

# Patch Aging and the S-Allee Effect: Breeding System Effects on the Demographic Response of Plants to Habitat Fragmentation

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**ABSTRACT:** We used empirical and modeling approaches to examine effects of plant breeding systems on demographic responses to habitat fragmentation. Empirically, we investigated effects of local flowering plant density on pollination and of population size on mate availability in a common, self-incompatible purple coneflower, *Echinacea angustifolia*, growing in fragmented prairie habitat. Pollination and recruitment increased with weighted local density around individual flowering plants. This positive density dependence is an Allee effect. In addition, mean mate compatibility between pairs of plants increased with population size. Based on this empirical study, we developed an individual-based, spatially explicit demographic model that incorporates autosomal loci and an S locus. We simulated habitat fragmentation in populations identical except for their breeding system, self-incompatible (SI) or self-compatible (SC). Both populations suffered reduced reproduction in small patches because of scarcity of plants within pollination distance (potential mates) and inbreeding depression. But SI species experienced an additional, genetic contribution to the Allee effect (S-Allee effect) caused by allele loss at the S locus, which reduces mate availability, thereby decreasing reproduction. The strength of the S-Allee effect increases through time (i.e., patches age) because random genetic drift reduces S-allele richness. We investigate how patch aging influences extinction and dis-

cuss how the S-Allee effect influences communities in fragmented habitat.

**Keywords:** self-incompatibility, pollen limitation, *Echinacea angustifolia*, spatially explicit model, prairie, mating system.

Habitat fragmentation isolates remnant populations and decreases their size, which leads to reduced reproduction in many species (Knowlton 1992; Noon and McKelvey 1996; Wells et al. 1998; Aizen et al. 2002). These dynamics may result in an Allee effect, a positive relationship between per capita population growth rate and density, which is hypothesized to increase extinction rates when population size or density is below a certain threshold (Allee 1931; Groom 1998; Courchamp et al. 1999). Because reproduction depends on the availability of mates, a population's breeding system influences the strength of the Allee effect (Bessa-Gomes et al. 2004). For example, recent work on small populations of animals found that reproductive rates were more sensitive to stochastic changes in sex ratio in monogamous species than in polygamous species (Sæther et al. 2004). Plants have many types of breeding systems, ranging from dioecy, which is analogous to most animal breeding systems (Renner and Ricklefs 1995), to self-compatibility, where an individual plant can set seed with its own pollen. Approximately 60% of plant species are self-incompatible (Hiscock and Kues 1999), having some genetic mechanism to avoid self-fertilization. How the Allee effect differs between self-compatible (SC) and self-incompatible (SI) plant species remains an open and important question, given that many plant populations are declining in size because of habitat fragmentation and other environmental changes.

Habitat fragmentation alters the ecological contexts that affect trade-offs among plant breeding systems. Habitat fragmentation may reduce population size, decrease local plant density, and alter pollen movement—especially by increasing pollen movement between relatives. Both SI and SC plants may suffer from pollen limitation because of a

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reduction in potential mates, the number of plants within pollination distance. Animal-pollinated plants may suffer from additional Allee effects because of pollinator limitation, but SC plants with autonomous self-pollination avoid this. Even though many SC plants produce inbred progeny by selfing or mating between relatives, they may nevertheless have reduced fitness when mates are sparse because a greater proportion of progeny result from inbreeding and thus experience inbreeding depression (Murawski and Hamrick 1991; Franceschinelli and Bawa 2000; Keller and Waller 2002). Self-incompatibility is an inbreeding avoidance mechanism that confers the fitness benefits of obligate outcrossing at the expense of limiting mate availability (De Nettancourt 1997; Hiscock and McInnis 2003). Self-incompatibility consists of a mate recognition system attributed to a genetic locus (*S* locus) that prevents both self-fertilization and cross-fertilization between individuals sharing an allele at this locus (De Nettancourt 1977). In general, fertilization occurs only when pollen and stigma carry different alleles at the *S* locus. Self-incompatibility thus prevents production of progeny from selfing and from mating between individuals with the same *S* alleles, thereby reducing inbreeding depression but also reducing mating opportunities with some unrelated plants. Self-incompatibility reduces the number of mates available to an individual from those within pollen dispersal distance (potential mates) to those that are compatible (compatible mates). Where reproduction is not limited by compatible mates or pollinators, the benefits of self-incompatibility have been demonstrated theoretically and empirically (Lande and Schemske 1985; Schemske and Lande 1985). Where mates are limited, however, the costs of reduced mate availability due to self-incompatibility may outweigh the benefits of avoiding inbreeding depression, in which case SC individuals gain a selective advantage (Baker 1955; Reinartz and Les 1994; Stephenson et al. 2000; Vallejo-Marín and Uyenoyama 2004).

Two separate lines of evidence generate the hypothesis that breeding system influences demographic response to habitat fragmentation. First, the prevalence of pollen limitation in many plant species, both SC and SI, suggests that Allee effects may be very common and sometimes strong, especially in fragmented landscapes (Groom 1998; Aizen et al. 2002; Ashman et al. 2004; Knight et al. 2005). Second, small populations created by habitat fragmentation lose genetic diversity by random drift (Wright 1931; Hartl and Clark 1989). The combination of the Allee effect and the effect of drift on mating-type diversity suggests that effects of habitat fragmentation on population dynamics could differ between SC and SI populations. Historical evidence has revealed that self-incompatibility and self-compatibility have evolved independently many times in many different plant families, suggesting that the

ecological contexts affecting the costs and benefits of each breeding system vary in space and time (Stebbins 1974; Vogler and Kalisz 2001; Goodwillie et al. 2005). Habitat fragmentation is one type of ecological change that could influence the costs and benefits of self-compatibility relative to self-incompatibility.

In this study, we combined empirical and modeling approaches to examine the effects of mating and breeding systems on demographic response to habitat fragmentation. Empirically, we investigated the effects of local flowering plant density on pollination and of population size on mate availability in the purple coneflower *Echinacea angustifolia* (hereafter *Echinacea*). Based on the empirical study, we developed and parameterized an individual-based, spatially explicit demographic model that incorporates autosomal loci and an *S* locus. The model enables us to identify and quantify three separate components of the Allee effect, the effect due to reduced abundance of potential mates (those within pollination distance), the effect due to reduced abundance of compatible mates, and the effect due to inbreeding depression. We use the model to compare how plant species that are identical in all life-history traits except their breeding systems (SI and SC, with six levels of selfing) respond to a sudden reduction in habitat area. We discuss how breeding system and habitat area can influence plant community composition through their effect on carrying capacities.

## Material and Methods

### *Study System*

*Echinacea angustifolia* (Asteraceae) was chosen as a model system to investigate basic ecological and evolutionary processes of the vast, but now fragmented, grasslands of central North America. *Echinacea* shares characteristics with many prairie plants, including pollination by generalist insects, reproduction by seeds only, the lack of a specialized seed dispersal mechanism, and self-incompatibility (Haverkamp and Whitney 1983; Molano-Flores 2004; Wagenius 2004). *Echinacea* has a sporophytic self-incompatibility system, which is one of the two main homomorphic self-incompatibility systems and has been well characterized in the Asteraceae and Brassicaceae, among other plant families (Uyenoyama 1995; Hiscock and McInnis 2003). Sporophytic self-incompatibility involves recognition between products of both maternal *S*-locus alleles in the stigma and both paternal *S* alleles in the diploid pollen coat protein. Mating compatibility typically requires that both maternal *S* alleles differ from both paternal *S* alleles. Long-lived herbaceous perennials dominate the flora of the great plains and prairie (Weaver 1954; Great Plains Flora Association 1986; Swink and Wilhelm 1994).

Detailed demographic information is known about very few prairie plants (Kerster 1968; Harper and White 1974), but *Echinacea* does not appear unusual with regard to longevity (16–44 years), years to initial flowering (2–9), or flowering frequency (not every year and environment dependent; Kerster 1968; Schaal and Levin 1976; Hurlburt 1999; S. Wagenius, personal observation). In addition to *Echinacea*'s biological characteristics, the recent history of its abundance and distribution is typical of many prairie plants. *Echinacea* was and is distributed widely from Texas to Canada between the Mississippi River and the Rocky Mountains (McGregor 1968). Before European settlement, the entire landscape offered apparently suitable habitat for *Echinacea*. Today, natural populations are sparsely scattered, and local population sizes are often small; *Echinacea* is not threatened or endangered, however.

In our 6,400-ha study site in western Minnesota farmland (centered near 45°49'N, 95°42.5'W), there are 48 prairie remnants with *Echinacea* population sizes ranging from one to several thousand flowering individuals. This fragmentation reduces reproduction in *Echinacea*, and inbreeding depression is evident (S. Wagenius, H. Hangelbroek, and R. G. Shaw, unpublished manuscript). Pollen limitation reduces seed production in isolated *Echinacea* plants (Wagenius 2006), but insect visitation does not appear to vary with population size or local plant density (S. Wagenius, unpublished data). This pattern is consistent with the hypothesis that isolated plants receive less compatible pollen rather than fewer visits from pollinating insects. Seeds from smaller populations tend to produce less vigorous plants than those from larger populations when grown in a common environment (Wagenius 2000; Geyer et al. 2007). Moreover, progeny resulting from mating between siblings grow more slowly and die at a greater rate than progeny resulting from random mating (S. Wagenius, H. Hangelbroek, and R. G. Shaw, unpublished manuscript). Adult flower production in remnant populations does not vary with population size (Wagenius 2004). Throughout this article, we use population- and individual-based measures of local plant abundance as appropriate for the modeled or empirically measured mechanism (Wagenius 2006). Population-based measures include population size and population mean plant density. Individual-based measures include the local density of flowering plants and the outcross mating potential (see "Juvenile and Adult Dynamics" and "Pollination," respectively).

#### Empirical Design

*Fine-Scale Spatial Patterns of Pollination.* We focused on the largest remnant population in our study site, the Stafanson Prairie Preserve, a 45-ha preserve owned and man-

aged by The Nature Conservancy. Plants in this remnant have presumably been influenced by fragmentation the least. In 1998, there were 2,300 flowering plants on the preserve (1,000 on the burned eastern unit and 1,300 on the unburned western unit). We mapped a sample of *Echinacea* plants growing in the preserve and characterized their flowering, pollination, and seed production. We observed style persistence of 63 flowering plants on a 600-m-long, 5-m-wide belt transect (51 on the burned eastern unit and 12 on the unburned western unit) every third day during the flowering season. We mapped the location of all flowering plants within 30 m of the transect (441 plants). For each plant on the transect we calculated the mean annual duration of style persistence (SP). Style persistence is a measure of pollen limitation (nonreceipt of compatible pollen) because a receptive style persists for up to 10 days unless it receives compatible pollen, in which case it shrivels within 24 h (Wagenius 2004). We collected seed heads from 50 plants (116 heads) along that transect.

In 2001, we germinated 45 randomly chosen seeds from each head of a randomly chosen subset of 26 plants (59 heads) from the eastern unit and all heads collected from the western unit (11 heads from nine plants). After the germination treatment, all remaining seed coats were dissected to estimate the fertilization rate for the plant, which is the fraction of seed coats that either germinate or contain an embryo. Two plants in this sample were diseased and produced no seeds, and one plant had too few observations of SP; these were excluded from further analysis. For each remaining plant, we have the following information: SP, fertilization rate, and the distance to all flowering plants within 30 m. For every plant, we have the distance to its six closest neighbors, but the seventh-nearest neighbor for some plants on the transect was more than 30 m away and thus unmapped.

*Estimating Population Mean Compatibility Rates.* In this experiment, we focused on 19 remnant populations during the summer of 2003. In each population, we chose six focal plants at random from all flowering plants in the population. We partitioned some populations on the basis of natural barriers or gravel roads and sampled six focal plants from each side. We then determined the six nearest flowering plants to each focal plant and designated them as pollen donors. Our goal was to determine compatibility between each focal plant and its six closest pollen donors. We attempted to do this in one 3-day crossing cycle but could not because focal plants did not always present enough styles and the donors' pollen production was not perfectly synchronous. On the first day of a cycle, for each focal plant we painted tips of bracts subtending pollen-producing florets with acrylic paint. Using colors to represent each pollen donor, we painted five or six bracts per

color and up to six colors per flower head. We put pollinator exclusion bags over all painted heads on each focal plant and over one head on each pollen donor. The next day, we collected pollen from pollen donors in microfuge tubes and used a toothpick to place pollen on the newly emerged styles whose bracts had been painted the day before. The third day, we scored the hand-pollinated styles as unchanged or shriveled. If necessary, we began a new cycle. All crosses with at least four scored styles were classified according to the number of styles that shriveled: 0 or 1, incompatible; 2 or 3, undetermined; and 4 or more, compatible. Styles with applied incompatible pollen occasionally shrivel because of contamination with compatible pollen or mechanical damage, and styles with applied compatible pollen rarely fail to shrivel (S. Wagenius, personal observation). Within one flowering season, we could not simultaneously determine the compatibility between pairs of plants and natural fertilization rates because bagging heads affects pollinator behavior. We tested the null hypothesis that compatibility rate is independent of population size, using a binomial family generalized linear model with a logit link function, implemented in the statistical package R (R Development Core Team 2004).

#### Model Description

We developed a stochastic, spatially explicit, and individual-based computer simulation model of plant population dynamics in a habitat that becomes fragmented (see appendix in the online edition of the *American Naturalist*). Although this model generalizes to species with a variety of life-history and ecological attributes, we detail the aspects of the model most relevant to *Echinacea*. Similarly, our parameterization and experimental runs focus on *Echinacea*'s prairie habitat and its recent fragmentation. We emphasize that this study species was chosen to represent a large class of common prairie plants, as described at the beginning of "Material and Methods." Each individual plant had seven diploid, autosomal loci. We used six loci to assess autozygosity. Each plant also had an *S* locus that determined compatibility. At the start of each simulation, each individual carried two unique alleles at each of the non-*S* loci, so that the total number of alleles per locus was equal to twice the number of individuals, and thus each individual was completely unrelated to all other individuals at the start of each simulation. We used these loci to calculate inbreeding; as time progressed, if individuals were homozygous at any locus, inbreeding was indicated. At the *S* locus, the program randomly assigned to each plant two nonidentical alleles from a pool of 25 codominant *S* alleles, a number consistent with other sporophytic self-incompatibility systems (Lawrence 2000) but

higher than found in colonist populations of *Senecio squalidus* (Brennan et al. 2006).

Runs began by simulating a relatively large, continuous habitat with 80 individuals assigned to random positions. We then ran the simulation until an approximate steady state for both population size and genetic composition was reached, at  $t = 500$ , at which point habitat area was reduced. Only plants located in the remaining habitat were retained, and their fate was followed during the transient phase after the perturbation. The simulation occurred in discrete time with one time step per year that included the following processes in sequence: pollination, fertilization, seed set, seed dispersal, establishment of seedlings, growth of juvenile plants, survival of adult plants, and overwintering mortality.

**Pollination.** For each plant  $i$ , we determined distances to and compatibility with all other flowering plants  $j$ . A weighted sum determined the outcross mating potential ( $P_i$ ) for each plant as

$$P_i = \sum_{j=1}^n e^{-\gamma d_{ij}} c_{ij}, \quad (1)$$

where the summation is over all  $n$  flowering plants  $j$  that are distance  $d_{ij}$  from plant  $i$ . The exponential decay parameter  $\gamma$  represents the reciprocal of the average pollen dispersal distance. The compatibility parameter  $c_{ij}$  is equal to 1 if plants  $i$  and  $j$  are compatible and 0 otherwise. We assumed that fertilization could occur only when all four alleles, two from the maternal plant and two from the paternal plant, at the *S* locus were different. This mimics the sporophytic incompatibility system that is common in the Asteraceae (Hiscock and Tabah 2003). The modified outcross mating potential,  $P_i^*$ , refers to  $P_i$  calculated with all  $c_{ij} = 1$ , that is, all mates assumed compatible.

**Fertilization.** The outcross mating potential ( $P_i$ ) was then converted into a probability of fertilization ( $F_i$ ),

$$F_i = (1 - s)\alpha \frac{P_i}{\kappa + P_i} + s\alpha, \quad (2)$$

where  $\alpha$  represents the maximum proportion of fertilized seeds,  $\kappa$  is the half-saturation constant, and  $s$  represents the selfing rate. For simulations representing species with an SI breeding system,  $s$  is equal to 0. In SC plants,  $s$  can range from 0 (obligate outcrossing) to 1 (100% selfing).

**Seed Dispersal and Recruitment.** The fertilization index was used to calculate the number of seeds each plant produces. If the maximum number of seeds is  $N$ , then plant  $i$  pro-

duces  $X_i$  seeds, where  $X_i$  is a Poisson variable with mean and variance equal to  $NF_i(1 - m\delta_i)$ , where  $\delta_i$  is the inbreeding coefficient of plant  $i$  (the proportion of non-S loci that are homozygous) and  $m$  is a scalar representing the magnitude of inbreeding depression for recruitment. Thus, we incorporate inbreeding depression as a reduction in seed set and mortality during early life-history stages.

The genotypes of each seed were assigned randomly by selecting one allele at each non-S locus from the maternal plant and one from a randomly chosen paternal plant. For seeds that were not produced from selfing, the paternal plant was chosen from a distribution where the probability of being chosen decays exponentially with distance,

$$\frac{e^{-\gamma d_{ij}} c_{ij}}{P_i}, \quad (3)$$

which is also the paternal plant's relative contribution to the maternal plant's outcross mating potential. The seeds from the remaining portion (i.e., those that resulted from selfing,  $\alpha\alpha/F_i$ ) were randomly assigned two alleles from the maternal plant. The distance each seed dispersed was chosen at random from an exponential distribution with parameter  $\lambda$ ; that is, the average seed dispersal distance was  $1/\lambda$ . The direction of dispersal was randomly drawn from a uniform distribution.

*Juvenile and Adult Dynamics.* Seeds that landed outside of a defined habitat area were discarded, while seeds that reached habitat spent three seasons in the juvenile phase. During the juvenile phase, each seed had a constant probability of mortality each season. If it survived for 3 years, it became an adult, provided that its local neighborhood was not too dense. To determine whether a juvenile plant became an adult plant, the local density was measured. Each plant  $j$  contributed to the local density of plant  $i$ ,  $D_i$ , with a weighting factor,  $\beta$ , that declined exponentially with distance to focal plant  $i$ ,  $d_{ij}$ , such that

$$D_i = 1 + \sum_{j=1}^n e^{-\beta d_{ij}}, \quad (4)$$

where  $n$  is the number of plants in the area. If the local density,  $D_i$ , was below a fixed threshold,  $K$ , the juvenile plant became an adult plant. If not, the juvenile plant died. Each adult plant had a fixed, density-independent mortality probability each year.

The simulation reported the genotype of every individual in the model and produced the following summary demographic and genetic parameters: population size, effective number of alleles at the compatibility locus (Hartl and Clark 1989), mean fertilization rate ( $F_i$ ), mean out-

cross mating potential ( $P_i$ ), mean modified outcross mating potential ( $P_i^*$ ), and mean proportion of compatible individuals ( $c$ ). We compared the genetic and demographic parameters that emerged from the model to our empirical results.

#### Parameter Fitting

When possible, parameters were estimated from the empirical study described above and from other observations of *Echinacea's* life history (Wagenius 2000). To parameterize the relationship between the local density of flowering plants and seed set, we estimated  $\kappa$  and  $\gamma$  with the data set generated from the empirical study. We solved equations (1) and (2) simultaneously, using all values of  $d_{ij}$  for  $j = 1, 2, \dots, 6$  and assuming  $c_{ij} = 1$  for all plant pairs. We used the method of least squares to determine the best-fit values for  $\kappa$  and  $\gamma$ . With our data set, many  $\kappa, \gamma$  combinations yielded high  $R^2$ . But with a given  $\kappa$ ,  $R^2$  was very sensitive to changes in  $\gamma$ , and vice versa. In all of our parameterizations, we set  $\alpha = 1$  to simplify estimation of  $\kappa$  and  $\gamma$ . These estimates were not particularly sensitive to  $\alpha$ , and a maximum rate of seed set approaching 1 is consistent with empirical observations (Wagenius 2004). This pollination model is appropriate for species pollinated by generalist insects, small bees, or wind, but it would be inappropriate for plants pollinated by specialist pollinators that fly longer distances as individual plants become sparser (Levin 1978).

Demographic parameters were fixed in the model and chosen to make the modeled population dynamics consistent with empirical observations. Because our main goal was to understand Allee effects during pollination,  $\beta$  and  $K$  were chosen to produce spacing of flowering plants that is consistent with empirical observations in natural populations: density-dependent threshold for seedlings,  $K = 1.005$  plants, near-neighbor weighting factor,  $\beta = 2.0 \text{ m}^{-1}$ . Maximum floret production,  $N = 80$ , seedling recruitment, and juvenile survival rates were based on empirical observations. As aggregated in the model, each flowering adult plant could annually produce a maximum of 2.8 flowering adults 3 years later, in the absence of pollen limitation, inbreeding depression, dispersal to nonhabitat, and competition with nearby neighbors. We know that inbreeding affects juvenile survival and growth rates. We also suspect that it affects time to initial flowering and adult survival and reproduction. Our estimate for the magnitude of inbreeding depression,  $m = 0.5$ , simplifies the known complex expression of inbreeding depression into one aggregated life-history transition. Adult mortality ( $0.05 \text{ year}^{-1}$ ) is consistent with empirical estimates of longevity for this species (Hurlburt 1999). Mean *Echinacea* generation time, the average age of the parents of all offspring produced, is

thus 24 years in our model. These parameters are suitable for modeling population dynamics of *Echinacea* and other sporophytically SI, long-lived prairie plants.

#### Experimental Model Runs

We used the model to investigate the effect of breeding system on the consequences of habitat fragmentation for plant population persistence and demography. Hereafter, we use the term “breeding system” to refer to both the SI and SC breeding systems, with the SI matings governed by the S locus and the SC matings modeled with six levels of selfing (0%–50%). These seven levels encompass breeding systems of many common prairie species (Havercamp and Whitney 1983; Molano-Flores 2004). We performed two simulation experiments: (1) demography of habitat area and breeding system, to investigate the effect of variation in habitat area and breeding system on population demography, and (2) breeding-system and population persistence, to elucidate the effect of breeding system on population persistence in a multipopulation system. These two experiments enable us to investigate individually based spatial processes that are directly relevant to the empirical study. The model as coded includes many constants that can be modified to enable further investigation into the dynamics of systems with other ecological, reproductive, or life-history characteristics.

**Demography of Habitat Area and Breeding System.** Our objective with this simulation experiment was to measure the effect of seven different breeding systems on the dynamical and genetic responses of populations when suddenly decreased to habitats with areas ranging from 100 to 2,500 m<sup>2</sup>, the areas of remnants in our study site. For each of the seven breeding systems, we started with an identical population in which every individual was unrelated at all six autosomal loci. We simulated the dynamics of this population in a relatively large habitat (50 m × 50 m) for 500 years (~25 generations), allowing demographic and genetic structure to stabilize. We then instantly reduced the habitat area and continued the simulation for another 500 years. We simulated five levels of habitat reduction for each of the seven breeding systems and replicated each breeding system by habitat reduction simulation five times. Our null hypothesis is that neither breeding system nor remnant area affects population demography. We recorded demographic information every 10 years.

**Breeding System and Population Persistence.** Our objective with this simulation experiment was to measure the effect of breeding system on population persistence. For each of the seven breeding systems, we simulated the dynamics of 50 isolated populations either until all habitat remnants

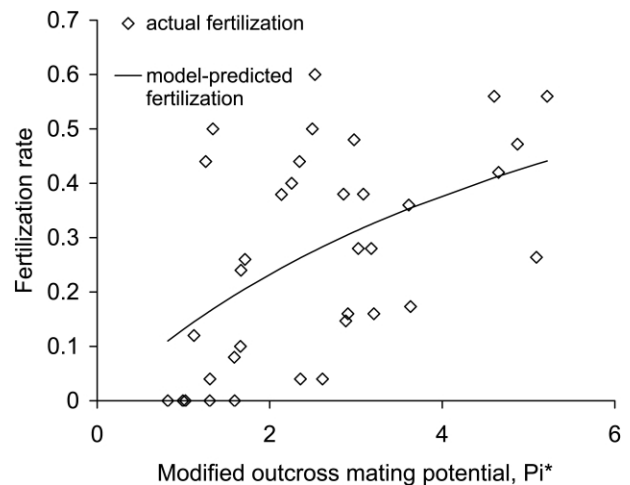
were unoccupied or for 1,000 years (whichever came first). Each isolated remnant (49 m<sup>2</sup>) was smaller than the habitat areas we used in the previous experiment. We repeated the simulation 10 times for each breeding system and computed the average number of remnants occupied at each time step. Using the average remnant occupancy, we estimated the extinction rate at time  $t$ ,  $E_t$ ,

$$E_t = -\frac{\ln(\bar{N}_t/N_0)}{t}, \quad (6)$$

where  $t$  is time,  $\bar{N}_t$  is the average number of occupied remnants at time  $t$ , and  $N_0$  is the initial number of occupied remnants (50; Neuhauser et al. 2003).

#### Results

Fertilization rates varied from 0% to 60% among individual flowering *Echinacea* plants on the Staffanson Prairie Preserve transect. Fertilization rates increased with the weighted local density of flowering plants,  $P_i^*$  (fig. 1). This positive density dependence is an Allee effect. Using the empirical results, we estimated pollen dispersal distance ( $1/\gamma$ ) to be 13.3 m. Furthermore, we estimated the effective number of pollen donors that yields a fertilization rate ( $\kappa$ ) of 0.5 to be eight individuals. Within one flowering season, we could not determine compatibility between pairs of plants,  $c_{ij}$ , and natural fertilization rates, thereby compro-



**Figure 1:** Relationship between fertilization rate and modified outcross mating potential ( $P_i^*$ ) of 35 individual *Echinacea angustifolia* plants from a transect on a nature preserve. Fertilization rate is the fraction of fruits that contain an embryo (i.e., successfully pollinated).  $P_i^*$  is the density of the six closest flowering *Echinacea* plants around the focal individual, weighted according to a negative exponential pollen dispersal distribution. The estimation of  $P_i^*$  is described in the text.

missing our estimates of  $\gamma$  and  $\kappa$ . So in these estimates, we assumed that all  $c_{ij} = 1$ .

Our empirical studies showed that mean compatibility between pairs of plants increased with population size over the range of sizes found in our study site:  $n = 19$ ,  $P < .0001$  (fig. 2A). Our empirical analysis offers no insight into patch aging because our results represent a snapshot in time and because we do not know the precise land use history of the study populations, except that fragmentation occurred primarily between 1870 and 1950.

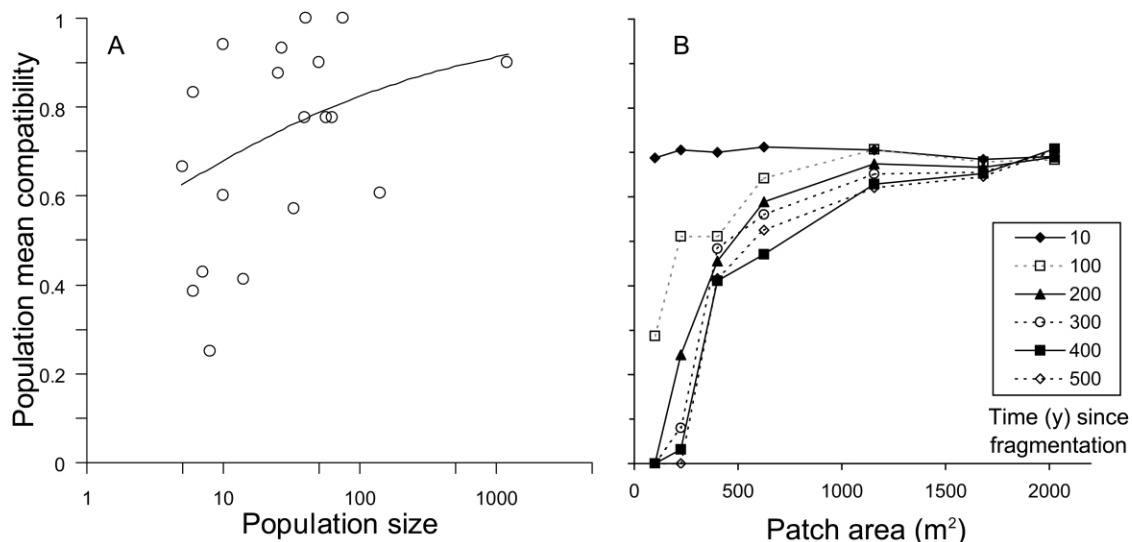
Our model results of mate compatibility mirror the pattern observed from our empirical study but offer additional information about the effect of patch age (fig. 2B). The effect of habitat area on compatibility increases with patch age. The mean compatibility rate in the smallest remnants declined with patch age, while it remained nearly constant in the largest habitat remnants. To compare model output with the empirical results, we used a model sampling scheme that mimics the empirical sampling of the six closest neighbors. But we also censused compatibility among all individuals in the model, instead of sampling, and the results were similar, suggesting that our empirical results estimate mean population compatibility rates well.

#### Demography of Habitat Area and Breeding System

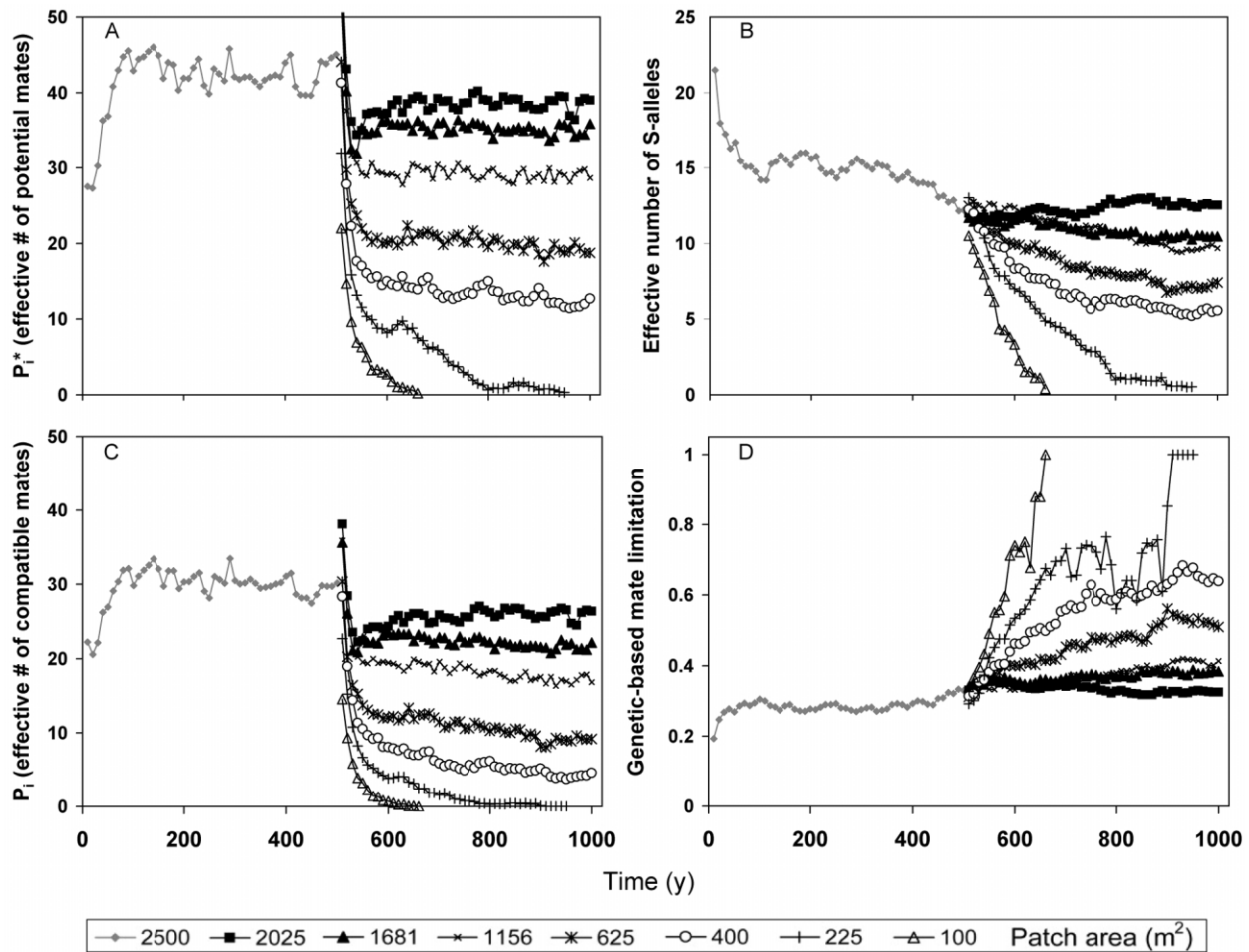
The results of our first simulation show that the effect of habitat fragmentation on *S*-allele diversity varies with the extent of fragmentation (remnant area) and increases over

time (fig. 3C). The reduction in *S*-allele diversity causes a reduction in the proportion of potential mates that are also compatible. The additional pollen limitation due to incompatibility among potential mates is caused by the loss of *S* alleles (fig. 3B). This time-dependent genetic effect is most pronounced in small remnants, and there appears to be a patch area ( $\sim 2,000 \text{ m}^2$  in our model) above which there is no discernible additional effect over the time simulated. If we ignore compatibility (i.e., assume that all  $c_{ij} = 1$ ) and calculate this modified outcross mating potential ( $P_i^*$ ), the result shows that there is a substantial habitat area effect on reproduction that is attributable to nongenetic causes—the traditional Allee effect (fig. 3A). The true outcross mating potential ( $P_i$ ) reveals a similar overall pattern, but the difference is greatest in the smallest remnants, where genetic drift has reduced *S*-allele diversity the most (fig. 3C). The proportional difference of these two indices ( $1 - P_i/P_i^*$ ; fig. 3D) quantifies the additional genetically based Allee effect and shows that the effect is greater in smaller remnants than in larger remnants and that the remnant size effect increases over time.

Compared to those in SC populations, reproduction and population growth rates in SI populations are more sensitive to habitat area. Furthermore, the effect of population size on reproduction and population growth rates changes with time; in other words, patches age. Soon after fragmentation, SC populations reach equilibrium fertilization rates, while fertilization in SI populations decreases over time and with decreasing habitat area (fig. 4A, 4B). In-



**Figure 2:** Mean compatibility rates versus population size or habitat area among the six closest flowering plants of six focal plants from (A) each of 19 remnant *Echinacea* populations in 2003 and (B) each of seven simulated populations at six patch ages (years since fragmentation). Note that mean *Echinacea* generation time in our model is 24 years. To present the model results, we use patch area as a proxy for population size for illustrative purposes. The variation in population size within a patch was small compared to the variation in population size between patches.



**Figure 3:** Effect of habitat area over time on four aspects of the Allee effect. *A*, Traditional Allee effect, a modified outcross mating potential,  $P_i^*$ , where all mating pairs are considered compatible (eq. [1] with  $c_{ij} = 1$ ). *B*, Effective number of alleles at the mating compatibility (*S*) locus. *C*, Traditional Allee effect plus the additional effect due to mating incompatibility as quantified by the outcross mating potential,  $P_i$  (eq. [1]). *D*, Proportional reduction in fertilization attributable to mating incompatibility among potential mates (plants within pollen dispersal distance), that is, the *S*-Allee effect. This simulation was run with a large area until year 500, when habitat area was reduced to the listed area. Data points were calculated once every 10 years as the mean of five simulated annual population means.

breeding rates for both SI and SC populations increase over time, and the effect is greatest in small populations (fig. 4C, 4D). Inbreeding rates are greater in SC than in SI populations. Recruitment decreases with time and decreasing habitat area in both SC and SI populations, but the effect of fragmentation is greatest in SI populations (fig. 4E, 4F). The net effect of fragmentation on plant demography is revealed in the response of population mean density to fragmentation. Self-compatible plants rapidly reach and maintain a steady population mean density over time, while population mean density in SI plants decreases with time, and the decrease is greatest in small remnants (fig. 4G, 4H).

#### *Breeding System and Population Persistence*

To further investigate the effects of breeding system in fragmented populations, we varied the breeding system to show that allowing selfing reduces population extinction rates by slowing the rate of patch aging (fig. 5).

#### Discussion

The results of our empirical study show that the number of nearby compatible mates increased with population size in remnant populations of the common, sporophytically SI purple coneflower *Echinacea angustifolia* growing in



fragmented prairie habitat. Pollination and recruitment increased with weighted local density around individual flowering plants in the largest remnant population.

The results of our model show that the strength of the Allee effect is greater in populations with sporophytic self-incompatibility than in SC populations. All species in our model, regardless of their breeding system, suffer reduced reproduction in small populations through scarcity of potential mates and increased inbreeding depression. But, in contrast to SC plants, where all potential mates are compatible, SI species suffer from an additional, genetically based Allee effect (*S*-Allee effect). This effect (fig. 3D) is caused by the loss of allelic diversity at the *S* locus, which reduces the number of compatible mates and is quantified as the proportional difference between the mating potential when mating compatibility among potential pollen donors is included (fig. 3C) and that when it is ignored (fig. 3A). Furthermore, the strength of this additional Allee effect increases through time because random genetic drift reduces allelic diversity at a rate inversely proportional to population size. In other words, the number of nearby compatible mates in old remnants is fewer than that in younger remnants. This “patch-aging” effect due to genetic drift has not emerged from a demographic model before, but patch aging by other means has been recognized as a detriment to metapopulation persistence (Hastings 2003).

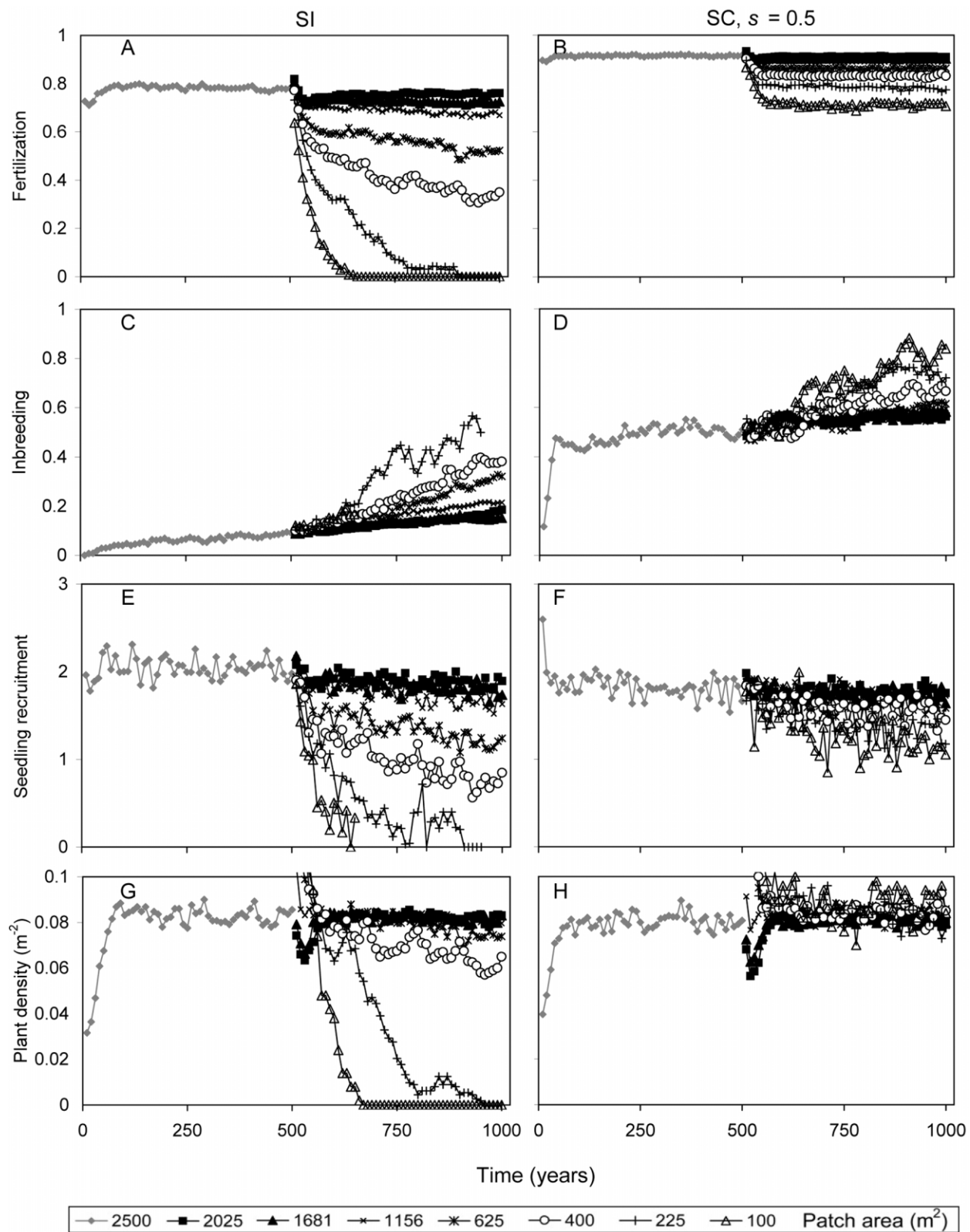
The Allee threshold requires a new interpretation in light of the time-dependent and genetically based *S*-Allee effect. The Allee threshold, the critical population density below which a population cannot persist, is a predicted feature of models and has been identified empirically (Lande 1987; Groom 1998; Keitt et al. 2001; Lennartsson 2002). Our work corroborates the work of others who have suggested that this threshold depends on a plant's breeding system (Byers and Meagher 1992; Widen 1993; Luijten et al. 2000; Fischer et al. 2003; Willi et al. 2005). Our model further suggests that the threshold changes over time in such a way that an isolated population's growth rate and estimated time to extinction depend on its breeding system and how long it has been isolated (fig. 5). For completely selfing species, which need no mates, there is no expected threshold because the inbreeding level is fixed. In SC species, as the intrinsic selfing rate ( $s$  in eq. [2]) decreases, the dependence of the Allee threshold on time increases (fig. 5) because inbreeding increases and the number of potential mates declines with population size. In SI species, we expect a higher and increasing threshold that depends on *S*-locus diversity: as inbreeding increases over time, the number of potential mates decreases and the number of compatible mates decreases. Thus, the difference between the SC and SI thresholds is expected to increase through time. In other words, the *S*-Allee effect increases the rate of patch aging in SI species relative to that in SC species.

The dependence of critical thresholds on spatial, temporal, and genetic parameters makes their empirical detection and interpretation complicated.

Our model explicitly incorporates genetic and ecological mechanisms in a demographic model, thus distinguishing it from other purely demographic models, for example, those based on the fundamental metapopulation model (Levins 1969). For example, Hanski's work on the metapopulation capacity incorporates population extinction rates that are independent of genetics and thus constant through time (Hanski and Ovaskainen 2000). Our work complements recent work that has investigated the effect of animal mating systems on Allee effects and population extinction (Engen et al. 2003; Bessa-Gomes et al. 2004; Sæther et al. 2004). Bessa-Gomes et al. illustrated the dependence of the Allee effect on sex ratios, which are modeled stochastically and arise from monogamous and polygamous social mating systems, but did not incorporate inbreeding. Plants have a variety of breeding systems, and self-incompatibility is present in some form in a majority of species (Hiscock and Kues 1999). In most self-incompatibility systems, mating types can be attributed to a single genetic locus.

Our model expands on previous genetic models of self-incompatibility (Wright 1939). Imrie et al. (1972) modeled the loss of *S* alleles by drift and found that populations of 16 individuals did not maintain enough alleles to persist but populations of 32 individuals maintained four alleles at equilibrium. Byers and Meagher (1992) developed a computer simulation model to test effects of small population size on *S*-allele frequencies and seed set. They found that mean seed set decreased and seed set variance increased in small populations. Reinartz and Les (1994) developed a spatially explicit computer simulation and showed that the distribution of seed set curves depends on the number of *S* alleles in the population. A recent paper investigated effects of drift at nuclear male-fertility-restorer loci on sex ratios in remnant prairie populations of a gynodioecious plant (not SI), *Lobelia spicata* (Byers et al. 2005). The results suggested that increased loss of male function via drift in small and isolated populations has potential to impede seed production. Vekemans et al. (1998) modeled mate availability in finite SI populations and found that the equilibrium numbers of *S* alleles per population depends on dominance relationships among *S* alleles and on the number of pollen genotypes available to each plant. None of these genetic studies modeled demographic processes, whereas our model showed that genetic drift at the *S* locus influences population dynamics, including extinction rates.

Our model complements a recent theoretical paper that modeled demographic processes in an SC plant with variable rates of outcrossing (Morgan et al. 2005). As in our



model, the model of Morgan et al. incorporated reproduction via both outcrossing and self-fertilization, inbreeding depression, and density-dependent pollination. Consequently, Allee effects and density-dependent pollen limitation are prominent features of both the self-compatibility model of Morgan et al. (2005) and our self-incompatibility model. In contrast to the self-compatibility model, our self-incompatibility model included population sizes, and thus drift played an important role in the genetic and demographic dynamics. By varying mating and breeding systems, our model demonstrated the dependence of patch aging on density and diversity of mates. In addition, we modeled discrete individuals whose pollination depended on local density, not population mean density.

Although we parameterized the model for *Echinacea*, we expect that the general results are relevant for the many other common prairie plant species that share similar life-history, ecological, and reproductive attributes. More generally, this model is appropriate for other SI plants that have limited pollen dispersal, such as those pollinated by generalist insects. Plants pollinated by specialist insects are expected to have pollinator visitation that is less density dependent than in our model (Levin 1978; Kunin 1997), but they too might experience *S*-Allee effects with habitat fragmentation if plants become pollen limited.

The genetic and reproductive features that we introduced to the basic demographic model are features common to many real-life organisms, indicating that a reduction in fertilization due to mate incompatibility is likely to be quite common. First, limited pollen dispersal and pollen limitation are ubiquitous, especially in the context of habitat fragmentation (Burd 1994; Larson and Barrett 2000; Aizen et al. 2002; Knight et al. 2005). Second, self-incompatibility is widespread generally, particularly in the prairie flora, especially in the grasses (Poaceae) and the Asteraceae (Li et al. 1997; McKone et al. 1998; Molano-Flores 2004). The extent of mate incompatibility among individual plants in nature is difficult to detect and has been assessed infrequently (Stevens and Kay 1989; Byers and Meagher 1992; DeMauro 1993; Brennan et al. 2003), and the breeding systems of most prairie species remain unknown (Haverkamp and Whitney 1983; Molano-Flores 2004). However, there is evidence that fecundity often var-

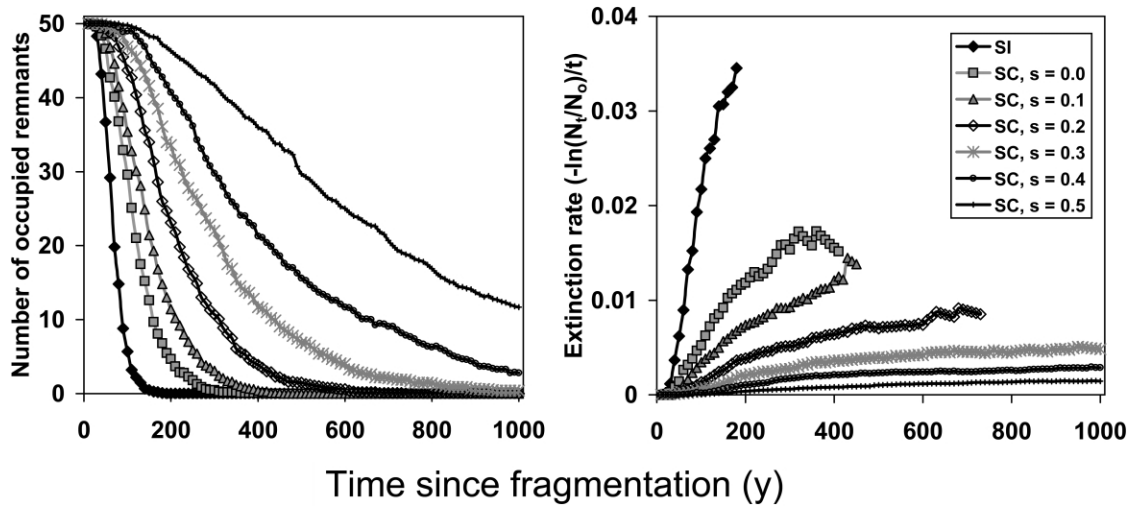
ies with density (reviewed in Kunin 1997), and researchers have attributed reduced fecundity and pollen limitation to many mechanisms, including self-incompatibility (Byers 1995; Kery et al. 2000; Groom 2001; Soons and Heil 2002; Johnson et al. 2004). Fischer et al. (2003) found that cross-compatibility rates increased with population size in a narrow endemic with sporophytic self-incompatibility. Third, circumstantial evidence of colonization limitation of species diversity in grassland and other habitat suggests that limited seed dispersal is common (Levin 1989; Foster and Tilman 2003). Seed dispersal is another feature that is challenging to measure directly. As habitat fragmentation becomes more extensive and interpopulation movement of seed and pollen becomes less frequent, the reduced reproduction attributable to mate incompatibility, as described here, and its tendency increase over time will play a greater role in the dynamics of plant populations.

The trade-off between avoiding inbreeding and avoiding mate scarcity is ubiquitous in plants, and our model reveals that the factor that limits population density may change from inbreeding depression in large remnants to mate limitation in small remnants. We calculated the mean relative population density in the largest and smallest fragments for each breeding system relative to the breeding system with the highest density (fig. 6). As selfing rate increased, relative fitness decreased slightly in the largest fragment but increased greatly in the smallest fragment, suggesting that as fragment size declines, breeding system becomes a better predictor of density. This result likely depends on the assumption that the magnitude of inbreeding depression is independent of breeding system, an assumption supported by Byers and Waller (1999), and provides important insight into potential changes in community structure as a function of remnant size.

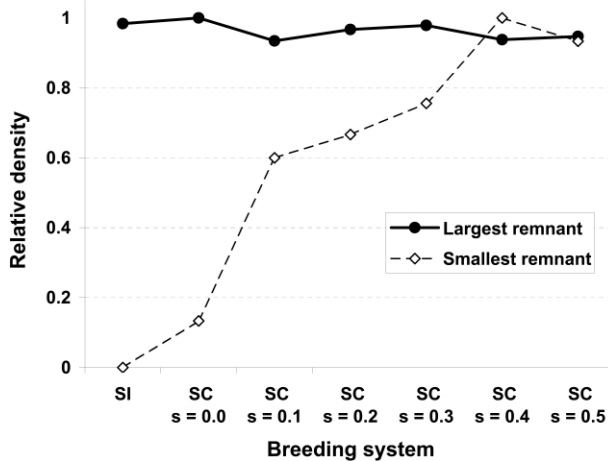
Our model shows that fragmentation alters the demographic consequences of inbreeding and mate scarcity. In unfragmented populations and in large remnants, SI and highly outcrossing species may have higher fitness and population mean density than predominantly selfing species because of differences in inbreeding (fig. 4C vs. fig. 4D). In smaller and older fragments, predominantly selfing species will likely have higher fitness and population mean density than SI and highly outcrossing species because of differences in mate limitation (fig. 4A vs. fig. 4B). In SC

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**Figure 4:** Effect of breeding system on four population mean demographic and genetic parameters. Each measure is shown for simulations with a self-incompatible (SI) population (left) and an otherwise identical self-compatible (SC) population with a 50% outcrossing rate (right). Fertilization (A, B) is the proportion of fruits with a fertilized ovule. Inbreeding (C, D) is the mean proportion of six autosomal loci that are autozygous. Recruitment (E, F) is the number of flowering 3-year-olds produced per plant, which is a product of the total fruits, the fertilization rate, juvenile survival, and inbreeding depression per plant. Population mean plant density (G, H) is the mean number of adult plants per square meter in the remnant. Each simulation was run with a large area until year 500, when habitat area was reduced to the listed area. All data points were calculated from annual means of five simulation runs.



**Figure 5:** The aging rate of a remnant population depends on its selfing rate. As the selfing rate increases, the predicted number of occupied remnant populations at any given time increases (A) and extinction rates become less dependent on time since fragmentation, that is, patch age (B). Self-incompatible (SI) populations age most quickly because of the continual loss of compatibility alleles by drift. The parameter  $s$  represents the selfing rate (eq. [2]). SC = self-compatible.



**Figure 6:** Effect of breeding system and remnant size on population mean density. Relative plant density, based on the breeding system yielding the highest mean density, is shown for each of seven breeding systems 500 years after fragmentation in the largest remnant (solid line, circles) and the smallest remnant (dashed line, diamonds). The selfing rate,  $s$ , is in equation (2). The figure shows that in the largest fragments, obligate outcrossing breeding systems have slightly higher mean density than selfing systems, while in the smallest fragments, greater selfing increases relative density. The figure illustrates that inbreeding may limit density (i.e., population mean fitness) in large remnants, while mate scarcity clearly limits density in small remnants.

species, fragmentation induces an Allee effect but not the additional time-dependent S-Allee effect, and so SC species suffer from habitat fragmentation but not as much as SI species. Thus, plant communities in fragmented habitat are expected to shift from outcrossing and SI species to selfing and SC species.

As habitat areas decrease and as the time since fragmentation increases, it becomes increasingly important to consider breeding systems when designing conservation plans. Although our model organism is a common plant chosen because of its typical life-history and reproductive traits, the results of this model are also relevant for threatened and rare species (Fischer et al. 2003). In addition, many common species have recently experienced reduced proximity and fewer potential mates because of habitat destruction and fragmentation. Recent changes in habitat area available to common species may be far greater in common plants than the changes experienced by rare or threatened species, which may have long histories of isolated habitats and low-density populations. Therefore, we expect that the S-Allee effect and its consequences are important in many species, including those that are considered common and not currently threatened. In addition, we expect detrimental effects to become more severe over time as patches age.

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