexes et les inégalités entre les valeurs moyennes. *Acta Mathematica* 30:175–193.
- Knight, T. M., J. A. Steets, and T. L. Ashman. 2006. A quantitative synthesis of pollen supplementation experiments highlights the contribution of resource reallocation to estimates of pollen limitation. *American Journal of Botany* 93:271–277.
- Knight, T. M., J. A. Steets, J. C. Vamosi, S. J. Mazer, M. Burd, D. R. Campbell, M. R. Dudash, M. O. Johnston, R. J. Mitchell, and T. L. Ashman. 2005. Pollen limitation of plant reproduction: pattern and process. *Annual Review of Ecology, Evolution, and Systematics* 36:467–497.
- Kozłowski, J., and S. C. Stearns. 1989. Hypotheses for the production of excess zygotes: models of bet-hedging and selective abortion. *Evolution* 43:1369–1377.
- Lau, T. C., and A. G. Stephenson. 1993. Effects of soil nitrogen on pollen production, pollen grain size, and pollen performance in *Cucurbita pepo* (Cucurbitaceae). *American Journal of Botany* 80:763–768.
- . 1994. Effects of soil phosphorus on pollen production, pollen size, pollen phosphorus content, and the ability to sire seeds in *Cucurbita pepo* (Cucurbitaceae). *Sexual Plant Reproduction* 7:215–220.
- Levin, D. A., and B. L. Turner. 1977. Clutch size in the Compositae. Pages 215–222 in B. Stonehouse and C. Perrin, eds. *Evolutionary ecology*. University Park Press, Baltimore, MD.
- Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences of the USA* 62:1056–1060.
- Lloyd, D. G. 1988. A general principle for the allocation of limited resources. *Evolutionary Ecology* 2:175–187.
- Mattila, E., and M. T. Kuitunen. 2000. Nutrient versus pollination limitation in *Platanthera bifolia* and *Dactylorhiza incarnata* (Orchidaceae). *Oikos* 89:360–366.
- May, R. M. 1978. Clutch size in plants. *Nature* 276:671–672.
- Micheneau, C., S. D. Johnson, and M. F. Fay. 2009. Orchid pollination: from Darwin to the present day. *Botanical Journal of the Linnean Society* 161:1–19.
- Neiland, M. R. M., and C. C. Wilcock. 1998. Fruit set, nectar reward, and rarity in the Orchidaceae. *American Journal of Botany* 85:1657–1671.
- Nepi, M., and M. Stpiczyska. 2007. Nectar resorption and translocation in *Cucurbita pepo* L. and *Platanthera chlorantha* Custer (Rchb.). *Plant Biology* 9:93–100.
- Pettersson, M. W. 1991. Pollination by a guild of fluctuating moth populations: option for unspecialization in *Silene vulgaris*. *Journal of Ecology* 79:591–604.
- Preston, K. A., and D. D. Ackerly. 2004. Allometry and evolution in modular organisms. Pages 80–106 in M. Pigliucci and K. A. Preston, eds. *Modularity and phenotypic complexity*. Oxford University Press, Oxford.
- Real, L. A., and S. Ellner. 1992. Life history evolution in stochastic environments: a graphical mean-variance approach. *Ecology* 73:1227–1236.
- Richards, S. A., N. M. Williams, and L. D. Harder. 2009. Variation in pollination: causes and consequences for plant reproduction. *American Naturalist* 174:382–398.
- Roberts, A. W., and D. E. Varberg. 1973. *Convex functions*. Academic Press, New York.
- Rosenheim, J. A., U. Alon, and G. Shinar. 2010. Evolutionary balancing of fitness-limiting factors. *American Naturalist* 175:662–674.
- Rosenheim, J. A., N. M. Williams, and S. J. Schreiber. 2014. Parental optimism versus parental pessimism in plants: how common should we expect pollen limitation to be? *American Naturalist* 184:75–90.
- Shi, X. J., H. J. Michaels, and R. J. Mitchell. 2005. Effects of self-pollination and maternal resources on reproduction and offspring performance in the wild lupine, *Lupinus perennis* (Fabaceae). *Sexual Plant Reproduction* 18:55–64.
- Stebbins, G. L. 1974. *Flowering plants: evolution above the species level*. Belknap, Cambridge, MA.
- Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253–279.
- Suzuki, N. 2000. Pollinator limitation and resource limitation of seed production in the scotch broom, *Cytisus scoparius* (Leguminosae). *Plant Species Biology* 15:187–193.
- Thomson, J. D. 1986. Pollen transport and deposition by bumble bees in *Erythronium*: influences of floral nectar and bee grooming. *Journal of Ecology* 74:329–341.
- Tremblay, R. L., J. D. Ackerman, J. K. Zimmerman, and R. N. Calvo. 2005. Variation in sexual reproduction in orchids and its evolutionary consequences: a spasmodic journey to diversification. *Biological Journal of the Linnean Society* 84:1–54.
- Tuljapurkar, S. 1990. *Population dynamics in variable environments*. Springer, Berlin.
- Vaughton, G. 1991. Variation between years in pollen and nutrient limitation of fruit-set in *Banksia spinulosa*. *Journal of Ecology* 79:389–400.
- Waites, A. R., and J. Agren. 2004. Pollinator visitation, stigmatic pollen loads and among-population variation in seed set in *Lythrum salicaria*. *Journal of Ecology* 92:512–526.
- Waser, N. M., and M. V. Price. 1984. Experimental studies of pollen carryover: effects of floral variability in *Ipomopsis aggregata*. *Oecologia* (Berlin) 62:262–268.
- Wesselingh, R. A. 2007. Pollen limitation meets resource allocation: towards a comprehensive methodology. *New Phytologist* 174:26–37.
- White, J. 1979. The plant as a metapopulation. *Annual Review of Ecology and Systematics* 10:109–145.
- Wirth, M., and C. L. Withner. 1959. Embryology and development in the Orchidaceae. Pages 155–188 in C. L. Withner, ed. *The orchids: a scientific survey*. Ronald, New York.
- Yang, C. F., S. G. Sun, and Y. H. Guo. 2005. Resource limitation and pollen source (self and outcross) affecting seed production in two louseworts, *Pedicularis siphonantha* and *P. longiflora* (Orobanchaceae). *Botanical Journal of the Linnean Society* 147:83–89.
- Zimmerman, M., and G. H. Pyke. 1988. Reproduction in *Polemonium*: assessing the factors limiting seed set. *American Naturalist* 131:723–738.

Associate Editor: John L. Maron

Editor: Susan Kalisz