

Plant Population Dynamics, Pollinator Foraging, and the Selection of Self-Fertilization

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ABSTRACT: Many flowering plants rely on pollinators, self-fertilization, or both for reproduction. We model the consequences of these features for plant population dynamics and mating system evolution. Our mating systems–based population dynamics model includes an Allee effect. This often leads to an extinction threshold, defined as a density below which population densities decrease. Reliance on generalist pollinators who primarily visit higher density plant species increases the extinction threshold, whereas autonomous modes of selfing decrease and can eliminate the threshold. Generalist pollinators visiting higher density plant species coupled with autonomous selfing may introduce an effect where populations decreasing in density below the extinction threshold may nonetheless persist through selfing. The extinction threshold and selfing at low density result in populations where individuals adopting a single reproductive strategy exhibit mating systems that depend on population density. The ecological and evolutionary analyses provide a mechanism where prior selfing evolves even though inbreeding depression is greater than one-half. Simultaneous consideration of ecological and evolutionary dynamics confirms unusual features (e.g., evolution into extinction or abrupt increases in population density) implicit in our separate consideration of ecological and evolutionary scenarios. Our analysis has consequences for understanding pollen limitation, reproductive assurance, and the evolution of mating systems.

Keywords: Allee effect, pollen limitation, bistability, population persistence, pollinator behavior, mixed mating system.

Plants in small or low-density populations can experience decreased pollinator visits, increased pollen limitation, and

decreased seed production (Aizen and Feinsinger 1994; Groom 1998; Hendrix and Kyhl 2000; Jacquemyn et al. 2002; Knight 2003). Such a decrease in per capita reproductive rate with decreasing population density is referred to as an Allee effect (Allee et al. 1949; Stephens et al. 1999; Dennis 2002). In plants, Allee effects might occur because of reduced density or quality of compatible mates (e.g., Agren and Ericson 1996; Ashih and Wilson 2001; Wolf and Harrison 2001) or scarcity of pollinators (e.g., Mustajarvi et al. 2001; Forsyth 2003). Many plants appear to be pollen limited (recently synthesized in Ashman et al. 2004), and more than 90% of all angiosperms rely on animal pollinators for pollen transfer (Buchmann and Nabhan 1996). For these reasons, Allee effects are likely to be particularly important in many animal-pollinated plants (Kunin 1997a; Knight 2003).

Pollinator behavior and self-fertilization influence Allee effects. Generalist pollinators may preferentially visit common plant species (Waser 1983). Pollinators may also spend more time foraging on many flowers of a single plant when plant density is low, increasing the proportion of ovules fertilized by self-pollen (geitonogamy; Ghazoul et al. 1998; Franceschinelli and Bawa 2000; Mustajarvi et al. 2001). In the presence of inbreeding depression, such pollinator-mediated selfing reduces plant population growth rates and exacerbates Allee effects. Few theoretical studies address generalized plant-pollinator systems (Ingvarsson and Lundberg 1995; Lundberg and Ingvarsson 1998; Feldman et al. 2004); most focus on mutualist interactions between plants and their obligate or specialist pollinators (e.g., Holland et al. 2002, 2004; Bronstein et al. 2003). The possibility of Allee effects with generalist pollinators, and in general the dynamics of multispecies mutualisms (Stanton 2003), remains unexplored.

Autonomous selfing offers an important way for plants to alleviate Allee effects (Lennartsson 2002) and plays a role in many scenarios of plant population dynamics (e.g., during colonization [Baker 1967] or metapopulation persistence of hermaphrodites [Pannell 1997b; Taylor et al. 1999]). Recent studies include population processes (e.g., providing an advantage to hermaphroditism in spatially

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structured populations [Wilson and Harder 2003] or selfing in metapopulations [Pannell 1997a; Pannell and Barrett 1998, 2001]). Yet evolutionary models of selfing (e.g., Lloyd 1979; Lloyd and Schoen 1992) do not explicitly include population dynamics and often only implicitly include pollinators. We know of no models that explicitly consider how trade-offs between outcrossing and selfing influence population dynamics and the Allee effects.

Here we ask how pollinator behavior and trade-offs between outcrossing and self-fertilization affect plant population dynamics and mating system (production of selfed versus outcrossed offspring) evolution. Our first step is to circumscribe Allee effects. We then develop an ecological model including selfing and inbreeding depression and the interaction between plants and their pollinators. The model is extended to allow for the evolution of plant selfing rates. We show how mating system and pollinator attributes influence the following: equilibrium plant population densities, presence and severity of Allee effects, opportunities for populations falling below the critical density required for pollinator visitation to persist through self-fertilization, consequences of plant and pollinator attributes for pollen limitation of plant reproduction, and evolution of selfing in density-regulated populations. Our results clarify how pollination, density-dependent population recruitment, and mortality contribute to plant population decline and how self-fertilization can ameliorate Allee effects.

Methods

Terminology

Several distinct concepts are often described as Allee effects (Stephens and Sutherland 1999; Dennis 2002; also Allee 1931). We use Allee effect to refer to the situation when, at low plant densities, per capita reproductive rates increase with density (fig. 1, *heavy line*). In our model, the increase in reproductive rate occurs when the frequency of pollinator visits increases. Although phrased in terms of population density, Allee effects can also be interpreted in terms of population numbers (e.g., when the area of a population is fixed, changes in density imply changes in number). The density-independent mortality shown in figure 1 is a simplifying assumption that allows us to focus on consequences of reproductive strategy. An extinction threshold occurs at the population density below which mortality exceeds recruitment, and population density decreases deterministically to 0 (fig. 1, *open circle*). It is possible for an Allee effect to occur without implying an extinction threshold (mortality μ_2 ; fig. 1). Extinction thresholds and increasing population growth rate at low densities may arise in other scenarios (e.g., involving

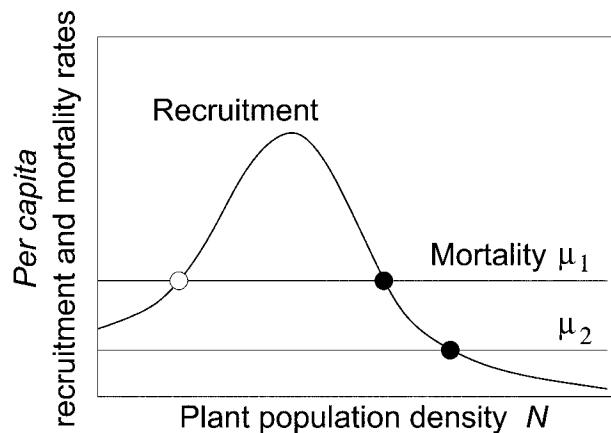


Figure 1: Concepts associated with the Allee effect include increasing recruitment at low density (*heavy line*) and an extinction threshold when mortality exceeds recruitment (*open circle*). Nonzero recruitment at low density (e.g., due to self-fertilization) and low mortality μ_2 result in an Allee effect without an extinction threshold.

density-dependent mortality), but these are not considered here.

Ecological Model Structure

Our model of plant population dynamics follows the density N of diploid plants and is described in per capita terms as

$$\frac{1}{N} \frac{dN}{dt} = \theta(S(N)w_s + T(N))R(N) - \mu \quad (1)$$

(variables and parameters are summarized in table 1). Plants produce ovules at rate θ . These are fertilized with probability $S(N)$ through selfing and $T(N)$ through outcrossing. Inbreeding depression reduces selfed seed production to an amount w_s relative to outcrossed seed production. Seeds are recruited into the population according to the function $R(N)$, which we model with a simple exponential function:

$$R(N) = e^{-N}. \quad (2a)$$

Recruitment is then a monotonically decreasing function of adult density; more realistic models (e.g., with stronger regulation of recruitment as seed production increases) would exaggerate the negative relationship between plant density and recruitment. All successfully recruited individuals experience density-independent mortality at rate μ . Equation (1) includes inbreeding depression prior to density-dependent recruitment but can be modified to allow inbreeding depression throughout the life history.

Table 1: Variables, summary functions, and parameters (and their default values) in the ecological model

	Symbol	Default value
Variables:		
Plant density	N	
Summary functions (per capita):		
Density-dependent population recruitment	$R(N)$	
Self, outcross seed maturation	$S(N), T(N)$	
Pollinator-mediated selfing	$g(N)$	
Pollination fraction	$V(N)$	
Pollinator foraging choice	$\phi(N)$	
Parameters:		
Mortality rate	μ	.1
Ovules production rate	θ	1
Prior selfing fraction	b	0
Pollinator-mediated selfing:		
Fraction (maximum)	g_0	0
Exponent	γ	0
Delayed selfing fraction	d	0
Selfed seed fitness	w_s	.6
Pollinator:		
Density	P	1
Switching density ⁻¹	ρ	1
Switching exponent	β	1

Self-fertilization and outcrossing are formulated to incorporate the major features of reproduction outlined by Lloyd (1979) and are summarized in equations (2b) and (2c):

$$S(N) = b + (1 - b)[V(N)g(N) + (1 - V(N))d], \quad (2b)$$

$$T(N) = (1 - b)V(N)(1 - g(N)). \quad (2c)$$

Ovules experience “prior” selfing (i.e., autonomous selfing occurring before pollinator visits) with probability b . Floral visitors arrive to pollinate the remaining $1 - b$ ovules with probability $V(N)$, which depends on pollinator density P and on pollinator foraging choice to include these plants in their diet $\phi(N)$. Floral visits are assumed to saturate as pollinator visits increase, as might occur if plant and pollinator encounters follow a Poisson process:

$$V(N) = 1 - e^{-\phi(N)P}. \quad (2d)$$

This “diminishing gains” relationship between plant or pollinator density and pollinator visitation probability might arise with imperfect floral constancy and consequent interspecific pollen transfer (e.g., Rathcke 1983); it is implied by limited pollen carryover curves (Harder and Thomson 1989). Pollinator foraging choice $\phi(N)$ reflects a strategy that depends on plant density:

$$\phi(N) = \frac{(\rho N)^\beta}{1 + (\rho N)^\beta}. \quad (2e)$$

Pollinator foraging choices that depend on plant density are often observed (e.g., Schiller et al. 2000; Castillo et al. 2002; Steven et al. 2003) and are expected under optimal foraging theory (e.g., Stephens and Krebs 1986). The parameters $\rho > 0$, $\beta \geq 1$ describe how pollinator foraging choice changes with plant density. We refer to $1/\rho$ as the switching density and to β as the switching exponent. Increasing ρ results in a higher plant population density required for pollinators to switch to include plants in their diet. Mathematically, the value of $1/\rho$ is the population density at which pollinator foraging choice results in visits to one-half of the plants encountered. Values of $\beta > 1$ make switching to include a plant in a pollinator diet (and hence visitation to the plant) an increasingly steplike function of plant density; very large values of β correspond to a threshold decision to include a resource in an optimal foraging diet (fig. 2).

Incoming pollen results in pollinator-mediated (e.g., geitonogamous or facilitated) selfing with probability $g(N)$. Increasing plant density (in addition to other factors such as reward structure) is likely to decrease the probability of geitonogamy. This decrease occurs because a flower visited at random by the pollinator is less likely to belong to the plant just visited by the pollinator and because optimal foraging considerations such as travel time

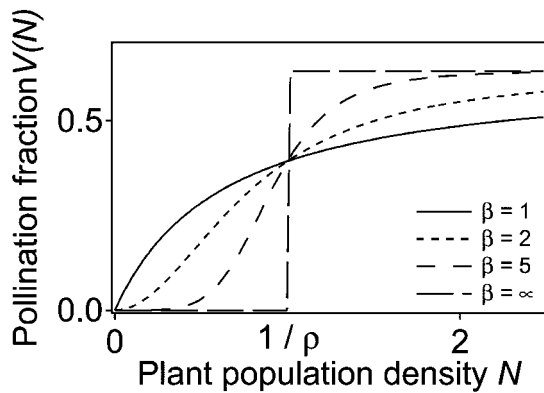


Figure 2: Relationship between population density N and pollination fraction $V(N)$. The intersection of the curves is determined by the switching density $1/\rho$ ($\rho = 1/3$ in the figure) corresponding to the density at which pollinators visit one-half of the plants they encounter. Pollinators exhibit increasingly abrupt switching with larger values of the exponent β .

(Stephens and Krebs 1986) are likely to encourage more frequent between-plant movement at higher plant density. Pollinator-mediated selfing is thus modeled as

$$g(N) = g_0 e^{-\gamma N}, \tag{2f}$$

where γ describes how pollinator-mediated selfing decreases with density and g_0 is the amount of pollinator-mediated selfing occurring even in very small populations. “Delayed” selfing occurs with probability d after pollinator visits. A combination of incomplete fertilization through outcrossing $V(N) < 1$ and partial prior and delayed selfing ($b, d < 1$) results in pollen limitation, because under these circumstances, a fraction $(1 - b)(1 - V(N))(1 - d) > 0$ of the θ ovules remains unfertilized.

Initial analysis of equation (1) involved numerical and graphical exploration to identify patterns of population dynamics. Major patterns are summarized in figure 3, as discussed below. The influence of model parameters on equilibrium results was determined by differentiating equation (1) with respect to model parameters.

Evolutionary Model Structure

Most model parameters are likely subject to evolutionary modification by natural selection on either the plant or pollinator. We explore the outcome of selection using the evolutionarily stable strategy (ESS; Maynard Smith 1976) and convergence stability (e.g., Geritz et al. 1998) criteria. To simplify initial analysis, we follow Geritz et al. (1998) and assume that ecological processes occur on a fast time-scale relative to evolutionary changes so that populations

are at their ecological equilibrium. Equation (1) closely approximates individual fitness but does not account for differences in the numbers of genes transmitted through selfing versus outcrossing. A modified equation correctly accounting for gene transmission, following Lloyd (1979), measures the fitness contribution of a rare individual adopting reproductive strategy i relative to the fitness contribution of common individuals adopting strategy 0:

$$\tilde{W}_i = \left[\theta_i S_i(N) w_i + \frac{1}{2} \left(\theta_i F_i(N) + \theta_0 F_0(N) \frac{M_i(N)}{M_0(N)} \right) \right] R(N) - \mu_i. \tag{3}$$

This equation allows selfing $S_i(N)$ to vary with the reproductive strategy (e.g., probability of selfing $b_i, g_i(N), d_i$). The outcrossing fraction $T_i(N)$ is expanded to account for the female $F_i(N)$ and male $M_i(N)$ pathways for transmitting genes to the next generation. The equation weights outcrossed seed production by a factor of one-half, because only one-half of the genes in outcrossed individuals are inherited from each parent. The term $F_i(N) = (1 - b_i)(1 - g_i(N))V_i(N)$ represents the probability that ovules available for outcrossing are fertilized (i.e., female outcross fertility). The term $F_0(N)M_i(N)/M_0(N)$ represents the probability an individual fertilizes ovules available for outcrossing (i.e., male outcross fertility). Here we set the function $M_i(N) = V_i(N)$. The evolutionarily stable strategy occurs when rare variants with reproductive strategy deviating slightly from the common strategy cannot increase in frequency. Mathematically, this translates into the conditions that

$$\left. \frac{d\tilde{W}_i}{dx_i} \right|_{N_i \approx 0, N_0 = N^*, x_i \approx x_0} = 0, \tag{4a}$$

$$\left. \frac{d^2\tilde{W}_i}{dx_i^2} \right|_{N_i \approx 0, N_0 = N^*, x_i \approx x_0} < 0, \tag{4b}$$

where x_i is any model parameter, $N_i \approx 0$ indicates rarity of type i , and N^* is the population dynamic equilibrium density. An additional condition, convergence stability, ensures that populations near the equilibrium identified by equation (4a) evolve toward it (Geritz et al. 1998). Directional selection occurs when equation (4a) cannot be satisfied; for example, selection always favors increasing values of a parameter x when the left-hand side of equation (4a) is positive for all values of x_0 .

Simultaneous Ecological and Evolutionary Dynamics

The evolutionary analysis conducted above assumes that populations are at ecological equilibrium. We explore re-

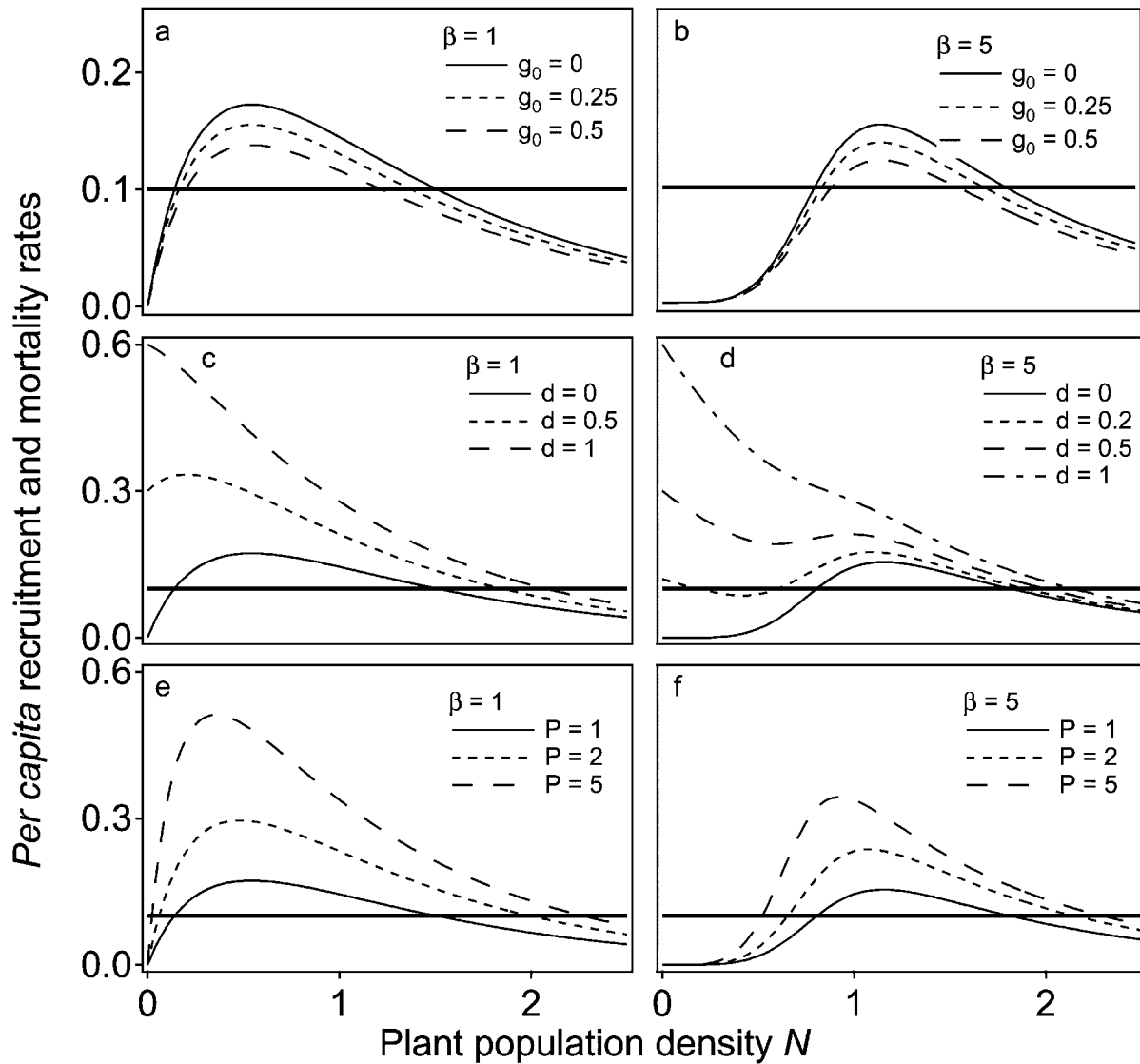


Figure 3: Influence of major model components on plant ecological dynamics (seed production and pollinator density scaled to 1, $\theta = P = 1$, and with density-independent mortality $\mu = 0.1$; the X -axis represents density, rather than absolute number, of plants; the scale on the Y -axis is directly proportional to seed production, θ). In each panel, the light solid line corresponds to random mating ($p = g_0 = d = 0$), with pollinator switching density $1/\rho = 1$; the heavy horizontal line represents density-independent mortality. *Top*, increasing pollinator-mediated selfing. *Middle*, increasing autonomous (delayed) selfing. *Bottom*, increasing pollinator density. *Left*, weaker pollinator switching exponents $\beta = 1$. *Right*, stronger pollinator switching exponents $\beta = 5$.

laxing this assumption by numerically integrating simultaneous equations for ecological and evolutionary change. This requires an explicit genetic model of parameter change. We assume a single genetic locus with two alleles, A_0 , A_1 . Alleles at the locus influence a single parameter (from those in table 1) and act such that the heterozygote has phenotype intermediate between the two homozygotes. We label A_0A_0 , A_0A_1 , and A_1A_1 as genotypes 1, 2, and 3, respectively.

Let N_i be the density of individuals of genotype i , with total density $N = \sum_i N_i$. Each genotype j produces offspring of genotype i in different proportions, depending on mating system parameters of the genotype, giving

$$\frac{dN_i}{dt} = \sum_j \theta_j N_j (S_{ij}(N) w_s + T_{ij}(N)) R(N) - \mu_i N_i. \quad (5)$$

The function $S_{ij}(N) = S_j(N) s_{ij}$ represents the likelihood

that genotype j produces a seed of genotype i through selfing. The expression $S_j(N)$ is the selfing probability function for genotype j , similar to $S(N)$ in equation (2b), while s_{ij} is the genetic probability that genotype j , when selfed, produces offspring of genotype i . Likewise, $T_{ij}(N) = T_j(N)t_{ij}(N)$ represents the likelihood that genotype j produces a seed of genotype i through random mating. Function $T_j(N)$ is the genotype-specific outcrossing probability similar to $T(N)$ in equation (2c). The probability t_{ij} is the genetic probability that genotype j , when outcrossed, produces offspring of genotype i ; t_{ij} depends on pollen allele frequency and hence genotypic densities in the population. The genetic transmission probabilities are

$$s_{ij} = \begin{bmatrix} 1 & 1/4 & 0 \\ 0 & 1/2 & 0 \\ 0 & 1/4 & 1 \end{bmatrix},$$

$$t_{ij} = \begin{bmatrix} p & p/2 & 0 \\ q & 1/2 & p \\ 0 & q/2 & q \end{bmatrix},$$

where the frequency of the A_0 allele in the pollen pool is $p = (N_0 + N_1/2)/N = 1 - q$.

We track changes in genotype frequency by numerically integrating equation (5). Populations start with frequencies 0.95, 0.05, 0 for genotypes $i = 1, 2, 3$, respectively.

Results

Ecological Structure

Key ecological features of the model are shown in figure 3. Per capita birth and mortality rates are shown as a function of plant population density; equilibria occur when per capita birth curves intersect the constant mortality line. Plants reproduce solely with the aid of pollinators in figure 3a and 3b. In many cases, there are two equilibria. The lower equilibrium is unstable: perturbations decreasing population densities result in extinction, whereas positive perturbations result in populations increasing to the upper equilibrium. The positive relationship between density and recruitment in the vicinity of this lower unstable equilibrium represents an Allee effect; that the unstable equilibrium occurs at positive density N means that there is an extinction threshold. Extinction occurs because, at low population densities, pollinator foraging choice $\phi(N)$ and consequently the fraction of flowers pollinated $V(N)$ are insufficient to offset mortality μ . The upper equilibrium is stable and occurs when decreasing gains in pollinator foraging choice and fraction of flowers pollinated, coupled with increasingly strong density-dependent recruitment $R(N)$, balance. Greater pollinator switching exponents (e.g., $\beta = 5$; fig. 3b) exacerbate the

extinction threshold while only moderately enhancing the stable equilibrium density.

Pollinator-mediated selfing does not change the qualitative dynamics of the model described in the previous paragraph. For instance, the solid line in figure 3a corresponds to random mating ($\gamma = 0$, $g_0 = 0$), whereas dashed curves represent increasing fractions of density-independent pollinator-mediated selfing (i.e., $\gamma = 0$, $g_0 = 0.25, 0.5$). As with random mating, pollinator-mediated selfing results in an Allee effect and an extinction threshold at low density and a single stable equilibrium at high density. Quantitatively, pollinator-mediated selfing (slightly) increases the extinction threshold while decreasing the upper equilibrium density. Both effects reflect inbreeding depression: pollinator-mediated selfing requires pollinator visits and hence is not likely to enhance birth rates (i.e., reproductive assurance; Lloyd and Schoen 1992), while inbreeding depression following selfing decreases per capita birth rates at all densities. Effects of pollinator-mediated selfing are similar when pollinators have switching exponent $\beta = 5$ (fig. 3b).

Autonomous selfing can qualitatively change model dynamics (fig. 3c, 3d). Particularly important is the possibility that autonomous selfing eliminates the extinction threshold. This occurs because autonomous selfing reduces plant reliance on pollinators, so per capita births remain above density-independent mortality even at low plant population density, providing reproductive assurance. The extinction threshold associated with the Allee effect is removed when

$$\left. \frac{1}{N} \frac{dN}{dt} \right|_{N \rightarrow 0} = \theta[b + (1 - b)d]w_s - \mu > 0. \quad (6)$$

This shows that high seed production, prior and delayed selfing (b, d), and low inbreeding depression ($1 - w_s$) enhance the possibility for eliminating the extinction threshold. In the absence of an extinction threshold, the upper equilibrium is globally stable. A second effect of autonomous selfing is to reduce the range of population densities where an Allee effect occurs; at high autonomous selfing probability (e.g., $d = 1$), the Allee effect is nearly eliminated. A final effect of autonomous selfing is that the upper equilibrium is increased slightly, even in the presence of inbreeding depression. This is in contrast to the consequences of pollinator-mediated selfing and reflects increased seed production associated with autogamy.

Larger pollinator switching exponents (e.g., $\beta = 5$) coupled with some autonomous selfing (e.g., $w_s = 0.6$, $d = 0.2$) can introduce a third, stable equilibrium into population dynamics (fig. 3d, *dashed lines*). The equilibrium occurs below the extinction threshold associated with

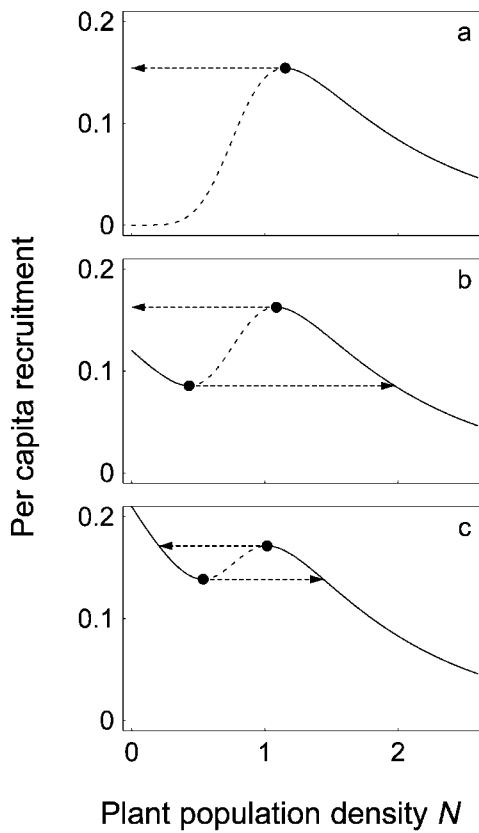


Figure 4: Allee effects and extinction thresholds in the presence of pollinator preference ($\beta = 5$) and autonomous (prior) selfing. In each panel, solid lines correspond to stable equilibria, dashed lines to unstable equilibria, and arrows to abrupt switches in plant density. *a*, With random mating ($b = d = 0$), there is a single abrupt extinction threshold. *b*, With some prior selfing ($w_s = 0.6$, $b = 0.2$), there is an abrupt extinction threshold as mortality increases in initially high-density populations and an abrupt mating system shift as mortality decreases in initially low-density populations. *c*, More substantial prior selfing ($w_s = 0.6$, $b = 0.35$) introduces an effect where increasing mortality in initially high-density populations results in an abrupt transition from partial outcrossing to selfing rather than population extinction.

the Allee effect and corresponds to populations persisting through selfing at a density below that required for pollinator attraction. The initial decrease in per capita recruitment reflects the regulatory effects of density-dependent population recruitment. Higher autonomous selfing ($d = 0.5, 1$) or reduced mortality can eliminate both the lower stable equilibrium and the Allee effect equilibrium.

Additional features of the pollinator switching exponent ($\beta = 5$) and autonomous selfing are explored with prior selfing in figures 1, 4, and 5. Note how, in figure 1, increasing mortality decreases the stable (upper) equilibrium density; mortality may increase because of deteriorating physical or biotic environments. In figure 4*a*, moving from

right to left along the solid line traces decreasing equilibrium density with increasing mortality. At the point where mortality exceeds recruitment (circle), population density abruptly declines to 0 (dashed arrow), and the population becomes extinct. Some autonomous selfing introduces a second threshold (fig. 4*b*; $w_s = 0.6$, $b = 0.2$). As in figure 4*a*, the equilibrium density of a primarily outcrossing population might, in the face of increasing mortality, abruptly decline to 0. Alternatively, a recently established population (e.g., through colonization of rehabilitated or novel habitat) may persist primarily through selfing (solid, downward sloping line at low density). If the habitat improves and mortality decreases, the population density increases and reaches a density sufficient for attraction of pollinators. The population abruptly shifts to an equilibrium density that includes a substantial outcrossing component (dashed right arrow). A third possibility occurs when autonomous selfing is more substantial (fig. 4*c*; $w_s = 0.6$, $b = 0.35$). Increasing mortality in an initially high-density population causes an abrupt mating system transition from partial outcrossing to selfing (fig. 4*c*, dashed left arrow). This effect, corresponding to an abrupt mating sys-

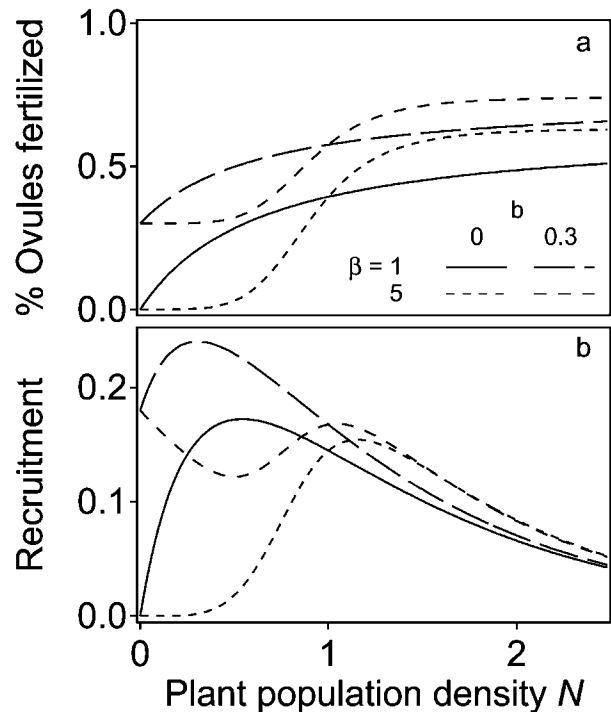


Figure 5: Percent of ovules fertilized (*a*) and per capita recruitment (*b*) under weaker ($\beta = 1$; lower pair of lines) and stronger ($\beta = 5$; upper pair of lines) pollinator preference and random mating ($b = 0$; lower pair of lines) or prior selfing ($b = 0.3$; upper pair of lines). Pollinator abundance is $P = 1.5$. With prior selfing $b = 0.3$, the selfing probability shifts from 100% at low plant density to $\approx 65\%$ at high density.

Table 2: Qualitative effects of increasing parameter values on the low-density equilibrium, the unstable equilibrium (extinction threshold), and the high-density equilibrium

	Low density	Extinction threshold	High density	Criterion
Mortality rate μ	↑	↓	↑	
Ovule production θ	↑	↓	↑	
Prior selfing b	↓	↑	↓	$w_s < \frac{V(N)(1 - g(N))}{1 - V(N)g(N) - (1 - V(N))d}$
Pollinator-mediated selfing:				
Fraction g_0	↓	↑	↓	
Exponent γ	↑	↓	↑	
Delayed selfing d	↑	↓	↑	
Self fitness w_s	↑	↓	↑	
Pollinator:				
Density P	↑	↓	↑	
Switching density ⁻¹ ρ	↑	↓	↑	
Switching exponent β	↑	↓	↑	$\rho N < 1$

Note: Criterion identifies conditions when specified relationships hold; calculations assume nonzero selfing (b , d , $g(N) > 0$) and inbreeding depression ($w_s < 1$).

tem shift to self-fertilization below a critical population density, contrasts with the extinction expected with lower selfing probability. Continued increases in mortality can drive the population to extinction, but decreases in mortality can result in an abrupt mating system shift to outcrossing (*dashed right arrow*). A final possibility is that the relationship between population density and recruitment is monotonically decreasing (as in fig. 3c, 3d, with $d = 1$). The population then smoothly transitions from outcrossing to selfing with decreasing density. These descriptions involve changes in mortality; below we explore analogous consequences when mating system evolution alters recruitment.

Plants capable of autonomous pollination and visited by discriminating pollinators ($\beta > 1$) may evolve to experience two different life-history phases (fig. 5). At low densities, reproduction occurs primarily through self-fertilization. At higher densities, plants increasingly reproduce through mixed mating. The distinction between completely selfing and mixed mating phases can be gradual or abrupt, depending on the strength of the pollinator switching exponent and amount of autonomous selfing.

It is important to consider evolutionary end points when interpreting figure 3. Analysis below (e.g., table 3; also Lloyd 1979, 1992) shows that evolution always favors 100% delayed selfing and either 0% or 100% prior selfing, depending on pollination and fitness parameters. Some of our most novel results (e.g., two stable equilibria) occur at parameter values that do not correspond to these evolutionary end points. The illustrated dynamics may nonetheless be relevant in species where factors not included in the model (e.g., life-history trade-offs or bet hedging in the face of environmental variation) result in inter-

mediate prior or delayed selfing or when species are in the process of evolving toward these end points.

Figure 3e and 3f summarizes consequences of pollinator density for population dynamics and equilibrium. Higher pollinator density increases per capita birth rates, shifting the extinction threshold to lower plant densities, reducing the range of densities exhibiting Allee effects, and increasing the equilibrium population density. Qualitatively, greater pollinator densities reduce the reliance on self-fertilization for population persistence. Since pollinator density is proportional to plant visits (eq. [2d]), increasing density usually increases the pollination fraction and reduces pollen limitation.

Qualitative effects of all parameters are summarized in table 2. As developed above, there are up to three possible equilibrium plant densities. The lower (“selfing”) and upper (“outcrossing”) equilibria can be stable, while the middle equilibrium is unstable and is associated with the extinction threshold of the Allee effect. Changes in parameters reducing mortality and increasing seed production (e.g., increased ovule number, delayed selfing, selfed fitness, pollinator density, and foraging choice) increase low and high equilibrium densities while reducing the density at which the Allee effect occurs. These parameters can be viewed as “stabilizing,” because they expand the range of densities over which populations reach stable equilibria. Parameters such as prior selfing in the face of strong inbreeding depression, pollinator-mediated selfing, and a larger switching exponent or lower switching density have the opposite effect. These parameters can be viewed as “destabilizing,” because they decrease the range of densities where stable equilibria are possible.

Evolutionary Modification

Simultaneous Ecological and Evolutionary Dynamics

Table 3 summarizes how selection changes model parameters over evolutionary time. Selection acting on different modes of selfing largely follows that in Lloyd’s (1979) analysis of purely evolutionary models. Delayed selfing is always favored (in the absence of between-year trade-offs; e.g., Morgan 2001), because otherwise unfertilized ovules contribute nothing to fitness. Pollinator-mediated selfing is only favored when selfed progeny have fitness greater than one-half that of outcrossed progeny. This is because pollinator-mediated selfing usurps opportunities for outcrossing, and the twofold gene transmission advantage of selfing is offset by reduced self fitness when $w_s < 1/2$. Prior selfing also experiences a threshold of selfed fitness required before being advantageous. The threshold depends on population numbers, because prior selfing usurps ovules that would otherwise be outcrossed, and this in turn depends on the pollination fraction. Lloyd (1979) notes a similar dependence, but his model does not explicitly include plant population dynamics or pollinator density and foraging.

Floral displays and rewards can influence pollinator behavior, so parameters such as the switching exponent β and switching density $1/\rho$ can change as plant traits evolve. Selection always favors a higher pollination fraction $V(N)$ (table 3), perhaps accomplished by evolution of characters changing the switching density $1/\rho$ (e.g., through increased or more readily accessible nectar reward). A higher pollination fraction also occurs with more abrupt switching (larger β) when the product ρN is < 1 . Because selection for more abrupt switching depends on plant density and to the extent that plants influence pollinator switching, it is possible for selection to favor an intermediate value of β .

Figure 6 illustrates simultaneous changes in genotype and population densities. Figure 6a serves to verify the numerical methods, with all genotypes having parameter values corresponding to the solid line of figure 3a. Populations starting below the extinction threshold become extinct, while those above the threshold evolve to the predicted equilibrium density. Figure 6b shows that alleles increasing the selfing parameter g_0 from 0.25 to 0.35 increase in frequency; this is as expected in table 3.

Simultaneous ecological and evolutionary change confirm dynamics implicit in the separate ecological and evolutionary scenarios. Figure 6c illustrates the dynamics implied in figures 3a and 4a when the mortality rate is elevated slightly ($\mu = 0.15$). A modifier increasing selfing parameter g_0 from 0.25 to 0.35 increases in frequency (because $w_s > 1/2$) but reduces population density (because this type of selfing does not increase seed production, and selfed seeds contribute less to changes in population density compared with outcrossed seeds). Total population density declines as the modifier spreads, eventually reaching the extinction threshold of figure 4a. The population moves abruptly to extinction. Figure 6d illustrates a situation like that in figures 3d and 4b. Parameters are chosen so that initially the population is at a low-density equilibrium, persisting primarily through some delayed self-fertilization. A modifier increasing the probability of delayed selfing d from 0.2 to 0.3 always increases in frequency. In the process, population recruitment rates increase, and population densities abruptly increase to the upper population dynamic equilibrium. As illustrated in figure 5, this transition is accompanied by an increase in the total number of seeds produced, so the fraction of selfed seeds actually decreases even while the probability of delayed selfing increases.

Table 3: Conditions favoring the selection of greater parameter values, based on analysis of equation (4a)

Selection increases	When
Mortality μ	Never
Ovule production θ	Always
Prior selfing b	$w_s > \frac{1}{2} \frac{V(N)(1 - g(N))}{1 - V(N)g(N) - (1 - V(N))d}$
Pollinator-mediated selfing ($g_0 \uparrow, \gamma \downarrow$)	$w_s > \frac{1}{2}$
Delayed selfing d	Always
Self fitness w_s	Always
Pollination fraction $V(N)$	Always
Switching density ⁻¹ ρ	Always
Switching exponent β	$\rho N < 1$

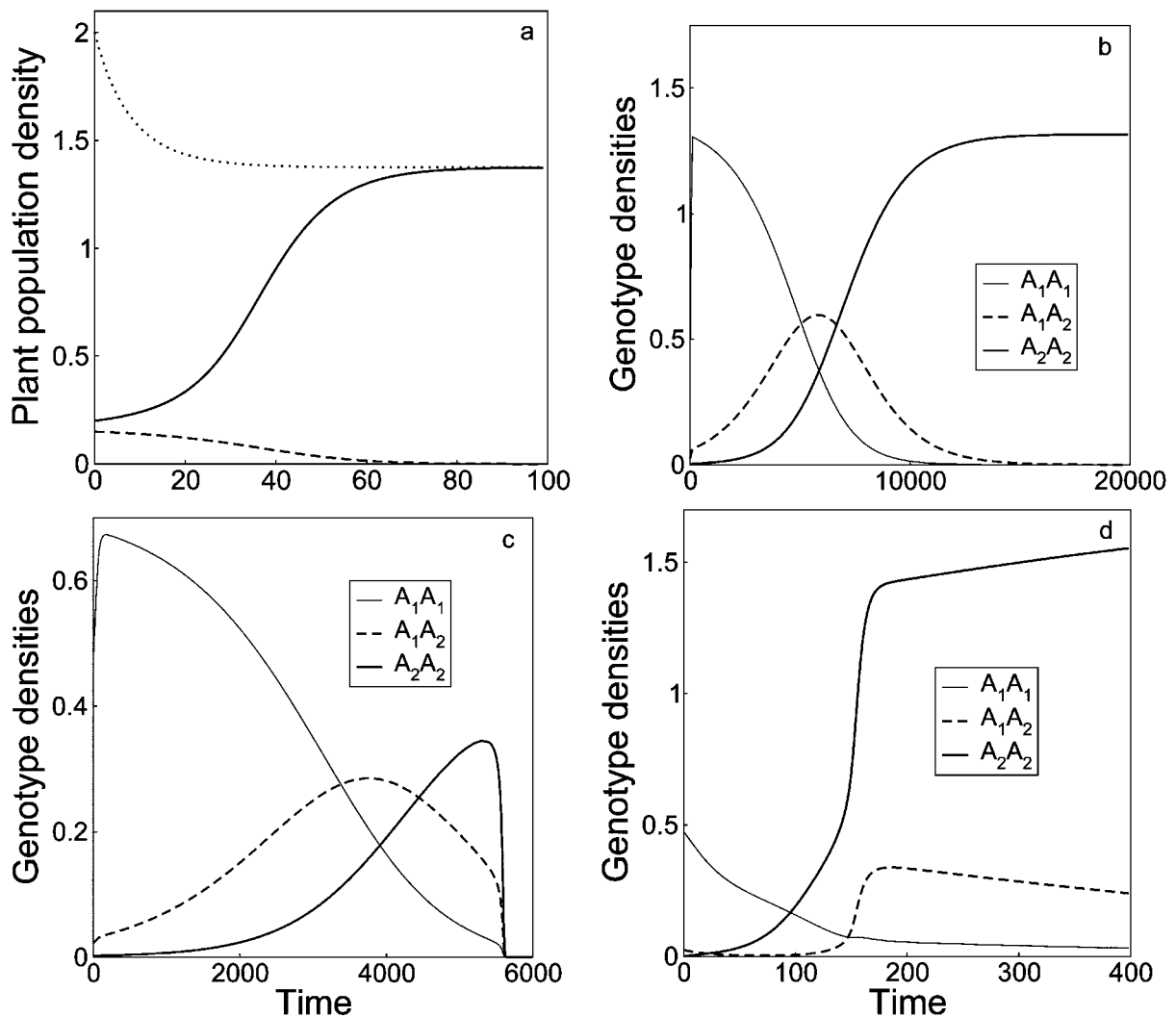


Figure 6: Simultaneous ecological and evolutionary dynamics of modifiers of the selfing probability. *a*, All genotypes with base parameter values of table 1 but with $g_0 = 0.25$; lines are total population densities starting at different initial densities. *b*, Genotype frequencies when a modifier genotype A_1A_1 with selfing parameter $g_0 = 0.35$ is introduced into the stable equilibrium population of *a*. *c*, As in *b* but with mortality $\mu = 0.15$ for all genotypes; spread of the modifier eventually leads to population extinction. *d*, Base parameters of table 1 but with strong pollinator preference $\beta = 5$ and some delayed selfing $d = 0.2$ and starting at the lower density equilibrium of figure 3*d*. A modifier increasing the delayed selfing probability of genotype A_1A_1 to $d = 0.3$ increases in frequency, leading to an abrupt increase in population density.

Discussion

We presented a model of plant population dynamics that includes pollinator-mediated reproduction and self-fertilization. In our model, reliance on pollinators for reproduction often results in an Allee effect (increasing per capita reproductive rate at low density). In random mating populations or in species capable of pollinator-mediated selfing, the Allee effect can be associated with a threshold

below which populations become extinct (fig. 3). Autonomous selfing moderates or eliminates the extinction threshold, although populations continue to exhibit Allee dynamics (figs. 3, 4). This change is particularly evident in species capable of autonomous selfing, where a second stable equilibrium can occur at low density. This equilibrium is associated with reproduction exclusively through

selfing (figs. 4, 5). A feature of our models is that pollen limitation and reproductive assurance are influenced by plant density, resulting in a transition between primarily selfing mating systems at low density and mixed mating systems at high density (fig. 5). Results of our evolutionary analysis are largely consistent with results anticipated in previous models (table 3). Low pollinator visitation can allow prior selfing to evolve even when inbreeding depression is greater than one-half. We thus provide a mechanism for a conclusion originally reached by Lloyd (1979). Numerical integration of coupled population and evolutionary dynamic equations supports the conclusions of our separate population and ESS analyses.

Allee and Related Effects in Plants

Plants illustrate important conceptual distinctions associated with reproduction at low densities. The Allee effect describes a positive relationship between per capita reproductive rate and population density as documented in, for instance, *Trillium grandiflorum* (Knight 2003). An extinction threshold is often associated with an Allee effect in models of random mating species. Distinguishing between Allee effects and extinction thresholds is particularly important in plants because autonomous selfing can remove the extinction threshold without compromising the presence of the Allee effect (fig. 3d). An additional feature occurs in the presence of autonomous selfing and switching exponent $\beta > 1$ (figs. 3d, 4). Under these circumstances, increasing mortality causes outcrossing populations to fall below an extinction threshold, but populations persist through selfing at an even lower density. There is an abrupt shift in the mating system equilibrium associated with this transition, from outcrossing to self-fertilizing in the face of increasing mortality and from selfing to outcrossing with decreasing mortality (fig. 4c). This switch might be reflected in shifting mating systems across environmental gradients (e.g., Barrett et al. 1989; Barrett 1993; Runions and Geber 2000; Fausto et al. 2001; below) or within-species variation in mating system (Schemske and Lande 1985). Analogous effects occur when evolution of the selfing probability influences recruitment (fig. 6).

Pollinator visits per plant might decline at very high density, as plants compete for limited pollinators. This “inverse Allee effect” would serve as a form of density-dependent regulation limiting plant density. We did not consider this explicitly in our model, but inverse Allee effects associated with pollinator visits probably do not change qualitative outcomes to the model. Mortality may not be density independent but may sometimes increase with density (i.e., exhibiting positive slope in figs. 1, 3). Again, the qualitative conclusions of our model are not

likely to change, provided mortality is not too strongly density dependent.

Pollen Limitation

A very large number of studies suggest that plants are routinely pollen limited; that is, plants are observed to receive inadequate pollen to fertilize available ovules (Ashman et al. 2004). A separate body of empirical literature indicates that reductions in plant density reduce pollination and reproductive success through mechanisms such as altered pollinator behavior (reviewed in Kunin 1997b). Our model combines these two broad empirical patterns. Our ecological model introduces pollen limitation because only a fraction of the θ ovules available are fertilized (except when prior or delayed selfing are complete; $b, d = 1$). Figure 5a shows that the extent of pollen limitation usually depends on plant density and is, in part, mediated by pollinator behavior. Many life-history features associated with recruitment (e.g., ovule production or pollination fraction) and survival (density-independent mortality) influence equilibrium plant density, which may thus help to explain the heterogeneity of observed pollen limitation.

Haig and Westoby (1988) introduced evolutionary ideas into the study of pollen limitation. These authors suggest that plants consistently faced with inadequate pollination evolve to adjust reproductive strategies from ovule production toward pollinator attraction (or, presumably, other life-history components that result in increased ovule fertilization probabilities; Ashman et al. 2004) until plants are simultaneously resource and pollinator limited. These evolutionary ideas of pollen limitation linked to allocation strategies can be incorporated into our formulation. One formulation close to that of Haig and Westoby is to posit an allocation r to attraction for the benefit of male and female functions and a fraction $1 - r$ for fruit production. Attraction can be included in the term relating plant abundance to pollinator foraging preference, equation (2e), as

$$\phi(N, r) = \frac{(r\rho N)^\beta}{1 + (r\rho N)^\beta}. \quad (7)$$

The fruit maturation allocation scales the number of ovules available for fertilization, $(1 - r)\theta$. The qualitative outcome from analyzing this model is a balance between pollen and resource limitation (cf. Haig and Westoby 1988; Ashman et al. 2004); the diminishing gains of the pollination fraction dictate that a portion of ovules remains unfertilized.

This model can be analyzed for the selection of self-fertilization and for the evolution of allocation to attraction r versus seed maturation $1 - r$ using methods like

those in equations (4). Conditions for the selection of various modes of self-fertilization are like those in table 3. Specifically, delayed selfing is always selectively advantageous and competing selfing advantageous when $w_s > 1/2$ regardless of attraction/seed maturation strategy. Selection of prior selfing follows the condition in table 3 but with visitation $V(N)$ and geitonogamy $g(N)$ involving the modified pollinator foraging preference of equation (7).

This extension can be analyzed, using numerical methods, for optimal allocation to attraction r under various mating system and population dynamic scenarios. In the presence of complete delayed selfing $d = 1$, $w_s > 1/2$ selects for allocation only to seed maturation (i.e., complete selfing), whereas $w_s < 1/2$ results in allocation to both attraction and seed maturation (i.e., mixed mating). In general, the optimal allocation to attraction r depends on population dynamic processes and is a function of parameters such as plant mortality and pollinator abundance. Figure 7 shows one example of the joint equilibrium of plant density and reward allocation as a function of plant mortality in a population with no selfing. For this set of parameters, plants facing greater mortality increasingly invest in pollinator attraction for reproductive success.

Reproductive Assurance

Pollinator visitation in our model decreases with plant density, and at low densities plants increasingly rely on selfing for reproductive assurance. Modes of selfing differ in reproductive assurance (e.g., Lloyd and Schoen 1992). In particular, autonomous selfing (e.g., prior selfing; fig. 5, *upper pair of lines*) offers reproductive assurance. Pollinators exhibiting abrupt switching ($\beta = 5$; fig. 5, *dashed lines*) expand the plant density over which reproductive assurance is important.

Explicit population dynamic models show how changes in plant density influence reproductive assurance and mating systems. Mixed mating can be achieved through intermediate levels of facilitated outcrossing (determined in part by plant density through $V(N)$, the pollination fraction) coupled with delayed selfing of ovules that were not outcrossed. A second way in which explicit population demographic models result in stable mixed mating involves density-dependent competitive interactions between self-fertilized and outcrossed individuals (Cheptou and Dieckmann 2002); these types of interactions are not included in our model.

Empirical surveys suggest that annual species are more likely to be self-fertilizing than perennial species (Stebbins 1950, pp. 176–181; Barrett and Harder 1996; Böhle et al. 1996; Bena et al. 1998). Reproductive assurance is sometimes invoked as an explanation for this association (Stebbins 1950). Morgan et al. (1997) note that self-fertilization

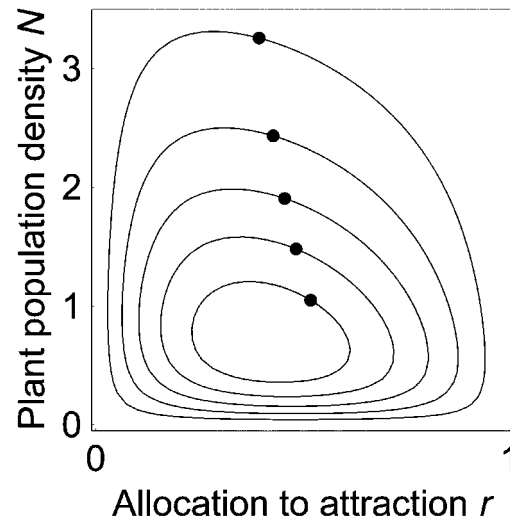


Figure 7: Zero growth isoclines of plant population density and reward allocation in a random mating population for the model extension developed in “Discussion” under different mortality rates. Each line corresponds to the combination of population densities and reward allocations resulting in constant population size; parameter combinations to the interior of the contours have positive population growth rates. Contours (from exterior to interior) are for mortality rates from $\mu = 0.01$ to $\mu = 0.05$ in steps of 0.01. Points represent the end point of ecological and evolutionary dynamics at a given mortality rate; reward allocations evolve to maximize individual fitness at r , while plant density changes so that recruitment and mortality balance. Greater mortality (contours to the interior of the figure) increases reward allocation while reducing equilibrium plant density.

that enhances reproductive output (i.e., providing reproductive assurance) is selectively favored in perennials as well as annuals. The model of Morgan et al. does not allow for population decline, since gene frequencies rather than population numbers are followed. From table 3, including population dynamics influences conditions for the evolution of prior self-fertilization. The effect is, however, indirect. Mortality μ (annuals necessarily have greater mortality rates than perennials; our model does not allow an explicit contrast between annual and perennial life histories) does not enter directly into conditions for the selection of prior selfing. Instead, decreasing per capita mortality increases population density. In this indirect sense, reproductive assurance contributes to the association of prior selfing and annual life history.

Reproductive assurance is an important component in explanations for geographic variation in mating system seen in several species. For instance, Barrett (e.g., Barrett et al. 1989; Barrett 1993) suggests that the evolution of stigma-anther polymorphism favoring selfing morphologies in *Eichhornia paniculata* occurs following expansion of *E. paniculata* outside the range of pollinators with suit-

able morphology and behavior for effective intermorph pollen transfer. A similar explanation, including evidence for reduced and density-dependent pollinator visits in areas with self-pollinating populations, describes the evolution of selfing in *Clarkia xantiana* (Runions and Geber 2000; Fausto et al. 2001). Ingredients for evaluating the theoretical validity of this explanation exist. For instance, Washitani (1996) shows through simulation how decreased pollinator density and increased pollen limitation favors selection for homostylous variants in *Primula sieboldii*. Pannell and Barrett (1998) show that metapopulation extinction and recolonization dynamics favor selfing because it provides reproductive assurance in newly established populations of a single individual. Our results suggest features likely to enhance selection for selfing promoted by reproductive assurance. Plants requiring specialized or discriminatory pollinators (as in heterostylous species) or exhibiting density-dependent recruitment (as in *C. xantiana*) are likely to have extinction thresholds at densities above a single plant. This suggests that selfing provides reproductive assurance in populations larger than the single individual assumed in Pannell and Barrett's (1998) description and that extinction and recolonization implied by metapopulation dynamics are not required for the evolution of selfing for reproductive assurance.

Future Directions

Several empirical studies have factorially manipulated both pollen and resource availability. Some find pollen is more limiting to reproductive success, whereas others find that resource limitation is most important (see Ashman et al. 2004); it may often be the case that pollen and resources simultaneously limit reproductive success (e.g., Campbell and Halama 1993). We reconcile these disparate results by assuming that, within species, pollen limitation decreases with increasing plant density (fig. 5a). However, few empirical studies test this assumption (but see Knight 2003 and references therein). Plants may also have the ability to respond plastically within a single growing season. For example, Campbell and Halama (1993) demonstrated that *Ipomopsis aggregata* produced more flowers and nectar per flower after resource supplementation, and plants given additional resources were therefore not more pollen limited than control plants. Thus, changes in reward allocations observed in figure 7 may occur in ecological time.

Our model describes the population-level effects of plant-pollinator interactions, whereas the majority of empirical work has focused on seed production and individual fitness. One solution to this problem has been to incorporate the effects of pollinators into a demographic matrix model of plant populations (Bierzychudek 1982; Ehrlen and Eriksson 1995; Parker 1997; Garcia and Ehrlen

2002; Knight 2004). There are limitations to what has been done to date. First, the demographic matrix models are density independent, which assumes that Allee effects do not occur. Second, seed quality (selfed versus outcrossed seeds) has not been explicitly incorporated into these models. Both limitations could be addressed with more empirical work and more detailed modeling.

Our models are deterministic, so it is not possible to reach conclusions about the probabilities or expected duration of population persistence (Dennis 2002). We do not include a metapopulation dynamic of gene flow between populations or of extinction and recolonization. Such processes can be important in long-term persistence of some natural populations (Brassil 2001; Lennartsson 2002) and in providing advantages to self-compatible species in a metapopulation (e.g., Pannell and Barrett 1998). Our models include selfing, but plants have a diversity of reproductive strategies. Evolutionary consequences of interactions between population dynamics and other reproductive strategies remain largely unexplored, although existing studies of androdioecy (e.g., Pannell 2000) and dioecy (e.g., Wilson and Harder 2003) suggest novel insights available from this approach.

Conclusions

We have developed models of plant population dynamics. Our models are unique in their inclusion of explicit pollinator foraging choice and in allowing for self-fertilization. We illustrate how autonomous selfing decreases, and pollinator switching exponent increases, the extinction threshold commonly associated with the Allee effect. We also show that autonomous selfing can introduce an effect where an abrupt shift to self-fertilization prevents population extinction expected with increasing mortality or decreasing pollinator service. One consequence of autonomous selfing and pollinator foraging choice is the opportunity for abrupt or gradual switches in mating system with changes in mortality.

Our evolutionary analysis supports key results from previous studies of the selection of selfing while explicitly relating population dynamic changes to the evolution of mating systems. As in previous models, we find that delayed selfing is always favored, while selection favoring pollinator-mediated selfing requires inbreeding depression less than one-half. Extending these results to include population density, we find that low density facilitates the selection of prior selfing while increasing the fraction of delayed self-fertilized ovules. We thus expect that plant density and pollinator foraging play important roles in understanding the variation and stability of mixed mating observed within some plant species.

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