



Evolution of Plant Mating Systems

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Introduction

Mating system has profound consequences for the ecology, distribution, and genetic structure of plant populations, and even the macroevolutionary fates of species and larger clades. “Mating system” is a notoriously ambiguous term, which we define operationally as the degree to which mating is random or nonrandom. This definition captures most of its common usage, at least as applied to plants. The most common form of nonrandom mating is inbreeding. When inbreeding is between separate but closely related individuals, it is called biparental inbreeding. Another form of inbreeding specific to hermaphroditic organisms is self-fertilization, also known as selfing. Although both forms are important, plant mating system research largely focuses on the rate of selfing. Inbred offspring are more homozygous than outcrossed offspring and thus exchange fewer alleles among their chromosomes when recombination occurs. Inbred populations have less allelic diversity than outcrossing populations, and the diversity they do have is sorted into homozygous lineages. Many plants have traits that reduce inbreeding, but why? Inbreeding depression—the decrease in offspring fitness caused by inbreeding—favors outcrossing. Selection to evade the expression of inbreeding depression by reducing inbreeding has in part shaped the remarkable diversity of floral architecture. Despite this, the evolutionary transition from outcrossing to self-fertilization is one of the most commonly traversed in flowering plants. What could overcome, repeatedly, the need for biparental sex that seems so common in eukaryotes? One of the most apparent theoretical advantages of self-fertilization over cross-fertilization is that a plant that can fertilize itself eliminates the liability of relying on pollinators or mates. This advantage might explain why selfing is more common in populations in which access to pollinators or conspecific mates is unreliable, such as frequently disturbed sites, edges of a species’ range, and locations reachable only by long-distance dispersal. A subtler advantage is that “selfers” may engage in a form of economic protectionism; pollen can fertilize self-ovules without needing to compete with pollen from other sires. Despite these advantages to an individual within a population, the reduction in genetic variation and effective recombination caused by selfing can limit future adaptation. Failure to adapt could lead to extinction. A species’ mating system, therefore, may be an essential determinant of its evolutionary lifespan.

General Overviews

The relative advantages of inbred and outbred mating systems in plants have been discussed since at least the 19th century. Barrett 2010 provides a detailed account of Darwin’s thoughts on mating system. In the 20th century, a series of canonical models for the evolution of self-fertilization arose from the field of population genetics. Charlesworth and Charlesworth 1979 clearly outlines the sequence of important models until the late 1970s, and Jarne and Charlesworth 1993 includes all current major models. Parallel to the development of theory, descriptive science has expanded the corpus of knowledge on the distribution of mating systems among taxa. Fryxell 1957 reviews mating system diversity in depth. Because both selfing and asexual reproduction require only a single parent, it is easy to conflate the two. Holsinger 2000 explains the key differences between selfing and asexual reproduction.

Barrett, Spencer C. H. 2010. Darwin’s legacy: The forms, function and sexual diversity of flowers. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:351–368.

This high-level review evaluates adaptive explanations of the morphological diversity of flowers. It extensively catalogs different types of floral adaptations, including those that are less well known. The author traces modern discussion of the topic back to Darwin, who explained most floral adaptations as a means of maximizing outcrossing.

Charlesworth, Deborah, and Brian Charlesworth. 1979. The evolutionary genetics of sexual systems in flowering plants. *Proceedings of the Royal Society of London B: Biological Sciences* 205:513–530.

The authors review the development of concepts in a chronological sequence of canonical models and relate how each built on previous work. This article provides the clearest view available of the historical context of models published previously.

Fryxell, Paul A. 1957. Mode of reproduction of higher plants. *The Botanical Review* 23:135–233.

This taxonomically broad review classifies angiosperm mating systems based on frequency of cross-fertilization, self-fertilization, and asexual reproduction through seed (see Outcrossing Rate). It gives a sense of the proportions of species practicing these forms of reproduction.

Holsinger, Kent E. 2000. Reproductive systems and evolution in vascular plants. *Proceedings of the National Academy of Sciences* 97:7037–7042.

This review provides an introduction to the population genetic consequences of mating system in land plants. In particular, the comparison of the effects of self-fertilization and asexual reproduction reveals important symmetries while pointing out potential sources of confusion between them.

Jarne, Philippe, and Deborah Charlesworth. 1993. The evolution of the selfing rate in functionally hermaphrodite plants and animals. *Annual Review of Ecology and Systematics* 24:441–466.

The authors of this review recommend a reorientation of mating system research toward an empirical focus. They argue that the possible theoretical advantages of selfing and outcrossing have been exhaustively described, but that basic data on selfing rate, inbreeding depression, and inbreeding coefficients are insufficient to decide their importance. The authors also explain the uses and limitations of some of the methods of estimating these parameters.

Selective Forces Controlling Mating System

One major disadvantage and two advantages are usually invoked to explain the evolution of plant mating system. Inbreeding depression is the main factor preventing transitions to selfing on the population scale. Although reproductive assurance and transmission advantage do not comprise an exhaustive list of the advantages of selfing, each is the basis of one of the two most popular competing hypotheses for the evolution of increased selfing. The reproductive assurance hypothesis attributes the advantage of selfing to the ability to reproduce when pollinators or mates limit reproduction. The transmission advantage hypothesis explains the success of selfing as an outcome of the outsize genetic contribution that selfers make to the next generation.

Inbreeding Depression

Inbreeding depression is one manifestation of genetic load, the degree to which individuals fall short of the fittest possible genotype. In an outbred, genetically diverse population, there is a genetic load because even if a perfect genotype could be constructed from the standing genetic variants, no individual will actually possess it. In the common case that inbreeding decreases fitness, inbreeding depression is defined as the difference in fitness of an average inbred offspring from the average (imperfect) outcrossed offspring in a population. When used without qualification, inbreeding depression usually refers to population level inbreeding depression; however, individual lineages within a population may suffer more or less family-level inbreeding depression than others (Kelly 2005). Inbreeding depression summarizes all consistent fitness differences between inbred and outcrossed progeny, regardless of how these fitness differences manifest (e.g., increased seedling mortality, decreased adult fecundity, or reduced vegetative growth). Although inbreeding depression in plants has long been recognized (Knight 1799), Darwin 1876 is the first work to explain its relation to natural selection. Darwin's argument has since become a central principle in mating system evolution: when inbred progeny are less fit, selection should act to minimize inbreeding. After

the rediscovery in the 20th century of Mendel's work, biologists attempted to explain how inbreeding depression could arise from genetics. Such explanations are models of genetic architecture, the genetic causes of variation in a trait. The simplest genetic model of inbreeding depression is that recessive deleterious alleles occur harmlessly in heterozygotes at a low frequency of μ/s in a randomly mating population, where μ is the mutation rate and s is the selection coefficient. Two randomly chosen parents are unlikely to carry and pass on the same rare allele, but inbreeding relatives or selfing individuals may easily do so. Alternatively, in a pattern called overdominance or heterozygote advantage, heterozygotes might be intrinsically fitter than either homozygote. Charlesworth and Willis 2009 supports a general role for both strongly and weakly deleterious recessive alleles but not for truly overdominant loci. Dudash and Carr 1998 shows most inbreeding depression in two species of monkey flower to be caused by partially recessive alleles. In addition to investigating the genetic basis of inbreeding depression, biologists have also sought to determine its severity in natural populations. Crnokrak and Roff 1999 finds the fitness of inbred offspring in a sample of plant species is about two-thirds that of outcrossed offspring.

Charlesworth, Deborah, and John H. Willis. 2009. The genetics of inbreeding depression. *Nature Reviews Genetics* 10:783–796.

The authors review whether inbreeding depression is caused mostly by increased homozygosity for deleterious recessives or by decreased heterozygosity at overdominant loci. Inbreeding studies reveal deleterious recessives in species, but studies showing overdominance rarely exclude the possibility that putative overdominant allele pairs are actually two pairs of linked beneficial and deleterious alleles, a phenomenon known as apparent overdominance or pseudo-overdominance.

Crnokrak, Peter, and Derek A. Roff. 1999. Inbreeding depression in the wild. *Heredity* 83:260–270.

The magnitude of inbreeding depression in wild populations is not well documented, but this review gives some sense of what is known. The authors calculate the average inbreeding depression in fifteen plant species and perform similar calculations for several groups of animals.

Darwin, Charles. 1876. *The Effects of Cross and Self Fertilisation in the Vegetable Kingdom*. London: John Murray.

Darwin describes a long series of small experiments comparing the general vigor (in terms of height, seed number, and other characters) of the offspring of self- and cross-fertilized plants of many angiosperm species. The author documents a general trend toward reduced vigor in selfed plants, with a few exceptional reversals in some individuals or species.

Dudash, Michele R., and David E. Carr. 1998. Genetics underlying inbreeding depression in *Mimulus* with contrasting mating systems. *Nature* 393:682–684.

This crossing experiment separates additive and nonadditive genetic variance for inbreeding depression in *Mimulus guttatus* and *Mimulus micranthus*. In one of the first few experiments to test the genetic basis of inbreeding depression in a wild plant, the authors find little of the nonadditive variance that would indicate overdominance.

Kelly, John K. 2005. Family level inbreeding depression and the evolution of plant mating systems. *New Phytologist* 165.1: 55–62.

This review makes the critical distinction between population-level inbreeding depression, a mean decrement in fitness, and family-level inbreeding depression, the set of individual observations of decrements. It also explains how the genetic architecture of inbreeding depression can be estimated from covariance among family-level inbreeding depression observations.

Knight, Thomas Andrew. 1799. An account of some experiments on the fecundation of vegetables: In a letter from Thomas Andrew Knight, Esq. to the Right Hon. Sir Joseph Banks, K. B. P. R. S. *Philosophical Transactions of the Royal Society of London* 89:195–204.

Inbreeding depression was recognized long before the discovery of either genetics or natural selection. This crossing study on *Pisum sativum* contains early experimental observations of inbreeding depression.

Reproductive Assurance

If inbred offspring are generally less fit than outcrossed offspring, then it is surprising that predominantly self-fertilizing taxa exist at all. Darwin 1877 provides one of the first attempts to reconcile the existence of selfing taxa with selection against inbreeding. Darwin hypothesizes that predominantly selfing taxa arise when selection for the ability to reproduce without pollinators or mates overcomes selection against inbreeding. This is the reproductive assurance hypothesis for the transition to self-fertilization. Field studies and experiments find pervasive evidence of reproductive assurance. Piper, et al. 1986 shows that pollen limitation is at least partly responsible for the inferior fecundity of highly outcrossing morphs of primrose. Moeller and Geber 2005 finds that *Clarkia xantiana* individuals with weak morphological barriers to self-fertilization show greater seed set than others in conditions adverse to cross-pollination, and Kalisz and Vogler 2003 detects reproductive assurance in *Collinsia verna*.

Darwin, Charles. 1877. *The various contrivances by which orchids are fertilized by insects*. 2d ed. London: John Murray.

Darwin's concluding remarks on floral adaptations for cross-fertilization contain one of the earliest statements of the reproductive assurance hypothesis. Self-fertilizing plant taxa are explained as the result of selection having favored selfing when pollinators were rare or absent.

Kalisz, Susan, and Donna W. Vogler. 2003. Benefits of autonomous selfing under unpredictable pollinator environments. *Ecology* 84:2928–2942.

This three-year study on wild populations of *Collinsia verna* in Pennsylvania uses combinations of experimental treatments (pollinator exclusion, emasculation, and hand-pollination) to disentangle causes of failure to set fruit. It illustrates the degree to which pollinator success and reproductive assurance can vary among organisms and through time and space.

Moeller, David A., and Monica A. Geber. 2005. Ecological context of the evolution of self-pollination in *Clarkia xantiana*: Population size, plant communities, and reproductive assurance. *Evolution* 59:786–799.

The authors of this experimental field study estimate the effect of population size and isolation on fitness of phenotypes predisposed to outcrossing or selfing. This study stands out because it establishes a basis for selection rather than merely showing that selection could have produced extant patterns.

Piper, John G., Brian Charlesworth, and Deborah Charlesworth. 1986. Breeding system evolution in *Primula vulgaris* and the role of reproductive assurance. *Heredity* 56:207–217.

This field study finds that outcrossing phenotypes do show pollen limitation compared to selfing phenotypes. Primroses are a model for the breakdown of an outcrossing phenotype in natural populations, and this study helps to establish that reproductive assurance is a major advantage of this breakdown.

Transmission Advantage

The other major hypothesized advantage of selfing is the transmission advantage proposed by Fisher 1941. In a self-fertilization event, an organism passes down two copies of each chromosome, whereas in an outcrossing event it only passes down one copy of each. Therefore, an allele that increases self-fertilization will spread through a population even if it confers no fitness benefit to the organism. Crosby 1949 shows how transmission advantage could explain transitions to a highly selfing condition in primrose. As Kimura 1959 first shows, alleles that increase selfing will, in fact, spread by transmission advantage even if selfing is deleterious, provided that inbreeding depression is less than one-half (i.e., offspring from outcrossing are no more than twice as fit as offspring from selfing). Holsinger 1988 shows that selfing can actually be favored below this threshold if there is genetic variation in inbreeding depression. The distinction between population and family level inbreeding depression (see Inbreeding Depression) partly explains this discrepancy; Kimura's model implicitly assumes zero variance in family-level inbreeding depression. Transmission advantage and reproductive assurance (see

Reproductive Assurance) are sometimes framed as competing hypotheses. However, as Busch and Delph 2012 points out, the difference between them is a question of the relative importance of two real advantages.

Busch, Jeremiah W., and Lynda F. Delph. 2012. The relative importance of reproductive assurance and automatic selection as hypotheses for the evolution of self-fertilization. *Annals of Botany* 109:553–562.

This review explains the underlying symmetry between models of selection for self-fertilization. All models account for transmission advantage. The “transmission advantage hypothesis” is merely the special case in which seed discounting is complete (see Pollination Biology, Pollen Discounting, and Seed Discounting), and transmission advantage is the sole advantage of selfing.

Crosby, Jack L. 1949. Selection of an unfavourable gene-complex. *Evolution* 3:212–230.

This combined theoretical and field study establishes the breakdown of highly outcrossing dimorphic floral phenotypes in English populations of the primrose *Primula vulgaris* as a model system for the transition to predominant selfing. Counts of style phenotypes from separate populations are consistent with different stages of a shared evolutionary trajectory toward a highly selfing monomorphic condition driven by transmission advantage.

Fisher, Ronald A. 1941. Average excess and average effect of a gene substitution. *Annals of Eugenics* 11:53–63.

This theoretical paper contains a proof-of-concept example that is perhaps the most important model of mating system evolution in the 20th century. An allele causing self-fertilization can spread to fixation by being transmitted to the organism’s own seeds through both pollen and ovules, even if the allele has no effect on viability or fecundity.

Holsinger, Kent E. 1988. Inbreeding depression doesn’t matter: The genetic basis of mating-system evolution. *Evolution* 42:1235–1244.

This mathematical study shows that the one-half inbreeding depression threshold (see Kimura 1959) disappears when fitness is determined by individual genotypes instead of a fixed population-wide inbreeding depression. Lineages that suffer less than average from inbreeding benefit more than average from selfing.

Kimura, Motoo. 1959. Conflict between self-fertilization and outbreeding in plants. *Annual Report of the National Institute of Genetics, Japan* 9:87–88.

This article builds on the transmission advantage model by incorporating inbreeding depression. It contains the first derivation of the classic threshold of inbreeding depression equal to one-half. Below this value, transmission advantage will drive any alleles that increase the selfing rate to fixation. Above this value, outcrossing will persist.

Pollination Biology, Pollen Discounting, and Seed Discounting

The specifics of how selfing is accomplished may affect the outcome of mating system evolution. If characters that increase selfing also limit the ability to pollinate other plants, then selfers’ transmission advantage may be counteracted by reduced success as a pollen parent (see Transmission Advantage). This disadvantage, now called pollen discounting, was first modeled in Nagylaki 1976 as an addition to Fisher’s transmission advantage model (see Fisher 1941, cited under Transmission Advantage). Charlesworth 1980 shows that if pollen discounting is greater than zero, inbreeding depression must be even lower than one-half in order for selection to favor an increased selfing rate. Harder and Barrett 1995 explains how pollen discounting could favor morphological and phenological adaptations that reduce self-pollination even when they seem redundant with molecular self-incompatibility (see Outcrossing Mechanisms). Analogous to pollen discounting, the idea of seed discounting is first described by Lloyd 1992. To a parental plant, inbreeding depression is only disadvantageous to the extent that inferior selfed seeds replace, rather than supplement, superior outcrossed seeds (see Inbreeding Depression). Seed discounting is the amount of potential outcrossed seeds sacrificed by a trait that increases selfing. Herlihy and Eckert

2002 uses emasculation experiments on *Aquilegia canadensis* to provide the first empirical demonstration of seed discounting. The theoretical outcome also depends on how selfing behavior is modeled. Holsinger 1991 models the selfing rate as a function that depends on pollen receipt from other plants instead of being intrinsic to each genotype and finds intermediate equilibria. Lloyd 1979 finds that the conditions under which selfing is favored critically depend on the timing of selfing relative to outcrossing, which the author terms the “mode of selfing.” Kalisz, et al. 2004 demonstrates that *Collinsia verna* achieves reproductive assurance through the delayed mode of selfing when pollinators fail (see Reproductive Assurance).

Charlesworth, Brian. 1980. The cost of sex in relation to mating system. *Journal of Theoretical Biology* 84:655–671.

This theoretical study demonstrates the disadvantages of biparental sex relative to asexuality and self-fertilization. In the self-fertilization model, Charlesworth modifies the pollen discounting model of Nagylaki 1976 to include inbreeding depression. Together, pollen discounting and inbreeding depression restrict the parameter space in which selfing is favored more than either factor alone restricts it.

Harder, Lawrence D., and Spencer C. H. Barrett. 1995. Mating cost of large floral displays in hermaphrodite plants. *Nature* 373:512–515.

The authors show experimentally that large floral displays are associated with increased pollen discounting in *Eichhornia paniculata*. They propose that some traits normally thought to be adaptations to reduce selfing actually might have been selected because they reduce pollen discounting. This would resolve the paradox of why such traits are present even in self-incompatible taxa (see Outcrossing Mechanisms), in which they would seem to be redundant.

Herlihy, Christopher R., and Christopher G. Eckert. 2002. Genetic cost of reproductive assurance in a self-fertilizing plant. *Nature* 416:320–323.

This field study of *Aquilegia canadensis* shows that self-fertilization increases seed set through reproductive assurance (see Reproductive Assurance), but it also decreases the proportion of ovules that are cross-fertilized (i.e., it causes seed discounting). Because both the most selfing and least selfing populations enjoy similar reproductive assurance, it remains a paradox that selection has not decreased the selfing rate.

Holsinger, Kent E. 1991. Mass-action models of plant mating systems: The evolutionary stability of mixed mating systems. *American Naturalist* 138:606–622.

Rather than choosing a selfing rate as a population-level parameter, this model uses the actual pollen receipt from neighbors to predict the evolution of the pollen export rate. Two possible outcomes are of special interest: alleles increasing pollen export can invade highly selfing populations, and stable intermediate selfing rates can occur as long as self-pollination leads to fertilization more often than cross-pollination does.

Kalisz, Susan, Donna W. Vogler, and Kristen M. Hanley. 2004. Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. *Nature* 430:884–887.

Because delayed selfing increases reproductive assurance without any intrinsic tradeoff (see Lloyd 1979), it is surprising how rarely it has been documented in nature. This field study uses emasculation experiments to demonstrate delayed selfing in a population of *Collinsia verna*.

Lloyd, David G. 1979. Some reproductive factors affecting the selection of self-fertilization in plants. *The American Naturalist* 113:67–79.

This theoretical study represents a step toward more biologically realistic models of the evolution of mating system. It distinguishes prior, competing, and delayed modes of selfing depending on timing relative to outcrossing. Previous models assumed competing selfing.

Lloyd, David G. 1992. Self- and cross-fertilization in plants: II. The selection of self-fertilization. *International Journal of Plant Sciences* 153:370–380.

This model incorporates an unusually extensive list of the advantages and disadvantages of selfing, including the novel concept of seed discounting. Selfing of ovules may create inferior offspring, but it is only disadvantageous to the parent if it also reduces the number of superior outcrossed offspring.

Nagylaki, Thomas. 1976. A model for the evolution of self-fertilization and vegetative reproduction. *Journal of Theoretical Biology* 58:55–58.

This modification of the model proposed by Fisher 1941 (cited under Transmission Advantage) is the first to account for an inferior ability of highly selfing organisms to sire offspring through cross-pollination, a consideration now called pollen discounting.

Purging

Simple models assume that inbreeding depression is a constant population-level parameter that decreases the fitness of all inbred progeny irrespective of their genotypes. Maynard Smith 1977 designs the first model in which inbreeding depression changes with multiple generations of selfing, and the author considers the possibility that it may eventually decrease. However, in this model, inbreeding depression varies arbitrarily through time instead of explicitly reflecting the action of selection. In the most important modification of the transmission advantage hypothesis (see Transmission Advantage), Lande and Schemske 1985 models the interaction of transmission advantage and an evolving inbreeding depression. Once deleterious recessives are united, selection will remove them from the population and decrease future inbreeding depression. This process is called purging. A historical episode of inbreeding or a population bottleneck can therefore increase homozygosity, purge inbreeding depression, and favor the evolution of even more inbreeding in a positive feedback loop. Several comparative and experimental studies support the claim that inbreeding causes purging. Barrett and Charlesworth 1991 empirically demonstrates purging by temporarily inbreeding historically outbred populations of *Eichhornia*. In a phylogenetically broad survey, Husband and Schemske 1996 finds that predominantly inbreeding populations suffer less inbreeding depression at the seed stage than outcrossing populations. However, purging should be ineffective on partially dominant or weakly deleterious components of the genetic load. Willis 1999 detects purging of strongly deleterious alleles in *Mimulus*, but the author finds only a minor effect on overall inbreeding depression. This is consistent with only a small role for strongly deleterious alleles in inbreeding depression. Additionally, several reviews do not favor a general purging effect of inbreeding. Byers and Waller 1999 finds that purging occurs occasionally, but not at all consistently. Winn, et al. 2011 does find evidence of purging in predominantly selfing taxa and populations, but not in those with intermediate selfing rates. This is contrary to the scenario of runaway selection described by Lande and Schemske 1985.

Barrett, Spencer C. H., and Deborah Charlesworth. 1991. Effects of a change in the level of inbreeding on the genetic load. *Nature* 352:522–524.

By repeatedly inbreeding populations of *Eichhornia paniculata*, the authors produce an early experimental demonstration of purging in plants. Consistent with a deleterious recessive model of inbreeding depression, a return to outcrossing in the final generation results in even greater fitness than that of the ancestral population.

Byers, Diane L., and Donald M. Waller. 1999. Do plant populations purge their genetic load? Effects of population size and mating history on inbreeding depression. *Annual Review of Ecology and Systematics* 30:479–513.

This review of empirical studies that tested purging provides a necessary caution against overgeneralizing the phenomenon of purging. Although there have been repeated demonstrations of purging, the authors find that these studies are in the minority compared to those that fail to show it.

Husband, Brian C., and Douglas W. Schemske. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50:54–70.

This review combines inbreeding depression and selfing rate data for fifty-four plant species to determine the effect of purging on inbreeding depression in different life stages. The authors argue that purging is common and occurs mostly in early stages of life history. This article helps to place purging in the context of the actual traits under selection, rather than an abstract fitness value.

Lande, Russell, and Douglas W. Schemske. 1985. The evolution of self-fertilization and inbreeding depression in plants: I. Genetic models. *Evolution* 39:24–40.

This theoretical paper is the first thorough treatment of the way in which purging of inbreeding depression can affect the ultimate outcome of mating system evolution in a population. The authors show that purging acts as a positive feedback loop that can favor selfing even in populations with initially great inbreeding depression.

Maynard Smith, John. 1977. The sex habit in plants and animals. In *Measuring selection in natural populations*. Lecture Notes in Biomathematics 19. Edited by Freddy B. Christiansen and Tom M. Fenchel, 315–331. Berlin and Heidelberg, Germany: Springer.

This theoretical work covers models of mating, breeding, and sexual system evolution (see Outcrossing Mechanisms). The selfing model is the first to include an inbreeding that can change over generations, although it uses arbitrary fitnesses as parameters rather than modeling the evolution of inbreeding depression itself.

Willis, John H. 1999. The role of genes of large effect on inbreeding depression in *Mimulus guttatus*. *Evolution* 53:1678–1691.

This greenhouse study on *Mimulus* differs from others of its kind in that Willis controls for greenhouse adaptation by measuring the change in inbreeding depression rather than overall fitness. The author finds only a small role for purgeable, strongly deleterious alleles in inbreeding depression.

Winn, Alice A., Elizabeth Elle, Susan Kalisz, et al. 2011. Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution* 65:3339–3359.

Most theoretical models predict that even moderate selfing rates will purge inbreeding depression substantially. This review of empirical estimates of inbreeding depression contradicts this prediction and shows that intermediate selfing rates are associated with inbreeding depression levels similar to those of predominant outcrossers.

Outcrossing Mechanisms

It is important to distinguish mating system from the related concepts of breeding and sexual system, although the terminology is not entirely standardized. Breeding system is defined as the characters that control which particular matings occur. Sexual system is defined as the division of male and female function among individuals. Mating system essentially describes the randomness of matings. Many morphological, phenological, and biochemical aspects of breeding and sexual systems also have a large effect on mating system. These may fairly be called “outcrossing mechanisms” because they currently prevent a fraction of potential self-pollinations or self-fertilizations. However, selection to avoid inbreeding may or may not have been their ultimate cause. One of the most extreme outcrossing mechanisms is dioecy, the sexual system in which each plant functions only as a pollen parent or as an ovule parent. Responding to arguments that dioecy could have evolved purely as a pollination or dispersal adaptation, Thomson and Barrett 1981 argue that dioecy evolved by selection against inbreeding. Dichogamy and herkogamy—respectively, the temporal and spatial separation of mature anthers and stigmas—are common among angiosperms. Lloyd and Webb 1986 and Webb and Lloyd 1986 argue that dichogamy and herkogamy are selected because they reduce mechanical interference between anthers and stigmas rather than because they reduce selfing. Self-incompatibility (SI) is the set of molecular mechanisms that reject self-pollen when it is received. It is controlled the S-locus, at which negative frequency-

dependent selection maintains many S-alleles at equal frequencies (Wright 1939). SI systems are classified as gametophytic (GSI) if the pollen's phenotype is determined by its own haploid genotype, or sporophytic (SSI) if it is determined by the genotype of its diploid parent. Whereas morphological outcrossing mechanisms have many independent origins in distantly related taxa, some SI systems shared among taxonomic families may be ancient homologies. Whitehouse 1950 even proposes the radical hypothesis that SI is ancestral to all flowering plants and that it is a key adaptation that propelled angiosperm diversification. Although the variety of molecular SI mechanisms contradicts a monophyletic origin of all SI, at least one SI system does seem to be old and conserved. Igić and Kohn 2001 concludes that the GSI ribonuclease (S-RNase) system is ancestral to the asterids and rosids because of the close relationship between the S-alleles of relatives as distant as Solanaceae and Rosaceae. Although these complex SI systems arise only rarely, they must have appeared at least once in each family that evolved SI independently. Using population genetic models, Charlesworth 1988 and Uyenoyama 1991 show how SSI and GSI, respectively, could have evolved in self-compatible populations.

Charlesworth, Deborah. 1988. Evolution of homomorphic sporophytic self-incompatibility. *Heredity* 60:445–453.

Extant SI mechanisms require multiple S-alleles to function; therefore, it is a challenge to explain how the first S-alleles arose. This theoretical study gives a plausible explanation for how a rare mutation conferring SSI could have established in a self-compatible population based on selection for outcrossing.

Igić, Boris, and Joshua R. Kohn. 2001. Evolutionary relationships among self-incompatibility RNases. *Proceedings of the National Academy of Sciences of the United States of America* 98:13167–13171.

This phylogenetic reconstruction of RNases supports a monophyletic origin of the GSI S-RNase ancestral to the rosid and asterid clades. If true, S-RNase genes must have been conserved since the common ancestor of the rosids and asterids, estimated at around 110 million years ago.

Lloyd, David G., and C. J. Webb. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms: I. Dichogamy. *New Zealand Journal of Botany* 24:135–162.

This review creates a clear classification of dichogamy based on such features as the level of synchronization between flowers and the duration of overlap between phases. The authors use the redundant co-occurrence of dichogamy with other outcrossing mechanisms to argue that it is not primarily favored because it reduces selfing.

Thomson, James D., and Spencer C. H. Barrett. 1981. Selection for outcrossing, sexual selection, and the evolution of dioecy in plants. *The American Naturalist* 118:443–449.

This is a good introduction to the case for dioecy being favored by selection for outcrossing. The authors' central point is that if either dioecy or self-incompatibility is sufficient to eliminate self-fertilization, selection against inbreeding should rarely lead to both. They argue that this is the observed pattern.

Uyenoyama, Marcy K. 1991. On the evolution of genetic incompatibility systems: VI. A three-locus modifier model for the origin of gametophytic self-incompatibility. *Genetics* 128:453–469.

This model posits a possible origin of GSI through the invasion of a modifier allele. This allele prevents a fraction of fertilizations between plants that match at a variable antigen locus. The resulting hypothetical scenario is biochemically more detailed than models in which functional S-alleles spring forth fully formed.

Webb, C. J., and David G. Lloyd. 1986. The avoidance of interference between the presentation of pollen and stigmas in angiosperms: II. Herkogamy. *New Zealand Journal of Botany* 24:163–178.

This follows Lloyd and Webb 1986. It mirrors their discussion of dichogamy in that article, but focuses here on herkogamy. The authors classify herkogamy based on the number of floral morphs and their distribution on different flowers or plants.

Whitehouse, H. L. K. 1950. Multiple-allelomorph incompatibility of pollen and style in the evolution of the angiosperms. *Annals of Botany* 14:199–216.

This article represents an early recognition of the importance of SI in driving other aspects of plant evolution. The author hypothesizes that SI is the ancestral state for the clade of all extant angiosperms.

Wright, Sewall. 1939. The distribution of self-sterility alleles in populations. *Genetics* 24:538–552.

This population genetic model of S-allele evolution predicts that balancing selection will favor rare alleles that allow compatibility with more mates. As new S-alleles arise, all extant S-alleles will equilibrate to equal frequencies. S-alleles provide one of the few clear examples of balancing selection in nature.

Outcrossing Rate

Although selfing is only one of several ways to inbreed, it is the one most often incorporated in population genetic models of plant mating system evolution. Therefore, the outcrossing rate is a convenient way to characterize real mating systems in light of theory. The outcrossing rate represents the proportion of ovules fertilized by non-self pollen. Theoretical models variously predict that the outcrossing rate will evolve toward extreme values or equilibrate at intermediate ones. Because biologists do not generally have access to complete pedigrees of natural populations, they must find methods to estimate population outcrossing rates through experiments or genetic data.

Estimation of Outcrossing Rate

As methodology has expanded, biologists have gained access to multiple means of estimating outcrossing rates of populations (see Fryxell 1957, cited under General Overviews). The simplest method of estimating the outcrossing rate is to measure a convenient proxy that is predicted to evolve in a particular direction in response to selection for outcrossing or selfing, such as the ratio of pollen grains to ovules (Cruden 1977). More direct methods infer the outcrossing rate from observed genotypes at marker loci (Clegg 1980). Gao, et al. 2007 develops a method for simultaneously estimating inbreeding and population subdivision. Once the outcrossing rate is known, it can be used to estimate other information. Ritland 1990 devises a method of estimating inbreeding depression from the selfing rate and the inbreeding coefficient (a measure of the probability of identity by descent of two homologous gene copies in a diploid).

Clegg, Michael T. 1980. Measuring plant mating systems. *BioScience* 30:814–818.

This review explains parameter estimation and hypothesis testing for the selfing rate under the mixed mating model, in which each ovule either is fertilized by pollen at random from the population or is fertilized by self-pollen with a constant probability.

Cruden, Robert William. 1977. Pollen-ovule ratios: A conservative indicator of breeding systems in flowering plants. *Evolution* 31:32–46.

Cruden describes a purely phenotypic estimate of outcrossing. Predominantly outcrossing plants produce pollen grains far in excess of the number of ovules, which partly might be explained as compensation for pollen wastage. If self-pollination avoids pollen wastage (such as loss in transit), the advantage of great pollen production disappears in highly selfing populations. Consistent with this prediction, a low pollen-to-ovule ratio is associated with taxa presumed to be highly selfing based on morphological characters. The pattern is also consistent with decreased pollen competition among sires, although Cruden does not address this point.

Gao, Hong, Scott Williamson, and Carlos D. Bustamante. 2007. A Markov chain Monte Carlo approach for joint inference of population structure and inbreeding rates from multilocus genotype data. *Genetics* 176:1635–1651.

Both habitual inbreeding and division of a population into local subpopulations produce deviations of genotype frequencies from expectations under random mating. Other popular software estimates population subdivision by assuming mating is random within each subpopulation. The authors provide an alternative that relaxes this assumption and estimates subdivision and inbreeding within subpopulations as separate parameters.

Ritland, Kermit. 1990. Inferences about inbreeding depression based on changes of the inbreeding coefficient. *Evolution* 44:1230–1241.

Ritland uses the key assumption that the inbreeding coefficient has reached equilibrium between generations to develop a method of estimating inbreeding depression using only the adult inbreeding coefficient and selfing rate for a single generation. The author applies this method to published data as an example.

Distribution of Outcrossing Rates

A contentious question is whether the distribution of outcrossing rates among plant taxa is bimodal. Lande and Schemske 1985 (cited under Purging) predicts only two stable outcomes of mating system evolution: if a population is sufficiently inbred, it will purge its inbreeding depression and evolve toward complete selfing; if it is insufficiently inbred, it will evolve toward complete outcrossing. Schemske and Lande 1985 provide early empirical support for bimodality in an initial review of outcrossing rates. However, contrary interpretations quickly arose. Aide 1986 points out that if wind-pollinated and animal-pollinated taxa are examined separately, only the wind-pollinated taxa show bimodal outcrossing rates. Later reviews have found substantial numbers of populations with intermediate outcrossing rates, which some authors have interpreted as inconsistent with a hypothesis of alternative stable states (Goodwillie, et al. 2005). Failure to detect bimodality might be caused partly by biased sampling. Igić and Kohn 2006 shows that the outcrossing rate literature reports a proportion of obligately outcrossing species smaller than the frequency of dioecious and self-incompatible species in community-level surveys. Although the extant distribution of outcrossing rates may seem to be a direct test of alternative stable states, a finer point is that this is only true if the extant distribution represents a static equilibrium. Igić and Busch 2013 (cited under Macroevolution) finds that equilibrium distributions can contain intermediate outcrossing rates even if there is continual turnover toward lesser outcrossing in the intermediate class. On a shorter timescale, estimates of the outcrossing rate collected at a single point in time may not be representative of the population's temporal average.

Aide, T. Mitchell. 1986. The influence of wind and animal pollination on variation in outcrossing rates. *Evolution* 40:434–435.

This critical response separates the data used in Schemske and Lande 1985 into wind- and animal- pollinated taxa. Aide finds that bimodality in wind-pollinated taxa is enough to drive the pattern, which is absent in animal-pollinated taxa considered separately.

Goodwillie, Carol, Susan Kalisz, and Christopher G. Eckert. 2005. The evolutionary enigma of mixed mating systems in plants: Occurrence, theoretical explanations, and empirical evidence. *Annual Review of Ecology, Evolution, and Systematics* 36:47–79.

This review covers a much larger set of outcrossing rates than that in Schemske and Lande 1985 and shows a more nearly unimodal distribution concentrated at high outcrossing rates.

Igić, Boris, and Joshua R. Kohn. 2006. The distribution of plant mating systems: Study bias against obligately outcrossing species. *Evolution* 60:1098–1103.

The authors of this literature survey argue that underrepresentation of obligate outcrossers in outcrossing rate studies might explain apparently unimodal distributions found in other reviews. If more self-incompatible taxa were included (see Outcrossing Mechanisms), bimodality might emerge.

Schemske, Douglas W., and Russell Lande. 1985. The evolution of self-fertilization and inbreeding depression in plants: II. Empirical observations. *Evolution* 39:41–52.

Lande and Schemske 1985 (cited under Purging) predicts a bimodal distribution of outcrossing rate as a result of purging of inbreeding depression. Published alongside that theoretical prediction, this literature review finds preliminary support for a bimodal distribution of highly selfing and highly outcrossing populations.

Genetic Diversity and Natural Selection in Selfing Populations

Selfing has several evolutionarily relevant population genetic consequences. Nonrandom sampling of gametes reduces genetic diversity and diminishes the effect of natural selection relative to stochastic genetic drift. Homozygosity reduces inter-chromosomal exchange of alleles, which prevents advantageous alleles from escaping mediocre genetic backgrounds and allows co-evolving natural enemies to adapt to common genotypes. Selfing also transmits the entire genome of a completely homozygous individual as a unit that lacks the competing evolutionary interests of two parents or of selfish genetic elements.

Allelic Diversity

Much of population genetic theory was formulated under the assumption of an ideal population of randomly mating hermaphrodites, but it can easily accommodate other populations with an appropriate transformation. The “effective population size” is the number of ideal randomly mating hermaphrodites that would evolve in the same way as the actual population is expected to evolve. Habitually inbreeding populations have smaller effective population sizes than equally large outcrossing populations. Gametes forming any given zygote are not drawn independently from the population gamete pool in habitually inbreeding populations. With fewer independent samples, neutral allelic variants are lost randomly by genetic drift more quickly, and thus there are fewer segregating alleles at any given time. Hamrick and Godt 1996 demonstrates this theoretical expectation in a review of predominantly selfing plant species. Because genetic loci share their evolutionary fate with loci in which they are in linkage disequilibrium, and because selfing slows the decay of linkage disequilibrium (see Consequences of Reduced Effective Recombination), selection can reduce diversity in wide swaths of the genomes of selfing populations. This process is called “linked selection.” Barrett, et al. 2014 argues that linked selection is an important cause of the observed lower allelic diversity in predominantly selfing populations. Nordborg 2000 explains an alternative formulation for the expectation of reduced diversity using a coalescent framework. In addition to being directly caused by mating system, lower allelic diversity may also result from the kinds of historical circumstances to which selfing populations are prone. Schoen and Brown 1991 concludes from a review of allozyme data that selfing populations have lower average diversity, but also greater interpopulation variance in diversity than outcrossing populations. This pattern can be explained if the low-diversity selfing populations, not the high-diversity ones, have gone through recent colonization bottlenecks. Although selfing populations may have lower within-population diversity, they are expected to have greater among-population differentiation because the neutral alleles that fix by chance are different in each population. Glémin, et al. 2006 finds both of these patterns in a review of DNA sequence data.

Barrett, Spencer C. H., Ramesh Arunkumar, and Stephen I. Wright. 2014. The demography and population genomics of evolutionary transitions to self-fertilization in plants. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 369.

This review and simulation study covers the demographic conditions in which transitions to selfing occur and the limitations of inferring these historical conditions using genetic data. The authors argue that the non-independent sampling of gametes that occurs in selfing populations is alone insufficient to explain their low allelic diversity, and that linked selection must be largely responsible.

Glémin, Sylvain, Eric Bazin, and Deborah Charlesworth. 2006. Impact of mating systems on patterns of sequence polymorphism in flowering plants. *Proceedings of the Royal Society of London B: Biological Sciences* 273:3011–3019.

Although selfing is expected to decrease diversity within a population, it is also expected to increase among-population differentiation by eliminating the cohesive effect of sex. This database search shows that empirical data on sequence diversity corroborate this expectation.

Hamrick, J. L., and M. J. W. Godt. 1996. Effects of life history traits on genetic diversity in plant species. *Proceedings of the Royal Society of London B: Biological Sciences* 351:1291–1298.

This review compares allozyme diversity among plant species, taking into account both mating system and life history traits. It corroborates in plants the general expectation that habitual self-fertilization is associated with high allelic differentiation among populations, but low allelic diversity overall.

Nordborg, Magnus. 2000. Linkage disequilibrium, gene trees and selfing: An ancestral recombination graph with partial self-fertilization. *Genetics* 154:923–929.

This theoretical study explores the expected effects of selfing on coalescence. It is possible that two homologous gene copies were inherited from the same ancestor; therefore, coalescence is faster, and allelic diversity is lower. Because effective recombination is rare, linkage disequilibrium can be substantial even at physically distant loci.

Schoen, Daniel J., and Anthony H. D. Brown. 1991. Intraspecific variation in population gene diversity and effective population size correlates with mating system in plants. *Proceedings of the National Academy of Sciences* 88:4494–4497.

This review shows that not all selfing populations can be characterized as having low allelic diversity. Although the authors find that selfing populations have a lower mean diversity than outcrossing populations, selfing populations vary enough to fall occasionally within the usual range of diversity for outcrossing populations.

Consequences of Reduced Effective Recombination

Selfing is associated with reduced genotypic diversity because whatever recombination does occur is likely to exchange identical alleles in the highly homozygous populations of predominant selfers. Such physical recombination does not contribute to effective recombination, the exchange of alleles among homologous chromosomes. In an influential model, Muller 1964 explains a consequence of the absence of recombination—the irreversible accumulation of deleterious mutations on even the fittest genotypes. This feature of non-recombining populations is known as “Muller’s ratchet” because it only cranks upward toward a greater genetic load (see Inbreeding Depression) of deleterious mutations. Applying the ratchet concept to purely selfing populations, the population genetic model Heller and Maynard Smith 1978 proves that the unloaded class of genotypes can actually persist at some frequency. As in Muller’s model (Muller 1964), however, whatever losses happen by chance will be permanent. Another effect of reduced effective recombination is that parents cannot easily produce rare offspring genotypes to which rapidly co-evolving natural enemies have not yet adapted. Levin 1975 hypothesizes that this individual-level disadvantage maintains biparental sexual reproduction. This hypothesis is now called the Red Queen hypothesis of sex because, like the Red Queen hypothesis of extinction proposed by Van Valen 1973, it involves a ceaseless coevolutionary arms race rather than progressive adaptation. Empirical corroboration of selection for biparental sex by pathogens has lagged behind theoretical proofs-of-concept, but Busch, et al. 2004 does find that the number of pathogen species is greater in outcrossing than in selfing taxa.

Busch, Jeremiah W., Maurine Neiman, and Jennifer M. Koslow. 2004. Evidence for maintenance of sex by pathogens in plants. *Evolution* 58:2584–2590.

This correlational study of published data on the number of fungal pathogen species for different plant species finds that, controlling for study bias and for phylogeny, outcrossing rate and pathogen diversity are positively correlated. This is the expected pattern if outcrossing is an adaptation to pathogens, assuming pathogen diversity is a proxy for the intensity of selection imposed by pathogens.

Heller, R., and J. Maynard Smith. 1978. Does Muller’s ratchet work with selfing? *Genetics Research* 32:289–293.

In this theoretical study, the authors find the equilibrium frequency of the class of genotypes with the least genetic load in a selfing population. This makes it possible to apply the concept of Muller's ratchet to selfing populations. If the least loaded class is small enough, it is possible that it may be lost by drift.

Levin, Donald A. 1975. Pest pressure and recombination systems in plants. *The American Naturalist* 109:437–451.

This argumentative review proposes a coevolutionary hypothesis for the advantage of sex and recombination. Levin hypothesizes that selection in stable environments will favor sex and recombination because they generate new genotypes to which natural enemies have not yet adapted.

Muller, H. J. 1964. The relation of recombination to mutational advance. *Mutation Research/Fundamental and Molecular Mechanisms of Mutagenesis* 1:2–9.

This model establishes that adaptation is faster in sexual than asexual populations. It is also the origin of Muller's ratchet, a central idea in the maintenance of sex. Asexual populations cannot recreate the genotypes with the fewest deleterious mutations once those genotypes have been lost.

Van Valen, Leigh. 1973. A New Evolutionary Law. *Evolutionary Theory* 1:1–30.

This paleontological review indicates a constant probability of extinction of major lineages through time. Van Valen explains this pattern by proposing the Red Queen hypothesis, in which adaptation in a species only temporarily prevents exclusion by its rivals.

Relaxed Selection

Because chance has a greater role in small samples, the expected outcome that the fittest alleles will rise in frequency is subject to greater chance deviation when effective population size is small. Furthermore, linked selection allows deleterious alleles to "hitchhike" on the success of beneficial alleles at other loci with which they are in linkage disequilibrium (see Allelic Diversity). Natural selection is therefore said to be relaxed in inbreeding populations. Glémin and Galtier 2012 provides an accessible introduction to the population genetic theory behind the concept of relaxed selection. Glémin 2007 analytically predicts that the net effect of selfing is to reduce the effect of selection under most realistic assumptions of dominance. Most genetic polymorphism is neutral and is expected to decrease with increased inbreeding. However, sites that normally would be constrained to a particular sequence by selection may instead maintain deleterious variants when selection is relaxed. Empirical studies have confirmed this effect of relaxed selection in some selfing populations. Qiu, et al. 2011 finds that selfing species of *Arabidopsis* and *Capsella* possess greater polymorphism for unpreferred degenerate codons. However, selfing is not expected to relax selection on every kind of allele. Haldane 1927 shows that selfing may intensify selection for beneficial recessives, just as it may against deleterious recessive alleles (see Purging).

Glémin, Sylvain. 2007. Mating systems and the efficacy of selection at the molecular level. *Genetics* 177:905–916.

This theoretical study illustrates two countervailing effects of selfing. It intensifies selection on recessive alleles, while also relaxing selection in general relative to drift. The overall effect of selfing on selection therefore depends on dominance. The author investigates how these effects influence sequence polymorphism and divergence among populations.

Glémin, Sylvain, and Nicolas Galtier. 2012. Genome evolution in outcrossing versus selfing versus asexual species. In *Evolutionary genomics*. Vol. 1. *Methods in Molecular Biology* 855. Edited by Maria Anisimova, 311–335. New York: Humana.

This book chapter explains the genomic and population genetic consequences of self-fertilization or asexuality. The authors provide a simple explanation of how highly selfing mating systems relax selection in terms of the population genetic concept of effective population size.

Haldane, J. B. S. 1927. A mathematical theory of natural and artificial selection: Part V. Selection and mutation. *Mathematical Proceedings of the Cambridge Philosophical Society* 23:838–844.

This population genetic model shows that beneficial recessive alleles are effectively neutral until they reach frequencies high enough to be united in homozygotes, an observation known as “Haldane’s sieve.” However, self-fertilization can generate homozygotes of even rare recessives, revealing their fitness effects. Self-fertilization fundamentally alters selection by minimizing the effects of dominance.

Qiu, Suo, Kai Zeng, Tanja Slotte, Stephen I. Wright, and Deborah Charlesworth. 2011. Reduced efficacy of natural selection on codon usage bias in selfing *Arabidopsis* and *Capsella* species. *Genome Biology and Evolution* 3:868–880.

Since even relaxed selection might still be strong enough to eliminate very deleterious mutations, the authors of this study examine genomic data on loci under weak selection (synonymous codons) to detect relaxed selection in selfing species of *Capsella* and *Arabidopsis*.

Parental and Intragenomic Conflicts

An allele may achieve greater representation in future generations in at least two ways. It may increase organismal fitness, or it may simply increase the rate at which it is transmitted. Selfish genetic elements are segments of the genome that spread through the second means while having a neutral or even deleterious effect on organismal fitness. Meiotic drive alleles do this by distorting segregation in meiosis or the transmission of meiotic products. Others, such as transposons, make multiple copies of themselves in the genome. Conflict can also arise between parents. Although the parents of an individual transmit equal nuclear genetic material, their investment of resources is not equal. A concentrated investment of energy or nutrients in particular seeds reduces the total fitness of the ovule parent by diverting resources from other seeds. However, such an uneven investment is a pure benefit for the favored seeds’ pollen parent because its investment is finished at fertilization. Self-fertilization can eliminate arenas of conflict between parents or between selfish genetic elements and the rest of the genome. Parental conflict is impossible if both parents are the same individual, mobile genetic elements may have no “uninfected” homologs to “infect” in highly homozygous individuals, and transmission-distorting alleles gain no benefit from biased transmission if they are already present on both homologs of a chromosome. A literature review of crossing studies between inbreeding and outcrossing species in Brandvain and Haig 2005 shows how the absence of parental conflict in selfing populations might drive patterns of unidirectional hybridization. Wright and Schoen 1999 finds that, in simulations, selfing decreases the equilibrium number of deleterious transposons under most models of the dominance pattern for fitness. Burt and Trivers 1998 uses population genetic models to predict correctly that deleterious supernumerary chromosomes, which are selfish genetic elements, are rarer in predominantly selfing than outcrossing plant taxa in the British Isles.

Brandvain, Yaniv, and David Haig. 2005. Divergent mating systems and parental conflict as a barrier to hybridization in flowering plants. *The American Naturalist* 166:330–338.

This review shows how parental conflict might affect reproductive isolation. The authors find several examples of pre-zygotic (e.g., selfer pollen failure on outcrosser stigmas) and post-zygotic (e.g., inviable paternally imprinted seed) barriers consistent with an absence of parental conflict in selfers.

Burt, Austin, and Robert Trivers. 1998. Selfish DNA and breeding system in flowering plants. *Royal Society Proceedings B: Biological Sciences* 265:141–146.

Supernumerary chromosomes called “B chromosomes” can spread through a population by biasing transmission despite being deleterious. This study uses a population genetic model to predict correctly that B chromosomes are rarer in inbreeding taxa of the British Isles. This provides empirical support for reduced genetic conflict in inbred populations.

Wright, Stephen I., and Daniel J. Schoen. 1999. Transposon dynamics and the breeding system. *Genetica* 107:139–148.

In most cases, selfing prevents the success of selfish genetic elements. This simulation of selection against transposons bears out this generality in the case of recessive or partially dominant deleterious effects, but it also suggests the unusual conclusion that selfing increases the number of transposons when heterozygotes are the least fit.

Selfing Syndrome

Several morphological and life history traits characterize most predominant selfers. These are collectively referred to as the “selfing syndrome,” which includes small and inconspicuous flowers, an annual habit, minimal pollinator rewards, and small quantities of pollen. Ornduff 1969 offers an extensive list of contrasts between selfing and outcrossing plants. These traits are logical consequences of the absence of selection for either pollinator attraction or avoidance of inbreeding, but at the same time, direct selection for these traits could incidentally increase self-fertilization. The selfing syndrome is interesting because it can show the effects of mating system on selection of other characters and because it is a naturally replicated series of adaptive genetic changes (Sicard and Lenhard 2011). Lloyd 1965 gives a classic example of the apparently recurrent evolution of selfing syndrome traits at the infraspecific level.

Lloyd, David G. 1965. Evolution of self-compatibility and racial differentiation in *Leavenworthia* (Cruciferae). *Contributions from the Gray Herbarium of Harvard University* 195:3–134.

This in-depth description of geographic races of two *Leavenworthia* species finds races that possess many traits of the selfing syndrome. The distribution of these traits is consistent with recurrent, convergent evolution of a selfing syndrome in multiple self-compatible lineages (see Outcrossing Mechanisms).

Ornduff, Robert. 1969. Reproductive biology in relation to systematics. *Taxon* 18:121–133.

This review focuses on the importance of mating, breeding, and sexual system characters in systematics. It also contains a thorough list of floral selfing syndrome characters.

Sicard, Adrien, and Michael Lenhard. 2011. The selfing syndrome: A model for studying the genetic and evolutionary basis of morphological adaptation in plants. *Annals of Botany* 107:1433–1443.

In this review, the authors argue that the recurrent evolution of the selfing syndrome is a model system for morphological evolution in general, and in particular its functional genetic basis. They also separate the selfing syndrome into two components—sex allocation and floral morphology—and summarize the literature on the selective pressures controlling the evolution of these two characters. This summary identifies an outstanding ambiguity—is increased self-fertilization itself the advantage of the selfing syndrome, or is it an incidental byproduct of adaptation to the physical environment?

Geographic Range and Local Adaptation

Henslow 1880 points out one of the earliest recognized geographical patterns of mating system—the tendency of predominantly selfing taxa to occupy a larger range than predominantly outcrossing taxa. A broad study by Grossenbacher, et al. 2015 supports this pattern. One means of range expansion in which selfing may be advantageous is dispersal to distant locations. Baker 1955 observes a consequence of the capacity for self-fertilization of such general importance that Stebbins 1957 (cited under Macroevolution) referred to it as “Baker’s Law.” Baker predicted that, because an organism capable of self-fertilization can found a colony without needing a mate, self-fertility should be more common in populations founded through long-distance dispersal (such as on oceanic islands). Carlquist 1966 argues that the prevalence of obligate outcrossers on islands, particularly the many dioecious plants in the Hawaiian flora, contradict Baker’s Law. Baker 1967 rebuts this critique on the grounds that dioecy could have evolved secondarily after dispersal. Baker also objects that individual examples of island inhabitants incapable of uniparental reproduction do not contradict his original prediction about relative prevalence, which, as a probabilistic rather than an absolute statement, might more accurately be called a “rule” than a “law.” Sporadic tests of Baker’s prediction have had mixed results, but an extensive survey by Grossenbacher, et al. 2017 finds support for it in the increased frequency of

self-compatibility (see Outcrossing Mechanisms) among island-inhabiting species. Another possible advantage of selfing is that it can decrease swamping of local adaptations by gene flow from non-adapted populations. Antonovics 1968 finds that metal-tolerant grass populations near mines show greater autonomous seed set than non-mine populations, consistent with selection to maintain local adaptation to harsh conditions.

Antonovics, Janis. 1968. Evolution in closely adjacent plant populations: V. Evolution of self-fertility. *Heredity* 23:219–238.

This field study documents significantly increased autonomous seed set in metal-tolerant *Agrostis* and *Anthoxanthum* mine populations compared to non-mine populations. This is the expected pattern if maintaining local adaptation by preventing gene flow is an advantage of selfing.

Baker, Herbert G. 1955. Self-compatibility and establishment after “long-distance” dispersal. *Evolution* 9:347–349.

This short article is the origin of an influential prediction on the geographic distribution of mating systems. Because organisms capable of uniparental reproduction can establish in distant locations without a mate, this ability will be more common in locations accessible only by long-distance dispersal.

Baker, Herbert G. 1967. Support for Baker’s Law—as a rule. *Evolution* 21:853–856.

This rebuttal to Carlquist 1966 gives some reasons to suspect that the high incidence of dioecy in the Hawaiian Islands is not fatal to Baker’s original prediction. Baker argues that, in most cases, dioecy evolved secondarily after the group reached the Hawaiian Islands.

Carlquist, Sherwin. 1966. The biota of long-distance dispersal: IV. Genetic systems in the floras of oceanic islands. *Evolution* 20:433–455.

This study points out a case that has become an enduring problem for the prediction in Baker 1955—the many dioecious plant taxa of the Hawaiian Islands. Carlquist argues that dioecious Hawaiian taxa are descended from dioecious colonists, and the ability to found a colony with a single individual is unimportant in determining successful colonization.

Grossenbacher, Dena L., Yaniv Brandvain, Josh R. Auld, et al. 2017. Self-compatibility is over-represented on islands. *New Phytologist* 215:469–478.

This survey of published breeding system data in the large plant families Asteraceae, Brassicaceae, and Solanaceae is the most comprehensive test of the prediction by Baker 1955, as of the mid-2010s. The authors compare the prevalence on islands and continents of self-incompatibility, which effectively prevents self-fertilization (see Outcrossing Mechanisms). Consistent with Baker’s prediction, species lacking self-incompatibility are disproportionately common among island-inhabiting species compared to their frequency on continents or in general.

Grossenbacher, Dena, Ryan Briscoe Runquist, Emma E. Goldberg, and Yaniv Brandvain. 2015. Geographic range size is predicted by plant mating system. *Ecology Letters* 18:706–713.

This study examines geographic ranges of sister pairs of selfing and outcrossing taxa. The results indicate that the pattern of larger ranges for selfers is general across genera and families. Controlling for ploidy and perennial or annual habit, selfing taxa have ranges that are twice as large as those of outcrossing sister taxa on average.

Henslow, George. 1880. On the self-fertilization of plants. *Transactions of the Linnean Society of London*. 2d series. *Botany* 1:317–398.

The author argues against the position that self-fertilization is usually maladaptive. Some of his points rely on a quasi-Lamarckian theory of inheritance, but one point is prescient of modern discussion. He observes that, within the flora of Britain, those taxa that have spread globally tend to be self-fertile.

Macroevolution

The evolution of mating system is peculiar in that transitions to predominant selfing occur extremely often in evolutionary history, and yet predominant selfing is the minority among extant species. This would not be puzzling in itself except that the reverse transition is rare. The selfing as a dead-end hypothesis explains why it has not become the norm in plants despite frequent permanent transitions to predominant selfing. According to this hypothesis, predominantly selfing lineages cannot keep pace with the higher diversification rates of predominantly outcrossing lineages. This is species selection in the sense that traits associated with a greater net proliferation of species into more species become more common among species. Early reviewers recognized that selfing could lead to extinction by eliminating the ability to generate genotypic variety (Mather 1943) and loss of biparental sex could prevent extensive radiation (Dobzhansky 1950). However, Stebbins 1957 is the first to advance a cohesive dead-end hypothesis. Reduced net diversification in selfing taxa could result from either decreased speciation or by increased extinction. Although Stebbins is careful not to link selfing to extinction, modern proponents of the dead-end hypothesis, such as Igić and Busch 2013, emphasize the role of extinction in limiting the proportion of selfing taxa. Goldberg, et al. 2010 estimates speciation and extinction rates for self-incompatible and self-compatible species in Solanaceae (see Outcrossing Mechanisms) and finds results supporting species selection against self-compatibility. Glémin and Ronfort 2013 models how selfing could lead to extinction through a reduced ability to track environmental changes, and Lynch, et al. 1995 shows that extirpation of selfing populations is possible purely through increased accumulation of deleterious mutations.

Dobzhansky, Theodosius. 1950. Evolution in the tropics. *American Scientist* 38:209–221.

This review contains a precursor to the selfing as a dead-end hypothesis of Stebbins 1957. The author considers the loss of biparental sex (asexuality in his example) to be a “blind alley” that achieves temporary adaptedness at the expense of the evolutionary flexibility needed to found large clades.

Glémin, Sylvain, and Joëlle Ronfort. 2013. Adaptation and maladaptation in selfing and outcrossing species: New mutations versus standing variation. *Evolution* 67:225–240.

This mathematical study explicitly models how failure to adapt to a changing environment could lead to extinction. The authors find that selfing can impede adaptation but can also promote it if adaptations arise from sufficiently recessive alleles.

Goldberg, Emma E., Joshua R. Kohn, Russell Lande, Kelly A. Robertson, Stephen A. Smith, and Boris Igić. 2010. Species selection maintains self-incompatibility. *Science* 330:493–495.

This phylogenetic study explains how self-incompatibility (see Outcrossing Mechanisms) can persist in a large proportion of taxa despite its frequent and apparently irreversible loss. The authors estimate speciation and extinction rates associated with self-incompatibility and self-compatibility from the phylogeny of the Solanaceae. Their results support species selection against self-compatibility.

Igić, Boris, and Jeremiah W. Busch. 2013. Is self-fertilization an evolutionary dead end? *New Phytologist* 198:386–397.

This review provides a clear explication of the premises of the selfing as a dead-end hypothesis, including the separate propositions that selfing decreases diversification and that transitions from outcrossing to selfing are far more common than the reverse. The authors review evidence on the hypothesis and find that it remains plausible.

Lynch, Michael, John Conery, and Reinhard Bürger. 1995. Mutational meltdowns in sexual populations. *Evolution* 49:1067–1080.

This mathematical study is one of the few to model extinction through accumulation of mutations that decrease the absolute fitness of a population (see Relaxed Selection). The authors find that, for most parameter choices, obligately selfing populations become extinct many times more quickly than otherwise similar randomly mating populations.

Mather, K. 1943. Polygenic inheritance and natural selection. *Biological Reviews* 18:32–64.

This review exemplifies the position that mating system is a tradeoff between the ability to maintain adaptive genotypes through inbreeding and the ability to produce a variety of genotypes that are adapted to environmental changes. The author reasons that sacrificing future adaptability must inevitably result in extinction.

Stebbins, G. Ledyard. 1957. Self fertilization and population variability in the higher plants. *The American Naturalist* 91:337–354.

This article is usually cited as the origin of the selfing as a dead-end hypothesis. The author argues that the advantages of reproductive assurance (see Reproductive Assurance), long-distance dispersal ability, and maintenance of fit genotypes favor selfing, but that the reduced potential to diversify makes selfing rarer than outcrossing.

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