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SELF-FERTILIZATION AND THE ESCAPE FROM POLLEN LIMITATION IN VARIABLE POLLINATION ENVIRONMENTS

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Abstract.—Seed production in many plants is pollen limited, likely because of unpredictable variation in the pollinator environment. One way for plants to escape the consequences of pollinator variability is to evolve mating systems, such as autonomous selfing, that assure reproduction without relying on pollinators. We explore this hypothesis through the construction and analysis of heuristic models of plant population dynamics in seed- or site-limited populations. Our analysis suggests several important points: the familiar rule that inbreeding depression greater than 0.5 maintains outcrossing significantly underestimates the threshold required under pollen limited conditions with prior selfing; variability in the pollination environment erodes the ability of inbreeding depression to maintain outcrossing; and variable pollination environments can result in stable intermediate rates of prior selfing. The results reflect the importance of geometric mean fitness (which in a variable environment is less than the arithmetic mean) in the face of temporal variation.

Key words.—Environmental stochasticity, inbreeding depression, pollen limitation, reproductive assurance, self-fertilization.

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Inadequate pollination is often invoked as a stimulus for the evolution of self-fertilization to provide reproductive assurance (Baker 1955, 1967; Stebbins 1974; Jain 1976; Richards 1986). Indeed, many studies suggest that inadequate pollination is the rule rather than the exception (Young and Young 1992; Burd 1994; Larson and Barrett 2000). A variety of factors may contribute to pollen limitation, but particularly prominent is the possibility that plants produce excess ovules or flowers as a bet-hedging strategy to maximize reproductive success during years of abundant pollination (reviewed in Ashman et al. 2004). Theoretical studies recognize that some forms of self-fertilization offer reproductive assurance (e.g., Lloyd 1979; Schoen and Brown 1991; Lloyd and Schoen 1992; Cheptou 2004), but none explicitly investigate how variation in the pollination environment selects for selfing.

Here we present a simple ecological context for investigating population dynamics in temporally variable environments. We then incorporate the selection of self-fertilization into this framework. Our analysis leads to important conclusions about the threshold inbreeding depression required to maintain outcrossing and the role of variability in facilitating the evolution of selfing and promoting stable mixed mating systems.

MODEL DEVELOPMENT

Population Dynamics and Regulation

To formulate our models of population regulation, we assume that individuals occupy a habitat with K sites, where each site contains zero or one individual (Table 1 lists variables and parameters). At time t , individuals of type i occupy $N_i(t)$ sites, and $E(t) = K - \sum_j N_j(t)$ sites are empty. We assume discrete time periods. A fraction $1 - \mu$ of each of the $N_i(t)$ individuals die following reproduction but prior to seed recruitment, so there are

$$E'(t) = E(t) + \mu \sum_j N_j(t) \quad (1)$$

empty sites available for new individuals. Each individual of type i produces $R_i(t)$ seeds, so the density of seeds per site is $\sum_j N_j(t)R_j(t)/K$. Assuming seeds occupy sites following a Poisson process, the probability of empty sites receiving at least one seed is $1 - \exp[-\sum_j N_j(t)R_j(t)/K]$. The fraction of empty sites newly occupied by type i is proportional to the representation of the type in the seed pool, $N_i(t)R_i(t)/\sum_j N_j(t)R_j(t)$. The change in number of individuals of type i over a single time period is then

$$\frac{N_i(t+1)}{N_i(t)} = 1 - \mu + E'(t) \left\{ 1 - \exp \left[- \sum_j \frac{N_j(t)R_j(t)}{K} \right] \right\} \times \frac{R_i(t)}{\sum_j N_j(t)R_j(t)} \quad (2)$$

We focus on two scenarios, characterized as seed-limited and site-limited population growth. Seed-limited growth occurs when most sites are empty, so $E'(t) \approx E(t) \approx K$, and the number of seeds produced is small compared to the number of sites, $\sum_j N_j(t)R_j(t)/K \ll 1$. The probability of empty sites receiving at least one seed is $1 - \exp[-\sum_j N_j(t)R_j(t)/K] \approx \sum_j N_j(t)R_j(t)/K$ and the growth rate of the i th type is

$$\frac{N_i(t+1)}{N_i(t)} = 1 - \mu + R_i(t) \quad (3)$$

Site-limited growth occurs when nearly all sites are occupied prior to mortality, so that $E(t) \approx 0$, $E'(t) \approx \mu \sum_j N_j(t)$ and there are many more seeds produced than sites, $\sum_j N_j(t)R_j(t)/K \gg 1$. Thus $1 - \exp[-\sum_j N_j(t)R_j(t)/K] \approx 1$ and the change in number of individuals of type i over a single time period is

TABLE 1. Parameters, variables, and additional notation in the pollination model, with biologically plausible values as indicated.

Variables, type i		
b_i	Prior selfing fraction	$0 \leq b_i \leq 1$
c_i	Competing selfing fraction	$0 \leq c_i \leq 1$
d_i	Delayed selfing fraction	$0 \leq d_i \leq 1$
Parameters		
$\bar{\pi}$	Average pollination fraction	$0 \leq \bar{\pi} \leq 1$
$\text{Var}(\pi)$	Variance in pollination fraction	$0 \leq \text{Var}(\pi) \leq \bar{\pi}(1 - \bar{\pi})$
w_s	Relative selfed seed fitness	$0 \leq w_s \leq 1$
μ	Mortality rate	$0 < \mu \leq 1$
Additional notation, type i at time t		
K	Total sites in the habitat	$0 < K$
$N_i(t)$	Number of individuals	$0 < N_i(t) \leq K$
$E(t), E'(t)$	Unoccupied sites	See text
$\pi(t)$	Pollination fraction	$0 \leq \pi(t) \leq 1$
$\lambda_i(t)$	Growth rate	$0 \leq \lambda_i(t)$
λ_{G_i}	Expected long-term growth rate	$0 \leq \lambda_{G_i}$
F	Per capita ovule production	$0 \leq F$
$R_i(t)$	Per capita seed production	$0 \leq R_i(t)$
$S_i(t)$	Per capita selfed seed fraction	$0 \leq S_i(t) \leq 1$
$T_i(t)$	Per capita outcrossed seed fraction	$0 \leq T_i(t) \leq 1 - S_i(t)$

$$\begin{aligned} \frac{N_i(t+1)}{N_i(t)} &= 1 - \mu + \mu \frac{R_i(t)}{\sum_j N_j(t)R_j(t) / \sum_j N_j} \\ &= 1 - \mu + \mu \frac{R_i(t)}{\bar{R}(t)}, \end{aligned} \tag{4}$$

where $\bar{R}(t)$ is the average seed production in the population at time t .

The change in number of individuals of type i after T time periods, with either seed or site limitation, is

$$\lambda_{G_i}^T = \frac{N_i(T+1)}{N_i(1)} = \prod_{t=1}^T \lambda_i(t), \tag{5}$$

where λ_{G_i} is the per capita geometric average growth rate and

$$\ln \lambda_{G_i} = \frac{1}{T} \sum_{t=1}^T \ln \lambda_i(t) = \langle \ln \lambda_i(t) \rangle. \tag{6}$$

The angle brackets denote expected value.

Evolutionary and Convergence Stable Strategies

In ecological models λ_{G_i} is familiar as the long-term population growth rate of the i th species. Here we treat λ_{G_i} as the long-term growth rate of the i th genotype. We then equate long-term growth rate with genotype fitness and use evolutionarily stable strategy (ESS; Maynard Smith 1976) criteria to identify reproductive strategies that maximize fitness.

Suppose that a particular life-history parameter x_0 predominates in a population, with resulting per capita growth rate λ_{G_0} . A rare variant is introduced, with life-history parameter $x_i \approx x_0$ and corresponding per capita growth rate (when rare) λ_{G_i} . The effect of the life-history variant on growth rate is then approximately

$$\left\langle \frac{d \ln \lambda_i(t)}{dx_i} \Big|_{x_i=x_0} \right\rangle. \tag{7}$$

The quantity in equation (7) represents the selection differ-

ential (see Morgan and Schoen 1997); new life-history strategies x_i increase in frequency when equation (7) is greater than zero. The life-history strategy \hat{x} is evolutionarily stable when

$$\left\langle \frac{d \ln \lambda_i(t)}{dx_i} \Big|_{x_i=x_0=\hat{x}} \right\rangle = 0 \tag{8}$$

and the second derivative evaluated at \hat{x} is less than zero,

$$\left\langle \frac{d^2 \ln \lambda_i(t)}{dx_i^2} \Big|_{x_i=x_0=\hat{x}} \right\rangle < 0. \tag{9}$$

The life-history strategy \hat{x} is convergence stable (i.e., populations with strategy x_0 different from the ESS can be invaded by types x_i closer to the ESS; e.g., Geritz et al. 1998) when

$$\left\langle \left[\frac{d^2 \ln \lambda_i(t)}{dx_i^2} + \frac{d^2 \ln \lambda_i(t)}{dx_0 dx_i} \right] \Big|_{x_i=x_0=\hat{x}} \right\rangle < 0. \tag{10}$$

Mating System Evolution

At the individual level, per capita seed production $R_i(t)$ depends on the number of ovules produced F_i , the fraction of these that are fertilized through selfing $S_i(t)$ and outcrossing $T_i(t)$, and the relative fitness of selfed progeny w_s :

$$R_i(t) = F_i[S_i(t)w_s + T_i(t)]. \tag{11}$$

Lloyd (1979) and Lloyd and Schoen (1992) recognized several modes of self-fertilization. Prior selfing occurs at rate b_i before any opportunities for outcrossing. Competing selfing (facilitated selfing in Lloyd and Schoen 1992) occurs at rate c_i during pollinator visits (occurring with probability $\pi(t)$) and only involves ovules that have not been fertilized through prior selfing. Delayed selfing occurs at rate d_i , after opportunities for prior or competing mating. Outcrossing involves ovules that are neither prior nor competing self-fertilized but rely on pollinator visits, $(1 - b_i)(1 - c_i)\pi(t)$. An assumption is that competing matings are linearly related to pollinator

visits $\pi(t)$. The components of reproductive success associated with mating strategy i are then:

$$S_i(t) = b_i + (1 - b_i)\{c_i\pi(t) + [1 - \pi(t)]d_i\} \quad \text{and} \quad (12a)$$

$$T_i(t) = (1 - b_i)(1 - c_i)\pi(t). \quad (12b)$$

Note that $S_i(t) + T_i(t)$ does not necessarily add to one; this occurs when not all ovules are fertilized. Variation in the pollination environment $\pi(t)$ influences the fraction of ovules self-fertilized through competing selfing and remaining for delayed selfing; it also influences the fraction of outcrossed ovules. The pollination fraction $\pi(t)$ can range between zero and one with a maximum variance $\text{Var}(\pi)$ equal to $\bar{\pi}(1 - \bar{\pi})$ when the pollination fraction is equal to one at some time periods and zero at others.

At the genetic level, our focus is on the fitness of rare individuals adopting reproductive strategy i in a population of individuals adopting an alternative strategy 0. Letting $M_i(t)$ represent pollen produced and exported at time t , the fitness of the i th individual is

$$R_i(t) = F_i S_i(t) w_s + \frac{1}{2} \left[F_i T_i(t) + F_0 T_0(t) \frac{M_i(t)}{M_0(t)} \right]. \quad (13)$$

The equation weights outcrossed reproduction by a factor of 1/2, because only half the genes in outcrossed seeds are inherited from each parent. The term $F_i T_i(t)$ represents outcrossed seeds produced by the i th individual. The term $F_0 T_0(t) M_i(t) / M_0(t)$ represents the rate the i th individual fertilizes ovules available for outcrossing (i.e., male outcross fertility); if there are $N_0 \gg 1$ individuals of type 0 and one individual of type i in the population, the fraction of available ovules fertilized by the i th type is $N_0 F_0 T_0(t) \{M_i(t) / [N_0 M_0(t) + M_i(t)]\} \approx F_0 T_0(t) [M_i(t) / M_0(t)]$. In the analyses that follow, we assume that there are no differences between types in ovule production, $F_i = F_0 = F$, and pollen production and export, $M_i = M_0 = M$. This assumption might be violated if, for instance, selfing strategies simultaneously influence reproductive allocation to male versus female function or if pollen discounting is a function of selfing rate.

Evaluating the selection of self-fertilization involves placing expressions (12a, b) and (13) into equations (7–10). Details of the analysis are presented in the Appendix.

RESULTS

Prior Selfing

A rich set of outcomes is possible when prior selfing occurs in seed-limited populations. From the selection differential for this scenario, equation (A4), an individual with some prior selfing can increase in frequency in an initially outcrossing population ($b = 0$) when

$$w_s - \frac{\bar{\pi}}{2} + \frac{1 - \mu + 2w_s}{2[1 - \mu(1 - \bar{\pi})]^2} \text{Var}(\pi) > 0. \quad (14a)$$

In contrast, invasion of a prior selfing population ($b = 1$) occurs when

$$w_s - \frac{\bar{\pi}}{2} < 0. \quad (14b)$$

In the absence of variation in pollen receipt, $\text{Var}(\pi) = 0$,

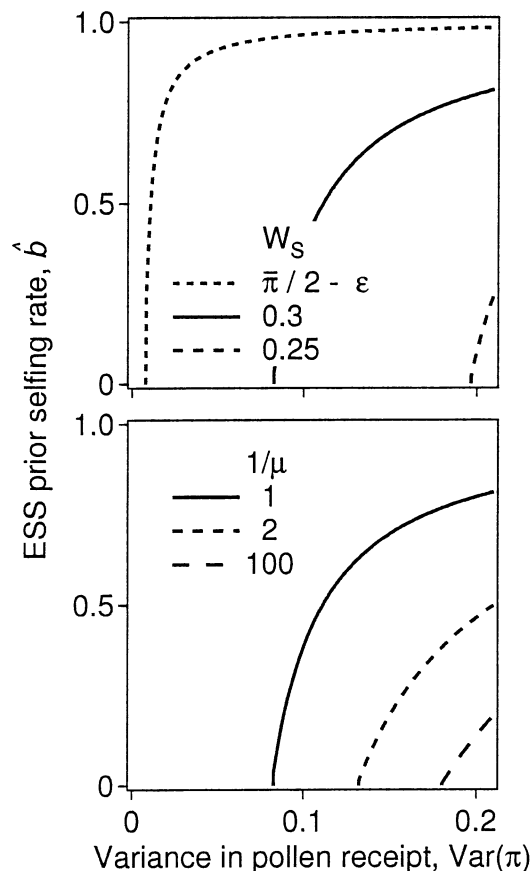


FIG. 1. Evolutionarily stable intermediate selfing rates \hat{b} under prior self-fertilization and seed-limited population regulation. Upper panel: effects of relative fitness of selfed progeny w_s in annuals $\mu = 1$; the upper line has $\epsilon = 0.005$, so that selfed fitness is just below that for prior selfing to be always advantageous. Lower panel: consequences of expected longevity $1/\mu$ with fitness of selfed progeny $w_s = 0.3$. Calculations assume average pollen receipt $\bar{\pi} = 0.7$; the maximum variance in pollen receipt $\text{Var}(\pi)$ is $\bar{\pi}(1 - \bar{\pi}) = 0.21$, and ovule production measured on a scale such that $F = 1$.

there is a threshold selfed fitness $w_s = \bar{\pi}/2$ below which outcrossing is always advantageous. Since average pollen receipt $\bar{\pi}$ is often considerably less than 100%, prior selfing can be favored even when the fitness of selfed progeny is considerably less than one-half that of outcrossed progeny. Variation in the pollination environment $\text{Var}(\pi) > 0$ allows condition (14a) to be satisfied more easily, so that variable pollination environments further erode the ability of outcrossing populations to resist invasion by prior selfing variants. Furthermore, $\text{Var}(\pi) > 0$ can allow both equations (14a) and (14b) to be simultaneously satisfied. This suggests that there is an intermediate ESS prior selfing rate, a result confirmed in equations (A4–A7). Figure 1 presents numerical examples illustrating the ESS. ESS prior selfing rates occur over a range of parameter values. Greater variation in pollen receipt results in higher prior selfing rates. Lower fitness of selfed progeny w_s increases the amount of variation required for prior selfing variants to spread and reduces the ESS prior selfing rate compared to higher selfed fitness. Perenniality ($\mu < 1$) increases the amount of variation required for initial

increase of prior selfing variants and reduces the sensitivity of the ESS to the amount of variation in pollen receipt.

Analysis in appendix equations (A8–A11) shows that prior selfing variants increase in an initially outcrossing site-limited population when $w_s < \bar{\pi}/2$, variation in the pollination environment erodes the ability of outcrossers to resist invasion by prior selfing types, and intermediate ESS prior selfing rates are possible. However, the site-limited ESS is independent of mortality μ and, in fact, equals the ESS under seed-limited regulation in annuals.

Competing and Delayed Selfing

As shown in the appendix, selection favors competing self-fertilization when $w_s > 1/2$ and outcrossing when $w_s < 1/2$, independent of variation in pollination environment or mode of population regulation. These results are the same as those in Lloyd (1979) and do not permit an intermediate stable selfing rate. Likewise, delayed selfing is always favored regardless of variation in pollination environment or population regulation. Variation in pollination environment does, however, influence the strength of selection for delayed selfing. As in models of delayed selfing without variation in pollen environment, some delayed selfing results in a mixture of selfed and outcrossed progeny whenever $0 < \bar{\pi} < 1$.

DISCUSSION

Our results show that variable pollination environments can have important consequences for the selection and evolution of prior self-fertilization but not for competing or delayed selfing. In a constant pollination environment, when $\text{Var}(\pi) = 0$, prior selfing invades outcrossing populations when $w_s > \bar{\pi}/2$. Since pollen limitation studies suggest that the fraction of ovules fertilized is only $\approx 70\%$ of that observed with supplemental pollination (Ashman et al. 2004), the threshold selfed fitness below which outcrossing is favored is likely to be 0.3 or less. This inbreeding depression ($1 - w_s = 0.7$) is considerably larger than the 0.5 commonly invoked as sufficient to maintain outcrossing; Holsinger (1991) notes that pollen discounting and mass-action selfing influence the threshold inbreeding depression and the maintenance of outcrossing. Variation in the pollination environment erodes the ability of outcrossing populations to resist the spread of prior selfing variants. Other important conclusions are that evolutionarily stable prior selfing rates are possible, and perenniality makes the evolution of prior selfing more difficult in seed-limited reproduction (Fig. 1).

Lloyd (1979) and Lloyd and Schoen (1992) recognized that prior and delayed selfing provide reproductive assurance but did not investigate variation in the pollination environment. Pannell and Barrett (1998) explicitly modeled consequences of population and metapopulation (extinction-recolonization) dynamics for reproductive assurance and the evolution of self-fertilization. Their study suggests that reproductive assurance selects for self-fertilization in newly established populations, with changes in population density generating the shift from conditions where selfing is favored (low density) to those where outcrossing is favored (high density). Our results show that reproductive assurance selects for self-fertilization over much broader conditions, even in site-limited

populations with strong inbreeding depression. In addition, our results rely on variation in pollinator visitation, rather than population growth, to maintain intermediate prior selfing rates. Reproductive assurance has been invoked for other breeding system shifts, especially the evolution of androdioecy (Pannell 2002; also Wolf and Takebayashi 2004). These studies have assumed metapopulation dynamics, but our results suggest that similar arguments apply in large populations experiencing fluctuations in the pollination environment.

A common observation is that annuals self-fertilize more than perennials (Stebbins 1974; Barrett et al. 1996). Our results are superficially consistent with this explanation, because variable pollination environments are less effective at establishing prior selfing in perennial than annual populations of seed-limited populations (Fig. 1). In addition, our model does not include differences in life history as individuals age (e.g., greater size, survivorship, or reproductive allocation) and does not allow for resource re-allocation following pollination failure (e.g., to growth in subsequent years). These factors likely reduce the range of parameters leading to stable intermediate prior selfing rates in perennials by lessening the variability in lifetime fitness (this suggestion requires investigation with explicit models). However, the annual habit may plausibly be associated with colonizing species with seed-limited reproductive success, but many perennials, especially trees, are likely to occupy site-limited habitats. In these conditions, life history μ influences the strength of selection on prior selfing (eq. A8) but never the sign of selection, and hence it does not have an influence when prior selfing is advantageous. The reason for this is because life history changes the fraction of the population replaced each generation without altering the between-individual competition for offspring establishment.

The mathematical mechanism responsible for the results obtained here is illustrated by a simple graph showing that the logarithm of the relative fitness advantage of prior self-fertilization decreases at a slower rate as the pollination fraction increases (Fig. 2). The logarithm of relative fitness transforms geometric population increase into a more intuitive additive scale. Because of the decelerating shape of the curve, decreasing the pollination fraction by a fixed amount (e.g., from 0.5 to 0.2 in Fig. 2) increases fitness of selfers relative to outcrossers more than increasing the pollination fraction by the same amount (e.g., from 0.5 to 0.8) decreases fitness. Keeping the average pollination fraction constant while increasing the variance therefore increases average relative fitness. This relationship, known as Jensen's inequality, drives results of many models of bet-hedging and temporal variation in selection, including models for the evolution of stable mixed mating systems due to temporal changes in inbreeding depression (Cheptou and Mathias 2001; Cheptou and Dieckmann 2002; Cheptou and Schoen 2002), reduced selection for delayed selfing in the presence of size-number trade-offs (Sakai and Ishii 1999), overproduction of ovules in variable pollination environments (Burd 1995; Sakai 1996), and mating advantages of hermaphroditism compared with dioecy (Wilson and Harder 2003). Proulx (2000) noted that many aspects of sexual reproduction are likely to exhibit conditions appropriate for this relationship in variable environments,

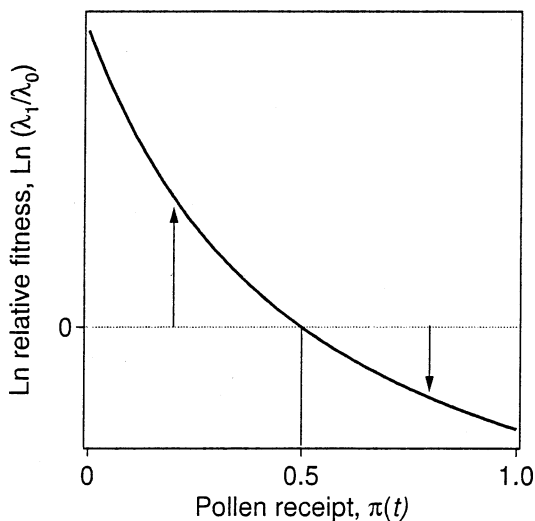


FIG. 2. The advantage to prior selfing, illustrating Jensen's inequality. When pollen receipt $\pi(t)$ is constant and equal to 0.5, a variant increasing the prior selfing rate to $b_1 = 0.1$ in an initially outcrossing population with $w_s = 0.25$, $\mu = 0.5$ is selectively neutral, as indicated by the natural logarithm of relative fitness equal to zero. If pollen receipt varies between $\pi(t) = 0.2$ and $\pi(t) = 0.8$ with equal frequency, the average pollen receipt $\bar{\pi} = 0.5$ remains unchanged but the fitness benefits of increased selfing at low pollen receipt (up arrow) outweigh the fitness costs at high pollen receipt (down arrow); the prior selfing variant increases in frequency.

especially when male and female fitness components respond differently to the pollination environment (e.g., because of differences in male and female gain curves, sensu Morgan and Schoen 1997). A variety of stable intermediate reproductive strategies, such as for life-history allocation (Zhang and Jiang 1997; Zhang 2000), sex allocation (Proulx 2000), or cleistogamy (Schoen and Lloyd 1984; Masuda et al. 2001), may then be expected.

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APPENDIX

We illustrate the analysis of the ESS criteria, equations (7–10), for prior selfing (b_i) and site-limited growth in the absence of competing or delayed selfing ($c_i = d_i = 0$; $i \in \{0, 1\}$). The expression for per capita fitness, from equations (3) and (13), is

$$\lambda_i(t) = (1 - \mu) + F \left\{ b_i w_s + \frac{1}{2} [(1 - b_i) + (1 - b_0)] \pi(t) \right\}, \quad (\text{A1})$$

and the derivative of the logarithm of the expected long-term growth rate of an initially rare variant, equation (7), is

$$\left\langle \frac{d \ln \lambda_i(t)}{db_i} \right\rangle_{b_i=b_0=b} = \left\langle \frac{w_s - \pi(t)/2}{1 - \mu + F[bw_s + (1 - b)\pi(t)]} F \right\rangle. \quad (\text{A2})$$

To evaluate this expectation, we write $\pi(t) = \pi + \delta(t)$. We then perform a second-order Taylor series expansion about $\bar{\pi}$. Each term in the expectation has the form

$$\frac{w_s - \bar{\pi}/2}{B} F - \frac{1 - \mu + F(2 - b)w_s}{2B^2} \left[F\delta(t) - \frac{1 - b}{B} F^2 \delta^2(t) \right] + O[\delta^3(t)], \quad (\text{A3})$$

where $B = 1 - \mu + F(bw_s + (1 - b)\bar{\pi})$. Taking expectations across terms, with the substitutions $\bar{\delta} = 0$, $\text{Var}(\delta) = \text{Var}(\pi)$ results in the selection differential defined by equation (7):

$$\frac{w_s - \bar{\pi}/2}{B} F + \frac{(1 - b)[1 - \mu + F(2 - b)w_s]}{2B^3} F^2 \text{Var}(\pi). \quad (\text{A4})$$

In this expression, $\bar{\pi}$ and $\text{Var}(\pi)$ are the expected value and variance of pollen receipt, respectively. Note that the coefficient on $\text{Var}(\pi)$ is always positive, so that variation in the pollination environment facilitates the evolution of prior selfing. An approximate candidate ESS solution is found by setting equation (A4) to zero and solving for $b = \hat{b}$,

$$\begin{aligned} & \{ -(1 - \mu + F\bar{\pi})(w_s - \bar{\pi}/2)(w_s - \bar{\pi}) + Fw_s \text{Var}(\pi)/2 \\ & + (1 - \mu + Fw_s)[\text{Var}(\pi) - \sqrt{R_b}/4] \} \\ & \div \{ F[(w_s - \bar{\pi}/2)(w_s - \bar{\pi})^2 + w_s \text{Var}(\pi)/2] \}, \end{aligned} \quad (\text{A5})$$

where $R_b = \text{Var}(\pi)[\text{Var}(\pi) - 16(w_s - \bar{\pi}/2)^2]$. Evolutionary and convergence stability conditions, equations (9) and (10), are

$$\frac{(w_s - \bar{\pi}/2)^2}{B^2} F^2 > 0 \quad \text{and} \quad (\text{A6})$$

$$\frac{(w_s - \bar{\pi}/2)(w_s - \bar{\pi})}{B^2} F^2 > 0. \quad (\text{A7})$$

From these equations, values of $0 < \hat{b} < 1$ will always be an ESS and are convergence stable when $w_s < \bar{\pi}/2$ (values of $w_s > \bar{\pi}$ also satisfy the convergence stability condition but result in $\hat{b} > 1$).

Analysis of site-limited regulation depends on interpretation of equation (4) when the invading type i is rare, so that population average seed production is approximately the seed production of the common type $\bar{R}(t) \approx R_0(t)$. Under prior selfing and space-limited regulation, the selection differential is then

$$\mu \left\{ \frac{w_s - \bar{\pi}/2}{bw_s + (1 - b)\bar{\pi}} + \frac{(1 - b)(2 - b)w_s}{2[bw_s + (1 - b)\bar{\pi}]^3} \text{Var}(\pi) \right\}. \quad (\text{A8})$$

Candidates for the ESS are then

$$\hat{b} \approx \frac{-\bar{\pi}(w_s - \bar{\pi}/2)(w_s - \bar{\pi}) + 3w_s \text{Var}(\pi)/4 - w_s \sqrt{R_b}/4}{(w_s - \bar{\pi}/2)(w_s - \bar{\pi})^2 + w_s \text{Var}(\pi)/2}. \quad (\text{A9})$$

Note that the solutions \hat{b} do not depend on life history, μ . Evolutionary and convergence stability conditions are

$$\frac{(w_s - \bar{\pi}/2)^2}{[bw_s + (1 - b)\bar{\pi}]^2} > 0 \quad \text{and} \quad (\text{A10})$$

$$\frac{(w_s - \bar{\pi}/2)(w_s - \bar{\pi})}{[bw_s + (1 - b)\bar{\pi}]^2} > 0. \quad (\text{A11})$$

As with seed-limited regulation, values of $0 < \hat{b} < 1$ will always be an ESS and are convergence stable when $w_s < \bar{\pi}/2$.

For competing selfing and seed-limited regulation, the selection differential at any time t , that is, each term in equation (7), is

$$\left(w_s - \frac{1}{2} \right) \frac{\pi(t)}{1 - \mu + F(1 - c + cw_s)\pi(t)}. \quad (\text{A12})$$

Since the sign of this expression is independent of $\pi(t)$, it follows that the sign of the long-term average selection differential is also independent of the mean or variance in pollination environment. Thus self-fertilization is always favored when $w_s > 1/2$, and outcrossing always favored when $w_s < 1/2$. Competing selfing with site-limited regulation has selection differential (eq. 7):

$$\mu \frac{w_s - 1/2}{1 - c + cw_s}. \quad (\text{A13})$$

Selection favors outcrossing when $w_s < 1/2$ and selfing when $w_s > 1/2$; there is no opportunity for $0 < \hat{c} < 1$.

Delayed selfing with seed-limited regulation has selection differential

$$\frac{w_s F}{D} \left[(1 - \bar{\pi}) + \frac{F(1 - dw_s)(1 - \mu + F)}{D^2} \text{Var}(\pi) \right], \quad (\text{A14})$$

where $D = 1 - \mu + F(\bar{\pi} + (1 - \bar{\pi})dw_s)$. This differential is always positive and increases with $\text{Var}(\pi)$, so variation in the pollination fraction increases the strength of selection for delayed selfing. The selection differential with delayed selfing under site-limited regulation is:

$$\frac{\mu w_s}{\bar{\pi} + (1 - \bar{\pi})dw_s} \left\{ (1 - \bar{\pi}) + \frac{1 - dw_s}{[\bar{\pi} + (1 - \bar{\pi})dw_s]^2} \text{Var}(\pi) \right\}. \quad (\text{A15})$$

Again, this expression is always positive, and variation in the pollination environment increases the strength of selection for delayed self-fertilization.