

MAJOR EVOLUTIONARY TRANSITIONS IN FLOWERING PLANT REPRODUCTION: AN OVERVIEW

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Evolutionary transitions are functionally significant changes in organismal traits that largely result from the action of natural selection. They first appear within populations when novel traits replace the ancestral state because of increased fitness. Evolutionary transitions take on broader significance and can be considered major when newly established traits persist, are maintained through multiple speciation events, and ultimately become well-established features of lineages. The shifts in character state that constitute an evolutionary transition are key elements of biological diversification, and the identification and study of major transitions during the history of life now represent an important research program in evolutionary biology (Maynard Smith and Szathmáry 1995).

Similar character state transitions often occur repeatedly among unrelated lineages, and these situations are of particular interest because they usually indicate equivalent selective mechanisms and convergence in function. Estimating the number of transitions using phylogenetic methods and character reconstructions can provide important information for more in-depth studies of the ecological basis of selection. Multiple transitions can also provide outstanding opportunities to investigate whether similar molecular and developmental mechanisms are responsible, although this area of study is still in its infancy. Another important issue concerns the polarity of transitions and to what extent particular changes are irreversible or evolutionarily labile. The developmental complexity of traits can play an important role in determining the degree of asymmetry, although this is not always the case. Finally, when transitions involve similar suites of characters, determining the order of acquisition of component parts can provide insight into adaptation and the ecological drivers of change. Research on the causes and consequences of character transitions are at the heart of modern evolutionary biology and, to be successful, require the integration of both microevolutionary and macroevolutionary approaches.

Among plant life-history traits, reproductive characters are particularly important in affecting microevolutionary processes and macroevolutionary patterns. These fundamental roles arise because reproductive characters influence genetic transmission, population genetic structure, selection response, and patterns of evolutionary diversification. Major reproductive transitions are often associated with changes to other components of life history and also with modifications in the genetic system. In flowering plants, resource allocation, pollination, and mating influence reproductive success in an integrated manner, and, as a result, functional correlations between these components of

reproduction are a pervasive feature of phenotypic evolution. Studies of reproductive trait transitions therefore should not be conducted in isolation from other changes to phenotype involving nonreproductive traits. In addition, phyletic history, development, and genetic architecture can all influence pathways of change and need to be considered.

Flowering plants exhibit exceptional diversity in floral traits and reproductive mechanisms, with closely related species often possessing different modes of sexual and asexual reproduction, contrasting pollination and mating systems, and diverse gender strategies. This variation was first studied in detail by Charles Darwin (1877) and was later exploited during the 1950s and 1960s by G. Ledyard Stebbins (e.g., 1974), Verne Grant (e.g., 1965), and Herbert Baker (e.g., 1959) during the golden era of plant biosystematics. These workers recognized that important insights into variation and evolution of reproductive traits within families and genera could often be obtained by careful studies of intraspecific variation, especially in wide-ranging species adapted to different ecological circumstances. The development of population biology in the 1970s led to field studies of natural selection (reviewed in Endler 1986) and the development of theoretical models investigating key parameters involved in the selective mechanisms responsible for particular reproductive transitions (e.g., Lloyd and Webb 1992). More recently, comparative and phylogenetic approaches have been used to investigate reproductive transitions in an effort to link macroevolutionary patterns of diversification with the ecology and genetics of species (reviewed in Weller and Sakai 1999).

Studies of major reproductive transitions in flowering plants are today the focus of considerable research in plant evolutionary biology. This special issue of *International Journal of Plant Sciences* highlights a selection of current work by leading authors in the field. The contributions feature new research findings, reviews, and synthesis and include diverse approaches for understanding the pathways of reproductive trait evolution in flowering plants. These include comparative and phylogenetic methods, theoretical models, investigations of structure and development, molecular genetics, and experimental studies of the ecology and genetics of wild populations. Given the exceptional reproductive diversity of flowering plants, it has not been possible to be comprehensive, and important major transitions involving flower morphology and development (e.g., evolution of zygomorphy), pollen biology (e.g., evolution of trinucleate pollen), life history (e.g., evolution of monocarpy), and fruit and seed dispersal (e.g., evolution of fleshy fruits) await future treatment. Instead this issue focuses on a selected group of topics, emphasizing how they can be tackled using

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complementary approaches. The issue is divided into three sections that in turn deal with flowers and pollination, mating patterns and gender strategies, and asexual reproduction and polyploidy.

Flowers and Pollination

Flowering plants exhibit spectacular variation in flower design and display, and much of the functional basis of this diversity is associated with the evolution of pollination systems. Mark Rausher begins the section on flowers and pollination by providing a comprehensive review of transitions in flower color in animal-pollinated lineages, focusing in particular on the change from blue to red flowers. He takes a critical approach to existing evidence about the mechanisms responsible for shifts in flower color and challenges the widespread assumption that these changes are inevitably related to pollinator-mediated selection and adaptation to novel pollinators. Although not disputing that pollinators may play an important role in flower color transitions, his review of the evidence indicates that a convincing case is still to be made. He proposes that some transitions in flower color could result from selection on the pleiotropic effects of flower color alleles by nonpollinating agents. Rausher also points out that transition rates from blue to red flowers are usually asymmetrical and associated with loss-of-function mutations and inactivation of branches of the anthocyanin pathway. His review provides a valuable lesson in the complexities of studying the evolution and adaptive significance of a seemingly simple trait such as flower color.

The next article, by James Thomson and Paul Wilson, also features changes in flower color from blue to red associated with pollinator transitions from hymenoptera, especially bees (melittophily), to pollination by hummingbirds (ornithophily). These transitions are commonplace, especially in western North America, where they have occurred at least 100 times in diverse lineages of herbs. Thomson and Wilson's approach is to consider the ecological and genetic mechanisms that might account for the destabilization of pollination syndromes, using *Penstemon*, *Mimulus*, *Ipomoea*, *Costus*, *Aquilegia*, *Silene*, and *Salvia* as examples. They focus specifically on three main topics: differences in pollen transfer efficiency among bees and birds, the role of mutations with large effects on floral phenotypes, and the ecological conditions that change visitation rates of pollinators and hence the nature of pollen dispersal. Among the various factors reviewed, Thomson and Wilson consider ecological change as the most likely initial driver of pollinator shifts but point out that little concrete information is currently available on precisely what these changes involve.

Risa Sargent and Jana Vamوسي take up this topic further in the next article by investigating the extent to which ecological context influences evolutionary transitions in the degree of pollinator specialization. They examine the hypothesis that ecological shifts to environments with different light conditions are accompanied by transitions in pollinator guild. Using phylogenetically independent contrasts and data collected largely from tropical forest environments, they examine the degree to which transitions in canopy position are associated with particular pollinators and pollinator guild size. Their analysis demonstrates that species that tend to occupy the

same position in the forest canopy are more closely related than would be expected by chance, as are species with particular pollinator syndromes (e.g., bee or bird). Transitions to generalist pollination are strongly associated with beetle and fly pollination and with position in the canopy above the forest floor. Their results suggest that evolutionary transitions between specialized and generalized interactions are unlikely to be subject to phylogenetic constraint or specific requirements for particular light environments.

In contrast to several of the major angiosperm reproductive transitions featured in this special issue (e.g., the evolution of selfing and dioecy), remarkably little is known about the evolution of wind pollination from animal pollination. This is surprising because this shift in pollination mode, with at least 65 independent transitions, represents one of the major transformations in the reproductive biology of flowering plants. Jannice Friedman and Spencer Barrett use comparative approaches to investigate the correlated evolution and order of trait acquisition between pollination mode and a range of ecological and reproductive characters. One of their most interesting findings is that wind pollination evolves more frequently in lineages that already possess unisexual flowers, and they propose a novel hypothesis to account for this association. Populations with unisexual flowers may evolve wind pollination as a mechanism of reproductive assurance ensuring more effective pollen dispersal between plants and relieving pollen limitation. Reproductive assurance is usually invoked to explain the evolution of selfing; however, the presence of unisexual flowers would prevent selfing by autonomous self-pollination in most groups. Pollen limitation may therefore promote strikingly different evolutionary transitions in pollination systems, depending on the sexual traits of ancestral populations.

In the next article, Lawrence Harder and Steven Johnson tackle the intriguing problem of why some flowering plants disperse their pollen in groups. The evolution from individual monads to pollen aggregation, including tetrads, polyads, pollen threads, and pollinia, has at least 39 independent origins and therefore represents a significant functional transition in angiosperm pollination. However, the adaptive benefits of pollen aggregation have not been explored either theoretically or empirically. It seems likely that transitions to pollen aggregation require special conditions because diminishing returns through male function during pollination, as well as the genetic benefits of multiple paternity, should favor the dispersal of individual pollen grains. Harder and Johnson explore the reproductive circumstances that are likely to favor the different forms of pollen aggregation and propose that this variation comprises alternative strategies for relieving contrasting limitations on siring ability. They also consider several aspects of plant reproduction that are consequences of the evolution of pollen aggregation, focusing in particular on the evolution of pollinia in orchids and proposing that the ability of orchid pollinia to reduce diminishing returns during pollination may explain the widespread occurrence of deceit pollination in this clade and its exceptional floral diversity.

In the last article in this section, William Friedman, Eric Madrid, and Joseph Williams provide a novel evolutionary and developmental perspective on the structural diversity of female gametophytes in angiosperms. They argue that female

gametophytes are iteratively expressed modular entities and that structural diversity results from variation in the relative timing of the establishment of modules as well as ontogenetic events that determine their number and degree of modification from the plesiomorphic condition. By linking structural diversity in the female gametophyte to endosperm biology, they demonstrate that variation in developmental patterns determines variation in endosperm genetics. Friedman and colleagues also review potential selective mechanisms that may drive changes in endosperm genetics. They show that hypotheses based on heterozygosity, ploidy level, and sexual conflict make similar predictions concerning the evolution of female gametophyte development. This article demonstrates that future investigation of evolutionary transitions in female gametophyte development and endosperm genetics cannot be examined independently.

Mating Patterns and Gender Strategies

The evolution of predominant selfing from obligate outcrossing has received more attention than any other reproductive transition in flowering plants. Indeed, Stebbins (1974) suggested that this transition has occurred more often than any other. This section begins with three contrasting articles concerned with various facets of this frequent change in the mating system of populations.

The self-incompatibility polymorphism is the principal and most effective mechanism preventing self-fertilization in hermaphroditic flowering plants. In the first article, Boris Igic, Russell Lande, and Joshua Kohn examine the breakdown of self-incompatibility and its evolutionary consequences. They begin by reviewing the available literature on the frequency distribution of self-incompatibility and find that it is reported from 100 taxonomically diverse families and ca. 39% of angiosperm species. They then consider why self-incompatibility is often lost but rarely, if ever, regained during angiosperm diversification. They suggest that loss of self-incompatibility occurs because transitions to self-compatibility are generally accompanied by losses in allelic diversity at the *S*-locus, because the variation becomes selectively neutral in self-compatible populations, and because of the accumulation of loss-of-function mutations, for which there is considerable evidence in *Arabidopsis* and *Solanum*. Assuming that the loss of self-incompatibility is irreversible, they develop a theoretical model that examines the evolutionary processes required to maintain self-incompatibility. They show that stable maintenance of self-incompatibility can only occur if it is associated with increased diversification relative to self-compatible lineages, with the balance of transition and diversification rates determining the frequency distribution of mating systems they consider. Lower diversification of self-compatible lineages may occur because mutations causing self-compatibility are commonly associated with increased selfing rates, and this can lead to lower genetic diversity and the possibility of an increased risk of extinction.

In the next article, Stephen Wright, Rob Ness, John Paul Foxe, and Spencer Barrett review the genomic consequences of selfing and outcrossing, picking up on the theme discussed in the preceding article regarding the influence of predominant self-fertilization on the evolutionary fate of populations.

They review available genomic data contrasting selfing and outcrossing populations and discuss opportunities for selfing populations to avoid an irreversible decline in fitness and extinction. Transitions to selfing are expected to cause a reduction in effective population size, an increase in fixation rates of slightly deleterious mutations, and a decrease in fixation of advantageous mutations; however, the existing evidence does not suggest a significant reduction in the efficacy of selection associated with high selfing rates. Although the available data are sparse, Wright and colleagues also examine evidence that recombination rates may evolve in response to changes in mating patterns, thus limiting the deleterious effects of inbreeding. The abundance and activity of selfish genetic elements may also be reduced in selfing lineages. A reduction in genomic conflict can increase mean fitness, reduce deleterious mutation rates, and reduce genome size. Using comparative data, Wright and colleagues show that highly selfing species have smaller genomes in comparison with outcrossing relatives, consistent with reduced activity and spread of repetitive elements in inbreeders. One of the main messages of this article is that as genomic data rapidly accumulate over the coming years, there will be exciting new opportunities to test evolutionary theory within a phylogenetic framework using comparative analyses of closely related selfing and outcrossing species.

Early theories on mating systems proposed that group selection favored some optimum level of recombination within species. Today, these ideas are no longer widely accepted, and models based on individual selection are used to explore the evolution of selfing from outcrossing. In the next article, Daniel Schoen and Jeremiah Busch reconsider the importance of group-level selection of mating systems. Their investigation is opportune in light of evidence, discussed earlier in this section, for differences in diversification and extinction rates of predominantly selfing versus outcrossing plants and the general observation that transitions to predominant self-fertilization may be unidirectional. Schoen and Busch develop models of mating system evolution using a metapopulation framework to investigate factors that may operate when group-level selection occurs. A particular focus of these models is to examine situations in which individual and group-level selection oppose one another, as well as those that result in stable mixed mating. They find that if group-level selection in a metapopulation is sufficiently strong, it may limit transition rates from outcrossing to selfing and therefore counteract individual selection for selfing through reproductive assurance. The models generally show that selection among populations can maintain outcrossing through higher extinction rates of selfing groups and through reduced transition rates from outcrossing to selfing. Further studies of the role of multilevel selection in the evolution of self-fertilization will require detailed information on the extent to which transitions to selfing influence population viability and longevity and also how genetic architecture and the details of floral development influence the tempo by which selfing variants can spread.

The remaining two articles in this section consider transitions in gender strategies, particularly the evolution of gender dimorphism from monomorphism. This represents a prominent transition in the sexual systems of plants that, in common with the evolution of selfing from outcrossing, has received considerable theoretical and empirical attention. John Pannell,

Marcel Dorken, Benoit Pujol, and Regina Berjano employ microevolutionary approaches to investigate transitions between sexual systems in the annual herb *Mercurialis annua*, in which dioecious, monoecious, and androdioecious populations occur in different parts of the European and North African range. This species complex has provided outstanding opportunities for investigating the ecological and genetic mechanisms driving sexual system evolution. Pannell and colleagues point out that hybridization and polyploidy have played an important role in initiating transitions between sexual systems. However, they also demonstrate that some transitions are not confounded with changes to the genetic system, and these can provide valuable insights into the ecological and demographic mechanisms involved. Investigations of geographical transitions between monoecious and androdioecious populations support a metapopulation model in which differential selection for reproductive assurance during colonization at the regional level plays a key role. Pannell and colleagues also present new experimental data that illustrate the importance of phenotypic plasticity in hermaphrodite sex allocation in regulating male frequencies in androdioecious populations. This contribution illustrates how the resource status of plants and their local mating environment can play critical roles in regulating gender strategies and sex ratios.

A complementary approach to understanding evolutionary transitions in gender strategies is to investigate genera or families that contain sexual system diversity using phylogenetic analysis and the reconstruction of character evolution. In their article, Andrea Case, Sean Graham, Terence Macfarlane, and Spencer Barrett address some of the difficulties associated with inferences about historical transitions in sexual systems using *Wurmbea*, a small genus of monocotyledons from the Southern Hemisphere. *Wurmbea* is divided into two well-supported clades, each defined by geography and variation in sexual system. Case and colleagues explore the influence of tree uncertainty, taxon sampling and extinction, the evolutionary lability of characters, and several other sources of ambiguity for maximum likelihood (ML)-based inferences of sexual system evolution. They find that the interspersed species across trees that vary in sexual system is the main cause of ambiguity in their historical reconstructions. Another source of uncertainty that they identify concerns the nonmonophyly of two sexually polymorphic species, *Wurmbea dioica* and *Wurmbea biglandulosa*. These geographically widespread taxa have been the subject of detailed ecological and genetic studies over the past two decades aimed at understanding the selective mechanisms driving the evolution of gender dimorphism from monomorphism. Clearly, the finding that these taxa are not monophyletic will have important implications for future interpretation of character transitions. This article provides examples of some of the challenges in linking macroevolutionary pattern with microevolutionary processes for evolutionarily labile traits in plant groups that possess diverse sexual systems. It should caution workers interested in reconstructing character evolution that using these approaches is not always as straightforward as is sometimes assumed.

Asexual Reproduction and Polyploidy

Asexual reproduction and polyploidy are both very widespread among flowering plant families and, in some groups,

are commonly associated. In the final section of this issue, evolutionary transitions to asexual reproduction and genome duplication through polyploidy are examined. In the first article, Jonathan Silvertown evaluates the costs and benefits of asexual and sexual reproduction in plant species that have both reproductive modes. He is intrigued by the fact that the evolutionary transition to clonal reproduction has rarely, if ever, replaced sexual reproduction entirely. Silvertown compares the genotypic diversity of populations, a proxy for the relative success of recruitment through sexual and asexual means, across a range of ecological conditions in 218 species from 74 families to determine why one mode of reproduction may be favored over the other. After controlling for bias resulting from marker type, scale of sampling, sampling design, and the number of populations sampled, Silvertown is able to make several generalizations from his data set. First, most populations in the survey are multiclonal, with populations of aquatic plants, especially those recently founded through vegetative dispersal, often the exception. Second, clonality occurs more commonly than sexual reproduction in older populations maintained by a lack of disturbance, in geographically marginal environments, and also in rare or alien species. Silvertown concludes by proposing that the shift to exclusive clonal reproduction is rare because clonality is not a substitute for sex but, rather, prolongs the time to extinction when restrictive ecological conditions prevent sex from occurring.

In contrast to clonal propagation, the evolution of asexual reproduction through apomixis has occurred frequently in sexual lineages, and in some polyploidy groups this can be obligate, although mixed reproductive modes are more common. Apomixis is reported from many angiosperm families, with particular concentrations of species in the Asteraceae, Poaceae, and Rosaceae. In the next article, Jeannette Whitton, Christopher Sears, Eric Baack, and Sarah Otto provide a comprehensive review of the evolution of apomixis, focusing on its genetic basis and on the population genetic and ecological factors that affect the spread of asexual lineages. They emphasize the importance of occasional bouts of sexual reproduction to the establishment and proliferation of asexuality and, specifically, the role that pollen plays in this context. Evidence indicates that many apomicts retain residual pollen function, providing opportunities for the spread of apomixis through male gametes. Whitton and colleagues also propose several hypotheses to explain the association between gametophytic apomixis and polyploidy and argue that determining whether polyploidy involves autopolyploidy or allopolyploidy may provide critical insights into the causal mechanism(s) responsible for this association. Review of their own work on two North American apomictic complexes in the Asteraceae illustrates some of the challenges in interpreting the origins and spread of apomixis in systems with complex phylogenetic histories. The article concludes by addressing general issues concerning the evolution of sex and the long-standing issue of why it is so prevalent. Future studies of apomictic plants should provide exciting opportunities for investigating these problems through experimental studies of the benefits of sex and the costs of asexuality.

Populations at range limits often reproduce primarily through asexual reproduction, and an important question is the extent to which this results in the dissolution of sex function. This problem has been considered for clonal species, but in

the next article, Stacey Lee Thompson, Gina Choe, Kermit Ritland, and Jeannette Whitton investigate the presence and extent of asexuality and recombination within populations of the polyploid apomict *Townsendia hookeri* (Easter daisy) at the extreme northern limit of the species range in Yukon Territory, Canada. Their study nicely illustrates some of the complexities that can arise as a result of the evolutionary transition to asexuality in apomictic lineages. Using genetic markers, surveys of genome size using flow cytometry, estimates of pollen viability, and a novel procedure for estimating long-term recombination, they demonstrate considerable variation within and among populations in ploidal level, male fertility, and the reproductive modes of populations. Of particular significance is their finding that in apparently male sterile polyploid populations, there is evidence of a low level of sexuality with an estimated equilibrium rate of approximately three sexual events every two generations. This study by Thompson and colleagues adds to a growing literature on apomictic polyploid groups that were initially believed to be strictly asexual but instead display cryptic sexuality.

The final article in this special issue, by Brian Husband, Barbara Ozimec, Sara Martin, and Lisa Pollock, brings together two recurrent themes featured in earlier articles—polyploidy and mating systems. Because polyploidy affects the entire genome, it is perhaps not surprising that it influences many aspects of the phenotype, including the mating system. However, although it has long been recognized that the evolutionary transition from diploidy to polyploidy may result in correlated changes in mating patterns, the theoretical and empirical evidence is limited and often contradictory. Several theoretical models predict an increase in the rate of self-fertilization in polyploids, and a survey of mating patterns in related diploid and polyploid congeners in this article provides support for this prediction. However, increased selfing was a feature only of allopolyploids and not autopolyploids, raising the important question of what factors limit selfing in autopolyploid species. To address this problem, Husband and colleagues use *Chamerion angustifolium* to compare the magnitude of inbreeding depression in established autopolyploids and neopolyploids synthe-

sized using colchicine. They find that the cost of selfing in neopolyploids is negligible compared with extant polyploids but that there is some evidence that inbreeding depression increases with the history of inbreeding. Their results suggest that any initial increase in selfing may be transient in autopolyploids and that selection may ultimately favor mixed or outcrossed mating. An important conclusion from this study is that the costs of selfing in polyploids are likely to be dynamic, changing with the age of the polyploid and history of mating.

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