Mating Systems in Flowering Plants

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Glossary

Cosexual The most common sexual system in flowering plants, in which a population is comprised of a single sexual class of hermaphrodites (cosexes) and on average individuals reproduce equally through female and male function.

Dioecy A sexual system in which a population is composed of female and male plants usually differing in secondary sex characters. At equilibrium the sexual morphs are maintained at equal frequency because of negative frequency-dependent selection.

Gender strategies The femaleness and maleness of individuals as reflected in their relative contribution to fitness through maternal and paternal investment.

Gynodioecy and androdioecy Two contrasting polymorphic sexual systems; gynodioecious populations are composed of female and hermaphrodite individuals, a sexual system that is not uncommon; in contrast, androdioecious populations contain male and hermaphrodite individuals, a sexual system that is extremely rare.

Inbreeding depression The reduction in viability and/or fertility of inbred offspring compared to outcrossed offspring as a result of the expression of deleterious recessive alleles in homozygous genotypes. Inbreeding depression is a key factor in determining mating system evolution, can occur throughout the life cycle, and is usually expressed most strongly when inbreeding occurs in a predominantly outcrossing species.

Linked selection Changes in allele frequency due to linkage with positively or negatively selected alleles at other loci, resulting in the loss of genetic diversity across genomic regions.

Modes of self-pollination The different ways that self-pollination can occur in flowering plants; distinguished primarily by the timing of self-pollination, whether pollinators are involved or not, and whether self-pollination occurs within or between flowers on a plant.

Pollen discounting The reduction in outcrossed male siring success caused by self-pollination within and between flowers on a plant.

Pollination The transfer of pollen between the male reproductive organ (stamen) to the receptive area (stigma) of the female organ (pistil). Pollination is necessary for mating but may not result in successful fertilization owing to post-pollination mechanisms, such as self-incompatibility.

Reproductive assurance An increase in seed set caused by self-pollination when conditions for outcrossing are unfavorable as a result of the absence of pollinators or compatible mates; requires that plants are self-compatible and also have the facility for autonomous self-pollination.

Self-incompatibility The inability of a fertile hermaphrodite plant to set abundant seed following self-pollination; the primary mechanism preventing self-fertilization in plants, and the opposite condition to self-compatibility in which plants can self-fertilize.

Sex allocation The parental expenditure of resources to sexual activities, including the relative allocation to female (ovules and seed) and male (pollen) function and also to floral display.

Introduction

Flowering plants (angiosperms) exhibit exceptionally diverse mating systems as a result of several distinctive features of their biology. First, because of their sessile habit plants depend on external agents to transfer male gametes (pollen) between individuals. This reliance has led to the evolution of diverse floral adaptations associated with the three main vectors for pollen dispersal: animals, wind, and water (Harder and Johnston, 2009). Pollination is a key reproductive process as it affects mating opportunities and fitness by determining the quantity and quality of pollen dispersed between flowers. Second, most plants possess hermaphroditic flowers and are therefore susceptible to self-pollination, often at the expense of cross-pollination as a result of pollen discounting (Harder and Barrett, 1995). Diverse morphological and physiological mechanisms have evolved in angiosperms to limit the harmful effects of self-fertilization and promote effective pollen dispersal between flowers on different plants. Finally, the modularity of plants and production of multiple reproductive structures introduces considerable mating complexity as a result of the subdivision of parental reproductive effort. Sexual plasticity and opportunities for combining hermaphroditic and unisexual flowers in different structural and temporal combinations has given rise to diverse gender strategies (Lloyd, 1979). As a result, the distribution of gametes within and between plants in a population is far more complicated than in animals, and reproduction can be highly promiscuous with individuals mating with numerous related and unrelated partners during their lifetimes, as well as themselves.

The term mating system is often used in different ways by reproductive biologists, depending on the organismal group. Perhaps the broadest definition, used primarily by researchers working with organisms with separate sexes, is simply "who mates with whom and how often." Biologists working with hermaphroditic groups (such as plants, worms, snails, slugs, or corals) often use a more restricted definition that simply involves the average frequency of cross- and self-fertilization in a

population. This definition of maternal mating success largely ignores information on male reproductive function (paternity or male outcrossed siring success) but has nevertheless provided important insights on the ecology and evolution of populations. The use of genetic markers over the past few decades has enabled quantitative measurements of selfing rates (s), or its complement the outcrossing rate ($t = 1 - s$), for several hundred angiosperm species representing diverse families, pollination systems, and life histories (Barrett and Eckert, 1990). This body of data has been valuable for testing theoretical models and for gaining insights on the ecological and demographic factors influencing the evolution of mating patterns.

In this article, we begin by considering mating patterns in plant populations with hermaphroditic sex expression (cosexuality), a condition that predominates among angiosperm taxa and is the ancestral state for most plant lineages. We focus on the causes and consequences of evolutionary transitions from outcrossing to predominant selfing, as this is the most common mating system transition among angiosperm families and has attracted considerable attention since Charles Darwin's seminal work on the topic. We then look at plant species with unisexual flowers in which populations are composed of various combinations of female, male, and hermaphrodite individuals. We review models and empirical evidence concerning how these polymorphic sexual systems are thought to have evolved from hermaphroditism and pay particular attention to the evolution of separate sexes from combined sexes.

Evolution of Mating Systems

Among life-history traits, reproductive characters that influence mating are of profound adaptive significance because they govern the character of genetic transmission between generations, the fitness of offspring and the amounts and distribution of genetic diversity in populations. The diversification of many angiosperm families (e.g., the orchid and phlox families) has been attributed to adaptive radiation of pollination and mating systems, often accompanying changes in the ecology of populations. Reproductive versatility is therefore a hallmark of angiosperm evolution and this is manifested by considerable inter- and intra-specific variation in mating systems. This variation implies frequent evolutionary transitions between mating systems, which are usually associated with changes to floral characters, pollination systems, and sex allocation in concert with life-history evolution. Ecological factors play a key role in driving the evolution of reproductive traits and in the maintenance of different mating systems. For example, long-lived tree species of stable plant communities are usually predominantly outcrossing whereas weedy colonists that occupy ephemeral environments are more commonly highly selfing. A major challenge is to determine the specific environmental, demographic, and genetic factors promoting changes in mating system.

The evolution of predominant self-fertilization (autogamy) from outcrossing represents the most important reproductive transition in angiosperms (Stebbins, 1974). There is evidence from numerous herbaceous families (e.g., the mustard and tomato families: Brassicaceae and Solanaceae, respectively) of multiple independent origins of autogamy and these transitions are often associated with the evolutionary breakdown of self-incompatibility, the primary genetic mechanism preventing selfing in plant populations. Investigation of evolutionary transitions from outcrossing to selfing is an active area of research today using comparative, experimental and genomic approaches, and theoretical models (e.g., Lloyd, 1992) on the selective mechanisms governing this transition have been particularly influential in guiding empirical research.

Why has the evolution of selfing from outcrossing been the focus of sustained interest for over a century? First, multiple independent transitions to selfing provide valuable opportunities to study convergent evolution, particularly the genetic and developmental basis of floral traits (e.g., small flowers, reduced floral display, and pollen production) that constitute the selfing syndrome (Sicard and Lenhard, 2011; Figure 1). Second, because selfing enables single plants to found colonies following long-distance dispersal, the shift to selfing can have significant biogeographical consequences (Figure 1), for example, by facilitating island colonization or migration to range margins where plant density may be low, a phenomenon known as Baker's Law (Baker, 1955). Third, selfing leads to restricted gene flow and reproductive isolation from ancestral outcrossing populations, potentially influencing speciation and lineage diversification (Wright et al., 2013). A persistent theme concerns the extent to which the evolution of selfing is an 'evolutionary dead end' as a result of the ephemerality of selfing lineages compared to those that are outcrossing (Igic and Busch, 2013). Finally, because predominant selfing reduces the effective rate of recombination and effective population size there has been much recent interest on the genomic consequences of transitions to selfing, and the demographic and genetic processes causing genome-wide reductions in diversity in populations (Wright et al., 2008).

Diverse reproductive, demographic, and genetic factors influence mating system evolution in plants. Of particular importance is the relative fitness of progeny that results from cross- versus self-fertilization, a phenomenon known as inbreeding depression. Darwin (1876) conducted controlled pollination studies on 57 species from 30 families and, in virtually all cases, discovered that selfed offspring performed less well compared with outcrossed offspring. Darwin used this observation to explain the function of numerous floral adaptations in angiosperms; they were outcrossing mechanisms limiting the harmful effects of self-fertilization. Today, it is understood that inbreeding depression is near ubiquitous in outcrossing species and largely results from the expression of recessive deleterious alleles in genotypes made homozygous as a result of inbreeding (Charlesworth and Willis, 2009). Inbreeding depression features in most models of mating system evolution and its magnitude plays an important role in helping to explain the observed distribution of outcrossing rates in nature, although explaining the occurrence of a significant number of species with a mixture of outcrossing and selfing (mixed mating) has resulted in considerable debate (Goodwillie et al., 2005). A current challenge is to determine ecologically relevant levels of inbreeding depression under
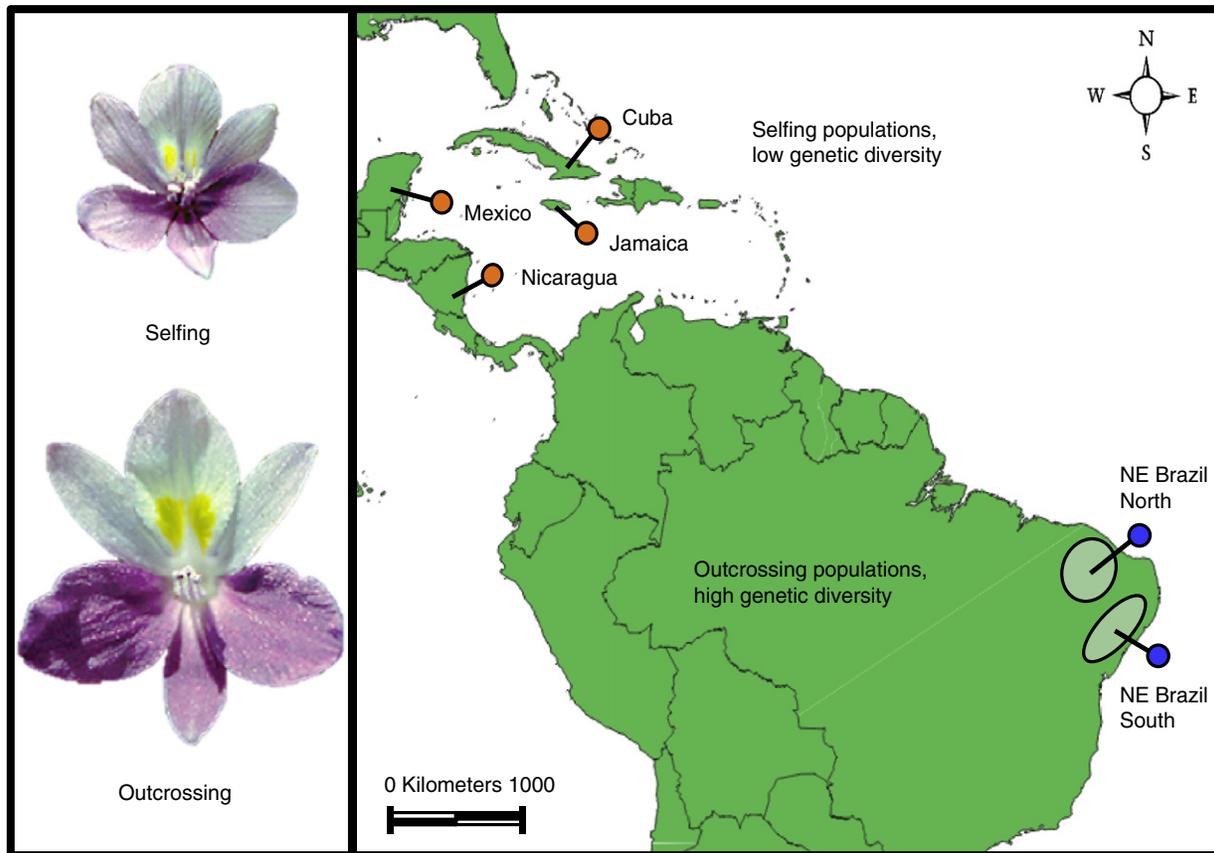
Figure 1 The phenotypic, biogeographical, and genetic consequences of evolutionary transitions from outcrossing to selfing, as exemplified by *Eichhornia paniculata* (Pontederiaceae). In this neotropical species, large-flowered outcrossing populations predominate in NE Brazil (bottom), and small-flowered selfing populations (top) have colonized the Caribbean and Central America. Outcrossing populations maintain high levels of diversity, whereas selfing populations are much less diverse. Further details are provided in Barrett *et al.* (2009).

field conditions as it is clear that comparisons conducted under glasshouse conditions significantly underestimate differences between selfed and outcrossed offspring (Dudash, 1990). Novel methods for estimating inbreeding depression in the field using genetic markers (Koelling *et al.,* 2012) may alleviate this problem, as should recent studies (e.g., Campbell *et al.,* 2013) on the extent to which biotic factors (pests and diseases) differentially influence the fitness of selfed and outcrossed offspring.

Inbreeding depression prevents the evolution of high selfing rates in most outcrossing populations. However, selfing evolves often and approximately 10–15% of flowering plants are predominant selfers, indicating that certain conditions can favor the selection of high selfing rates. The two most general mechanisms to explain the transition to selfing are: (1) The 'reproductive assurance hypothesis,' which traces back to Darwin and is the most frequently invoked explanation for why selfing often evolves under conditions of low density. It proposes that selfing is favored whenever pollen vectors and/or compatible mates are absent, limiting seed set by cross-pollination. (2) The 'automatic selection hypothesis,' which is based on R.A. Fisher's idea that a gene for selfing has a 3:2 transmission advantage when it arises in an outcrossing population. Determining the relative importance of these two hypotheses empirically is not straightforward, particularly if

both processes operate during the transition to high selfing rates, as it requires determining the modes of self-fertilization in a population, and whether selection of genetic modifiers of the mating system occurs through pollen and/or seed (Busch and Delph, 2012). As yet, this has not been attempted in any species in which the transition to selfing has been investigated.

It has also been suggested that molecular data might be useful for distinguishing the two main hypotheses for the evolution of selfing. The demographic and genetic processes associated with reproductive assurance may result in a different genomic signature than those associated with automatic selection. This is based on the idea that when selfing evolves by reproductive assurance genetic bottlenecks causing the genome-wide loss of diversity should be common (Schoen *et al.,* 1996). However, recent work demonstrating that linked selection can also reduce genome-wide diversity rapidly following the transition to selfing casts doubt on whether it will be possible to use molecular data to distinguish the two main hypotheses for the evolution of selfing (Barrett *et al.,* 2014). It seems likely that reproductive assurance plays a more important role than automatic selection in initiating the transition to selfing; however, at present the case rests largely on correlative ecological evidence on the geographical distribution of selfing populations and their occurrence under conditions of low density. Experimental evidence on the

selective mechanisms driving the transition to selfing is generally lacking, despite a rich theoretical literature on the topic.

Sexual Systems and Gender Strategies

Most angiosperm species possess flowers with both male and female sexual organs and only ∼10% have unisexual flowers (dicliny), with either female or male sex organs. There has been repeated evolution of dicliny across the angiosperm phylogeny, and variation in the temporal and spatial arrangement of unisexual flowers within and between individuals has given rise to the remarkable diversity of sexual systems found in flowering plants (Barrett, 2002). A population producing entirely unisexual flowers can be hermaphroditic if both male and female flowers are present on the same individuals (examples include maize and squash). This sexual system, termed monoecy (Figure 2(a)), prevents within-flower self-pollination and allows greater flexibility in the amount, location and timing of female and male investment in response to environmental cues during growth, or as a result of individual condition. Unisexual flowers can also be separated on different individuals, giving rise to male and female sexual morphs (dioecy; Figures 2(b) and 2(c)); examples include kiwifruit and marijuana. However, in some species unisexuals are maintained in populations with hermaphrodite

plants, resulting in gynodioecious (females and hermaphrodites; e.g., many members of the mint family, Lamiaceae) and androdioecious (males and hermaphrodites; e.g., annual mercury, *Mercurialis annua*) sexual systems. Finally, all three sex phenotypes can sometimes coexist within a population (subdioecy; e.g., broadleaf arrowhead, *Sagittaria latifolia*), although the extent to which this sexual system is stable over evolutionary time is unclear. Subdioecy is most often associated with evolutionary transitions from gynodioecy to dioecy, as discussed further below (and see Figure 3).

From the perspective of mating patterns it is often more informative to consider the gender strategy of a population, an approach that involves a functional as opposed to morphological definition of plant sexual systems. The term gender strategy concerns the genetic contribution that each plant in a population makes to the next generation through maternal versus paternal expenditure and hence their 'femaleness' or 'maleness' (Lloyd, 1979). Although it is challenging to measure the true functional gender of individuals using genetic markers, many workers obtain a rough approximation of female and male mating success by describing the phenotypic gender of populations, which involves estimating allocation to alternate sex functions. Using this approach it is evident that all plant sexual systems can be divided into two fundamentally distinct strategies involving either gender monomorphism (Figure 2(d)) or gender dimorphism (Figure 2(e)).
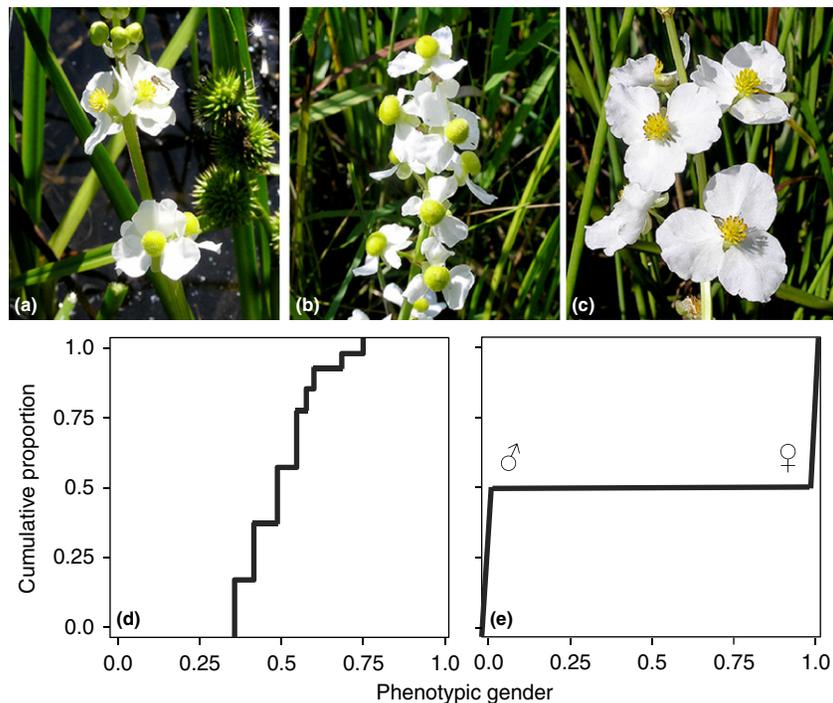

Figure 2 Intraspecific variation in sexual systems in a plant species: in *Sagittaria latifolia* (Alismatacae) three sexual phenotypes occur, with the majority of populations containing either hermaphroditic plants with separate female and male flowers (monoecy) as in (a), or unisexual plants (dioecy) that are either female (b) or male (c). (d) and (e) Illustrate phenotypic gender variation within and among populations of *S. latifolia*, based on allocation to female and male flowers. In (d) gender is monomorphic with continuous variation, whereas in (e) the distribution is dimorphic with approximately equal numbers of male and female plants. In some parts of the range populations with females, males and hermaphrodites also occur (subdioecy; Yakimowski and Barrett, 2014). See Lloyd (1979) for further details on the measurement of gender in plant populations and Sarkissian *et al.* (2001) for details of gender variation in *S. latifolia*.
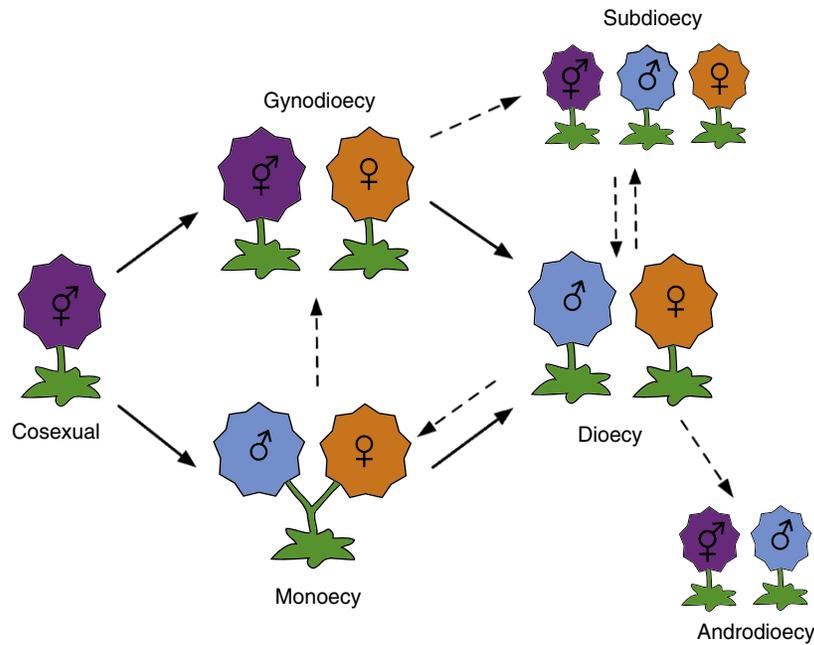
Figure 3   The primary evolutionary pathways by which polymorphic sexual systems originate from cosexuality in flowering plants. In the gynodioecy pathway (above), the first step is the invasion of females into hermaphrodite populations resulting in gynodioecy. This is followed by subsequent loss of female function in hermaphrodites giving males. This second step may often involve an intermediate stage in which hermaphrodites coexist with both females and males (subdioecy), although this condition can also arise from dioecy. The monoecy pathway (below) commences with increased specialization of female or male function by the origin of female and male flowers on hermaphroditic plants (monoecy). This is subsequently followed by gender specialization through gradual alteration in floral sex ratios and the evolution of unisexual plants (females and males). The monoecy pathway may occasionally involve an intermediate gynodioecious stage in which females invade monoecious populations, and occasional reversions from dioecy to monoecy are also known. Androdioecy is most commonly associated with the breakdown of dioecy, with females regaining male function and coexisting with males. For further details of the evolution of sexual system diversity see Barrett (2002).

In populations with gender monomorphism there is continuous (quantitative) variation in gender, with the average individual contributing genes equally through female and male function. All hermaphroditic plant species exhibit gender monomorphism. In contrast, in populations with gender dimorphism there is a bimodal distribution of gender, with a clear distinction between the gender of individuals belonging to different sexual morphs. Clearly, gender dimorphism occurs in dioecious populations, where male and female plants achieve all fitness through their particular gender and on average females and males contribute equally to the next generation, as every seed has both a mother and a father. However, gender dimorphism also occurs in gynodioecious and androdioecious populations, because the presence of unisexual individuals results in hermaphrodites contributing genes to the next generation mostly through the opposite gender to the particular unisexual morph in the population, rendering them functionally more male (gynodioecy) or female (androdioecy). Thinking about plant sexual systems in terms of gender strategies highlights the flexible and frequency-dependent nature of plant mating, with hermaphrodites acting 'more male' or 'more female' depending on the frequency of sexual phenotypes in the population, and this approach provides a functional framework for understanding the mating biology of plants.

The evolution of gender dimorphism from monomorphism requires the invasion of either males or females into a population of hermaphrodites, leading to androdioecy or gynodioecy, respectively. The frequency of these two dimorphic sexual systems is remarkably different among angiosperms families: gynodioecy occurs in ∼7% of species and in many families, whereas only a handful of examples of true androdioecy are known. Furthermore, most cases of androdioecy involve a reversion from dioecy via the reacquisition of male function in females (Figure 3), rather than through male invasion of hermaphrodite populations, although this pathway does appear to occur rarely (Pannell, 2002).

Why then is gynodioecy much more common than androdioecy? This question can be addressed by considering the conditions that allow a unisexual individual to invade a hermaphrodite population, and how these conditions differ between the sexes. Intuitively, for a female or male individual to invade a population of hermaphrodites they must be at least twice as fit as hermaphrodites through female or male function, respectively (Lloyd, 1975). An important component in models for the evolution of gynodioecy is therefore the presence of inbreeding depression lowering the fitness of hermaphrodites. If hermaphrodites are self-compatible and through selfing suffer inbreeding depression this will lower the threshold over which a female can invade, because all offspring from females must necessarily be outcrossed and will therefore avoid inbreeding depression. However, in the case of androdioecy in a partially selfing population there will be

fewer ovules available for males to fertilize, which limits the potential siring success of invading males. Theoretical models indicate that with some degree of inbreeding depression females are not required to produce twice the number of ovules in order to invade a population of hermaphrodites, whereas males always have to produce at least twice the amount of pollen (Charlesworth and Charlesworth, 1978). Another constraint that reduces the frequency of male invasion relative to female invasion arises from the genetic mechanism causing the loss of male or female function. Cytoplasmic male sterility, where the sterility mutation occurs in either plastid or mitochondrial DNA as opposed to nuclear DNA, is a common phenomenon in plants, and is used in the production of hybrid seed in many crops. Unlike nuclear mutations, these mutations are inherited solely through the maternal line, making it unavailable as a mechanism of female sterility, as required for androdioecy. Furthermore, if male sterility is determined this way, only a slight advantage in female fertility is required for females to increase in frequency in the population (Lewis, 1941). Altogether, the conditions under which females can invade a hermaphrodite population are much less stringent than for males, explaining why gynodioecy is considerably more common than androdioecy in flowering plants.

Only ~6–7% of flowering plant species have separate sexes (Renner and Ricklefs, 1995). Despite being relatively uncommon, dioecy has a scattered distribution across the angiosperm phylogeny occurring in ~40% of all angiosperm families. This indicates that separate sexes have evolved independently many times from hermaphroditism, in concert with a suite of ecological and life history correlates (Vamosi et al., 2003). The common occurrence of dioecy on the tips of phylogenetic trees and the apparent lower species richness of dioecious clades compared to their sister groups has led to the idea that dioecy, like predominant selfing, is an 'evolutionary dead end' either due to the high extinction rates or low speciation rates of dioecious clades (Heilbuth, 2000). However, this idea has recently been challenged based on comparative evidence that dioecious clades actually have a slightly higher net diversification rate than non-dioecious clades, and the phylogenetic distribution is instead a result of a combination of low transition rates to dioecy, as well as frequent losses (Käfer et al., 2014).

The evolution of separate sexes requires two independent sterility mutations affecting female and male fertility, making it improbable that dioecy would arise directly from a hermaphrodite population without any intermediate stages. There has therefore been considerable interest focused on the evolutionary pathways that give rise to separate sexes, with the two most frequently invoked routes being the gynodioecy and monoecy pathways (Figure 3). In the gynodioecy pathway, females invade a hermaphroditic population leading to gynodioecy and subsequent selection on hermaphrodite sex allocation increases their 'maleness,' giving rise to an intermediate and often unstable stage of subdioecy and ultimately the evolution of dioecy (Spigler and Ashman, 2012), as has been shown in Fragaria, the strawberry genus (Liston et al., 2014).

In contrast, the sequence of changes involved in the monoecy pathway is less well understood. It has often been suggested that disruptive selection on quantitative genetic variation in floral sex ratios within monoecious populations drives the evolution of different degrees of femaleness and maleness and ultimately results in completely separate-sexed plants (Figure 3). However, other evidence suggests that dioecy can sometimes evolve from monoecy via the gynodioecy pathway owing to large effect male sterility mutations and female invasion (e.g., broadleaf arrowhead, Sagittaria latifolia; Dorken and Barrett, 2004). Although the gynodioecy pathway has been well studied both theoretically and empirically, much less is known about the monoecy pathway, despite the strong correlation between dioecy and monoecy within clades, which has led to the suggestion that most transitions to dioecy follow this route (Renner and Ricklefs, 1995). However, there are two caveats that need to be considered in accepting this interpretation. First, in many clades the ancestral state is not clear and the polarity could therefore sometimes be reversed, with monoecy being derived from dioecy (e.g., in Momordica, the bitter gourd genus; Schaefer and Renner, 2010). Second, it is also possible that similar conditions promote the evolution of both monoecy and dioecy, resulting in a correlation independent of any particular transition sequence. What is clear is that more work is needed before a clear picture emerges of the evolution of dioecy via the monoecy pathway.

See also: Angiosperm Phylogeny and Diversification. Mating Systems in Plants, Genome Evolution and

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