

Modeling the Role of Plant Breeding System in the Emergence of Extinction Risk

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Introduction

Populations of a single species can be considered complex systems of interactions between individuals. The persistence or extinction of a population over a given time interval is the emergent outcome of individual life histories, which are the result of multiple genetic, demographic and stochastic processes. Feedbacks between genetic and demographic effects influence the trajectory of the system, particularly where reproduction is concerned. Despite these interactions, evolution and demography have traditionally been considered different disciplines. Because many of the feedback loops between genetics and demography intensify with decreasing population size, neither aspect can be neglected in small populations.

Given the ubiquity of habitat fragmentation, it is increasingly important to understand the factors that contribute to the persistence or extinction of small, isolated populations. It is not immediately evident after a fragmentation event whether a population is at elevated risk of extinction. Population declines may last over a century before extinction or rebound occurs (Tilman *et al* 1994). In contrast, most empirical fragmentation studies are short (< 14 years), and longer studies do not approach the durations over which this extinction debt operates (Debinski and Holt, 2000). Because long term trends are not necessarily apparent in short-term studies, a theoretical framework that distinguishes between populations that are likely to persist and those that are not would be useful from a conservation standpoint.

Small populations exhibit certain well-understood patterns that increase extinction risk. Genetic drift leads to the loss of alleles from a population, due to random changes in allelic frequency that occur between each successive generation. The Allee effect describes the positive correlation between per capita reproductive rates and population density, below a saturation threshold (Wagenius *et al* 2007). The extent to which genetic drift and Allee effects influence extinction risk is dependent upon population size and density. In sufficiently small populations, the combined strength of genetic drift and Allee effects is greater than that of natural selection. These processes lead to population declines by suppressing reproduction via inbreeding depression and mate limitation respectively (Wagenius *et al* 2007). Reproductive rates are key in determining whether genetic drift and Allee effects intensify or weaken over time. In plant populations, reproduction depends on proximity to neighbors, the dispersal distance of pollen, and breeding system.

Estimating the influence of breeding system on reproductive rates is a non-trivial task because breeding systems impose a tradeoff between maximal reproductive output and minimal inbreeding depression (Wagenius *et al* 2007). Plant breeding systems range from full self compatibility (SC) to full self incompatibility (SI). Self incompatibility reduces the risk of inbreeding depression by limiting the number of compatible mating pairs, while self compatibility eliminates mate limitation by allowing each individual to self-fertilize. Because breeding system is implicit in the tradeoff between mate availability and inbreeding depression, it is expected to be an important factor in the persistence of fragmented plant populations. Empirical and theoretical studies have confirmed this (Aguilar 2006, Wagenius *et al* 2007).

Self incompatibility in flowering plants is typically controlled by a single S-locus containing two S-alleles. Both alleles are present in the stigma and other female tissues. Fertilization occurs only when contact occurs between stigma and pollen that do not express any common S-alleles. Species in which the pollen carries a single S-allele are termed gametophytic; those in which the pollen possesses both alleles are

sporophytic (Hiscock and McInnis 2003). Because of this, gametophytic systems are less restrictive, exhibit greater mate availability and are subject to higher inbreeding risk.

It is not uncommon among sporophytic species for dominant and recessive S-alleles to occur, such that the former masks the expression of the latter. Because self incompatibility systems require relatively large numbers of S-alleles to function, numerous dominance patterns are possible. Cases in which there is a clear dominance hierarchy among alleles are classified as linear. Where no such hierarchy exists, dominance is nonlinear. Dominance interactions are typically asymmetric, following different patterns in female and male tissues. Mate limitation is relaxed in the presence of S-allele dominance because masked alleles shared by the pollen and stigma do not prevent fertilization. Although this elevates inbreeding risk, it has been hypothesized that dominance interactions are adaptive in populations with few S-alleles (Brennan *et al*, 2002).

Previous work has treated all self incompatible systems as equivalent, despite the differences in mate availability that arise in each case. Because breeding system influences population persistence in fragmented habitats, it is important not to overlook these differences.

Methods

To investigate the role of breeding system in the persistence of fragmented populations, I have extended the software model described by Wagenius *et al* (2007). This model individual-based, stochastic and spatially explicit. Each individual contains 6 autosomal loci and an S locus, which are used to calculate the constraints on seed set due to inbreeding depression and mate limitation respectively. Alleles are randomly passed on to offspring from compatible parents. The model as described by Wagenius *et al* simulates both self compatible and sporophytic self incompatible breeding systems. In order to compare the effects of mate limitation between self incompatible systems, I have added dominance interactions and gametophytic self incompatibility.

In each simulation run, a population is created in a large, continuous habitat (2500 m²) and allowed 500 years to reach genetic and demographic stability. At this point, habitat area is reduced to 100m² and the individuals outside of the remnant area discarded. The population is then followed for an additional 500 years. Each simulated year is comprised of a set of processes, including pollination, fertilization, seed set, seed dispersal, establishment of seedlings, growth of juveniles, survival of adults and overwintering mortality. The program records population size and density, mean number of compatible mates, probability of fertilization, seed set, juvenile recruitment, homozygosity, and effective number of S-alleles every ten years.

To compare influence of self incompatibility mechanism on the persistence of fragmented populations, I ran the model five times with each of the following breeding systems: self compatible with a 50% selfing rate, sporophytic SI with no dominance, sporophytic SI with linear dominance and gametophytic SI.

Results

Prior to fragmentation, all populations reached similar population densities of about 0.05 plants/m² (Fig 1). Homozygosity was similar in large self incompatible populations, regardless of mechanism. Habitat loss led to decreased population density, reduced mating and increased homozygosity in all populations, but only those with sporophytic self incompatibility became extinct. Because inbreeding levels were lowest for sporophytic populations with no dominant S-alleles, it is likely that mate limitation is a more important component of extinction risk. As expected, gametophytic populations exhibited behavior that fell between the self compatible and sporophytic extremes.

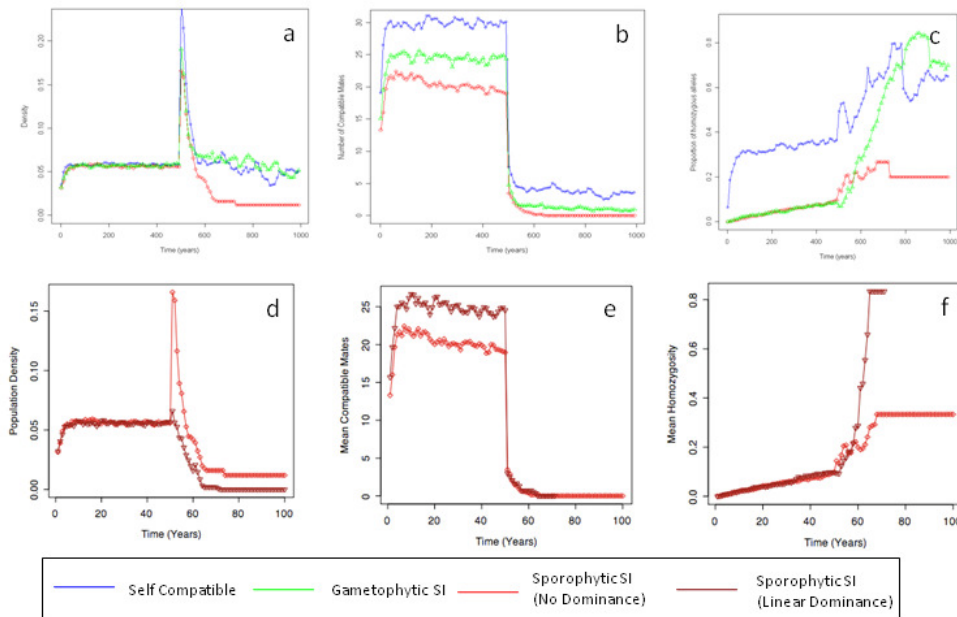


Figure 1. Outcomes of habitat fragmentation in various breeding systems. Self compatible, gametophytic and sporophytic (no dominance) systems are shown in the top row of graphs. Sporophytic systems with no dominance and linear dominance are compared in the bottom row. Graphs (a) and (d) show population density, graphs (b) and (e) show the mean number of compatible mates available to an individual, and graphs (c) and (f) show the proportion of homozygous loci in the population. Each data point is a ten-year mean, averaged over five simulation runs.

Sporophytic populations with linear dominance behaved similarly to gametophytic populations, with respect to inbreeding and number of compatible mates. Increased mate availability, however, did not mitigate extinction risk relative to sporophytic populations without dominance. It is possible that sporophytic populations are inherently less resilient to inbreeding depression than those with other breeding systems. Future investigation using dominance patterns taken from empirical studies will provide insight into whether other dominance patterns successfully mitigate extinction risk in fragmented populations.

References

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