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The Ecology of Mating and Its Evolutionary Consequences in Seed Plants

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Abstract

Mating in seed plants arises from interactions between plant traits and the environmental and demographic context in which individuals reside. These interactions commonly cause nonrandom mating, including selfing and promiscuous outcrossing within local neighborhoods. Shared features of seed plants, specifically immobility, hermaphroditism, and modularity, shape the essential character of mating mediated by animals, wind, and water. In addition, diverse floral strategies promote cross- and self-mating, depending on environmental circumstances. Extrinsic ecological factors influence all stages of the mating process—pollination, pollen-tube growth, ovule fertilization—as well as seed development, determining offspring quantity and quality. Traditionally, measures of plant mating systems have focused on a single axis of variation, the maternal outcrossing rate. Instead, we argue for an expanded perspective encompassing mating portfolios, which include all offspring to which individuals contribute genetically as maternal or paternal parents. This approach should expose key ecological determinants of mating-system variation and their evolutionary consequences.
1. INTRODUCTION

Across the tree of life, mating occurs when various processes unite sperm and eggs to produce zygotes, with diverse consequences for offspring, parents, and populations. For offspring, mating establishes their genotype and potential fitness. For parents, mating determines offspring quantity (fertility) and quality (mean and variance of offspring performance) and hence parental reproductive success. The aggregate distribution of parental outcomes, or who mates with whom and how often, comprises a population’s mating system. For populations, mating establishes and perpetuates pedigrees and genetic lineages, thereby determining population genetic structure and effective population size. Through these diverse influences, mating plays key roles in the demographic and genetic dynamics of populations, guiding evolutionary trajectories, including the scope for local adaptation, speciation, and extinction.

Mating and mating systems of seed plants (hereafter termed plants) have a distinctive nature associated with a suite of shared characteristics. Central among these is immobility, which necessitates the participation of a third agent, the pollen vector, enabling mating between individuals (outcrossing). Pollen dispersal by vectors typically results in nonrandom, promiscuous mating within local neighborhoods (Ghazoul 2005), which favors hermaphroditism (Wilson & Harder 2003), the most common sexual system among seed plants. Hermaphroditism introduces the opportunity for self-fertilization (selfing), which can relieve problems associated with immobility. However, hermaphroditism also risks interference between the sex roles (Barrett 2002) and, for self-compatible species, inbreeding depression (Charlesworth & Willis 2009). The costs and benefits of hermaphroditism are especially germane for most angiosperms, because of the proximity of female and male organs within flowers. Additional distinctive aspects of plant mating arise from their characteristic mode of development and resulting body plan. Plants grow by repeated addition and elaboration of meristems, each of which is totipotent and has the capacity to contribute to the germline. This modularity allows production of multiple sex organs and facilitates clonal propagation. Finally, for angiosperms, the closed carpel imposes intimate interactions between male gametophytes and pistils of sporophytes during the progamic phase of mating (Williams 2012), which intensify male-male competition (Lankinen & Skogsmyr 2001) and may allow female mate choice (Bhattacharya & Baldwin 2012) and opportunities for sexual conflict (Lankinen & Larsson 2009). Together, these plant features constrain plant mating while creating opportunities for unique evolutionary solutions reflected in the reproductive diversity of seed plants.

Although mating refers generically to the processes that generate zygotes, biologists use the terms mating and mating system differently, depending on the organism they study. For animals that couple, mating typically refers to copulation, and the mating system represents the number of different individuals with which an individual couples (e.g., monogamy and polyandry). In contrast, for seed plants coupling results from pollination, a stage for which mate identity is generally difficult to assess. Zygotes are even harder to genotype, so plant mating is usually defined operationally on the basis of seed or seedling genotypes, which reflect both mating and seed development (Maki 1993). Because most plants mate promiscuously, the zoological classification of mating systems is largely uninformative. In addition, because most plants are hermaphrodites, selfing is often a key mating-system component. Indeed, studies of seed-plant mating have historically focused on the relative frequency of cross- and self-fertilization, and this frequency has been widely used to depict plant mating systems (Goodwillie et al. 2005). However, this perspective ignores the diversity of female and male partners with which a plant outcrosses, which can vary greatly.

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1The concepts presented in this review apply generally to seed plants, despite differences in the structure and organization of their reproductive organs. For brevity, we refer to these organs using angiosperm terminology.
The recent availability of highly polymorphic genetic markers enables measurement of siring success and mate diversity (Ashley 2010), fostering a more comprehensive view of plant mating that extends beyond the classic outcrossing-selfing paradigm (Barrett 2003). Here, we review plant mating from this broader perspective.

Although mating is an explicitly genetic outcome, the representation of maternal and paternal alleles in seeds is an emergent property of the largely ecological processes that deliver pollen to ovules to generate zygotes, and of the physiological processes of seed development (Figure 1). This feature of plant mating has two implications. First, the mating system is not fixed for an individual or population. Instead, it depends on local abiotic and biotic environmental conditions that establish overall mating opportunities and realized outcomes (Figure 1). Second, the mating system evolves through intergenerational change in traits that affect gamete production, pollination, progamic processes, and seed development (Figure 1). In particular, selection on these traits commonly generates associations between traits that affect pollination (Rosas-Guerrero et al. 2014), progamic processes (Williams 2012), or both; between reproductive traits and the mating system (Goodwillie et al. 2010, Gervasi & Schiestl 2017); and between the mating system and life-history characteristics (Munoz et al. 2016). Such associations shape macroevolution, including the diversification of clades.

Figure 1
Processes that govern plant mating (purple arrows), and environmental characteristics (orange) and plant traits (green) that influence mating outcomes.
and reproductive traits. Consequently, a complete understanding of mating systems and their evolution requires appreciation of the proximate ecological mechanisms underlying mating success.

Here, we provide a synthetic overview of mating by seed plants, especially angiosperms. Recent reviews have focused on the paradox of mixed mating (Goodwillie et al. 2005), the evolutionary interplay of mating with clonality (Vallejo-Marín et al. 2010) and herbivore defense (Johnson et al. 2015), and the transition from outcrossing to selfing and its genomic (Barrett et al. 2014) and evolutionary (Wright et al. 2013) consequences. Instead, we explicitly consider the ecological dimension of mating, particularly how essential traits interact with the mating environment to determine the character of mating by individual plants, establishing opportunities for mating-system evolution. First, we provide a brief synopsis of mating options and their associated benefits and costs. Then, we identify the roles of key plant traits as fundamental intrinsic determinants of both the incidence of selfing and cross-mate diversity. Finally, we illustrate how environmental interaction shapes mating outcomes and consider the mating consequences of future environmental change.

2. FUNDAMENTALS OF PLANT MATING

Plant mating systems vary extensively, because many mechanisms cause selfing, and outcrossing commonly involves unequal genetic contributions from various numbers of partners.

2.1. Self-Mating

Selfing offers two quantitative advantages related to the representation of parental alleles in offspring: A parent contributes both allele copies to selfed offspring, rather than only one (transmission advantage); and selfing allows mating regardless of outcrossing opportunities (reproductive assurance). Mating, genetic, and resource costs offset these benefits. Mating costs accrue if self-pollination uses pollen or ovules that otherwise would have been available for outcrossing (pollen and ovule discounting, respectively). The severity of these costs differs among modes of self-pollination, being most detrimental when pollen vectors facilitate self-pollination, either within (facilitated autogamy) or among (geitonogamy) flowers, or if it occurs autonomously before (prior autogamy) or simultaneously (competing autogamy) with outcrossing (Lloyd 1992). In contrast, autonomous self-pollination after outcrossing (delayed autogamy) has no mating costs. Various aspects of floral design and display reduce the mating costs of self-pollination (see Section 3.3).

Regardless of the mode of self-pollination, genetic costs arise after self-fertilization. Selfing increases homozygosity, allowing expression of deleterious recessive alleles and causing inbreeding depression (Charlesworth & Willis 2009). The incidence and severity of inbreeding depression (\(\delta\)) depend on the frequency of such alleles in the population, or the mutational load, and can vary with environmental stress (Cheptou & Donohue 2011). Because plant meristems are totipotent, mitotic mutations preceding a meristem’s switch to reproductive function can be incorporated into gametes descended from it, increasing a plant’s potential to transmit deleterious mutations to offspring as it grows (Scofield & Schultz 2006). Expressed deleterious alleles are exposed to purifying selection, so that mutational load evolves, depending on mutation rates, population size, and inbreeding history. If \(\delta < 1\), selection can purge mutational load, reducing the genetic cost of selfing. Consequently, inbreeding depression varies positively with outcrossing rate (Husband & Schemske 1996). However, when inbreeding depression approaches \(\delta = 1\), because of limited inbreeding, deleterious mutations at many loci limit fitness variation among selfed individuals, precluding selection against specific mutations (selective interference; Lande et al. 1994). Mutational load then increases beyond the frequency required to eliminate all selfed offspring before they reproduce, and purging is possible only if selfing is sufficiently frequent to reduce the equilibrium number of deleterious alleles.
Several nongenetic costs also vary positively with inbreeding depression, further offsetting benefits associated with allelic transmission and reproductive assurance. Genetic death of selfed embryos causes seed discounting if outbred embryos have a better chance of developing into viable seeds (Herlihy & Eckert 2002, Layman et al. 2017). Seed discounting also imposes a resource cost proportional to the resources invested both in extra ovules to compensate for genetic deaths and in inbred seeds with poor prospects (Harder et al. 2008). Self-incompatibility protects against the genetic and resource costs of self-fertilization, but not the mating costs of self-pollination, whereas dioecy (populations with separate female and male plants) eliminates all selfing costs.

### 2.2. Cross-Mating

Outcrossing offers qualitative benefits related to the genetic diversity of offspring genotypes, but it is less efficient and success varies more than for selfing owing to the vagaries of pollen dispersal (Richards et al. 2009), pollen germination, and tube growth (Harder et al. 2016). Direct genetic benefits can accrue to outcrossed individuals from heterozygosity and beneficial interlocus associations. Heterozygosity guards against the expression of deleterious recessive alleles and increases the chances of overdominant allelic interactions that contribute to heterosis (Charlesworth & Willis 2009). Outcrossing also increases recombination, which, coupled with selection, can generate beneficial associations between alleles at loci that promote outcrossing and those at loci that enhance viability (Uyenoyama & Waller 1991, Takebayashi & Delph 2000). Such associations can arise if the performance of outcrossed offspring in competition with inbred individuals varies positively with their frequency (Cheptou et al. 2001). This type of epistasis may also explain the superior progamic performance of outbred over inbred male gametophytes (Losdat et al. 2014), even though all alleles are exposed to selection during the haploid phase, at least in diploids (Husband 2016).

Genetic diversity of offspring also arises from mating with multiple partners. From the male perspective, multiple mating provides obvious quantitative advantages, as mating opportunities typically constrain male success, regardless of limits on seed production. This basic tenet of sexual selection probably underlies selection of diverse reproductive traits, including those influencing pollinator attraction (Harder & Wilson 1994) and male-male competition after pollen deposition (Williams 2012). Less established and more contentious is whether multiple mating also confers qualitative benefits for both sex roles. Mating with multiple males creates opportunities for female choice among developing pollen tubes, at least for angiosperms. However, conclusive evidence of mate choice is elusive (although see Bhattacharya & Baldwin 2012), because of the difficulty in distinguishing its effects from those of competition among male gametophytes from different donors (Nora et al. 2016). As an added complication, mate choice may correlate with gametophytic competition, because pistils establish the competitive environment (Lankinen & Skogsmyr 2001). To the extent that either process promotes fertilization by higher-quality pollen, multiple mating can elevate mean offspring quality and hence parental fitness (Nora et al. 2016). Furthermore, within-family diversity should be beneficial if environments for seedling establishment vary temporally or spatially. In particular, with temporal variation, fitness depends on geometric mean offspring success, which varies negatively with variance in success (Simons 2011). In the face of environmental variation, offspring diversity increases the chance that some offspring succeed, reducing the variance in offspring success and enhancing the geometric mean (Garcia-Gonzalez et al. 2015). Such diversification bet-hedging offers benefits similar to those of a diversified investment portfolio in an unpredictable stock market, generally enhancing an investor’s/parent’s geometric mean fitness in the face of stochasticity. The variety of benefits from mate diversity illustrates that outcrossing conveys advantages beyond the genetic consequences associated with heterozygosity.
Mate diversity comprises the number of mates, their relative allelic contributions, and their phenotypic characteristics. Individuals can outcross randomly with respect to their reproductive traits, or partners could be more similar (assortative mating) or less similar (disassortative mating) than expected by chance. The number of mates and their relative contributions to a parent’s offspring can differ both among individuals and between the sex roles for hermaphrodites (see Figure 2). For animal-pollinated plants, two processes determine mate number. Most obviously, mate number generally increases with pollinator visitation, to the extent that pollinators follow different paths among plants. Also, individual pollinators usually carry pollen from multiple plants, because each stigma removes only a fraction of a pollinator’s pollen load, causing pollen carryover to multiple flowers (Richards et al. 2009) and deposition from multiple donors on individual stigmas (Mitchell et al. 2013). Typically, the representation of different male mates among seeds within fruits differs from that among the pollen received by the associated stigmas owing to unequal performance by genetically different male gametophytes and embryos (Ruane 2009).

2.3. Mating Portfolios and Systems

The preceding overview proposes that an individual’s lifetime mating success generates a portfolio of its contributions to offspring genomes (Figure 2). The breadth of options for portfolio composition ranges continuously from the highly consolidated extreme of a family of only self-fertilized offspring to the diversified extreme in which all offspring are half siblings. Most mating portfolios lie between these extremes, with a mixture of full and half siblings, perhaps also including some self-fertilized offspring. For hermaphrodites, an individual’s family, and hence its mating portfolio, includes all offspring to which it contributed genetically as a maternal or paternal parent. Given this perspective, the mating system of a population or species represents the mean and variation in mating portfolios of the constituent individuals. Minimally, the scope of mating portfolios and mating systems can be ordered along two axes: genetic contributions to selfed versus outcrossed zygotes, and the number of mates that donated alleles to outcrossed offspring within families. However, a complete characterization would also depict the relative contributions of different mates.

The portfolio perspective is difficult to elaborate with existing data. Four aspects of traditional approaches to studying mating systems limit understanding of the influences on variation along these axes. First, most studies estimate parameters from the female perspective for populations rather than enumerate allelic contributions of individuals through all relevant sex roles. This approach ignores the fact that every seed has a mother and a father, and averaging over among-individual variation renders it inaccessible to analysis of mating effects of traits and environment. The historical focus on population estimates of female parameters largely reflects the limitations of allozymes as genetic markers. However, the advent of hypervariable markers enables estimation of the paternity of individual seeds (selfed or outcrossed, paternal identity; Wang et al. 2012), which can be used to assess maternal and paternal mating outcomes of individuals and their environmental and trait associations (Kulbaba & Worley 2012). Second, most theoretical and empirical analyses of selfing and outcrossing implicitly assume that ovule production limits seed production (Harder et al. 2008). Given ovule limitation, self- and cross-fertilization must vary negatively, whether measured as proportions or numbers of offspring. However, plant reproduction is not generally ovule limited. Seed production is commonly limited by pollination (pollen limitation; Knight et al. 2005) or resources for seed development (Hove et al. 2016). Ovule limitation of male success is even less likely because of the many ovules available on all potential mates. Without ovule limitation, allele contributions to selfed and outcrossed offspring can vary positively with overall female or male success, even though the associated proportions vary negatively. This allows paradoxical associations, such as positive covariation of self- and outcross
Figure 2
Contrasting mating portfolios for two hermaphroditic plants (A, B) and two females (C, D) and two males (E, F) of a dioecious species. The area of a red-outlined box depicts overall female mating success, and the included rectangles represent the relative contributions of different male mates. Similarly, blue-outlined boxes depict overall male mating success and the relative contributions to female mates. Numerals in parentheses indicate an individual’s number of female and male outcross mates, respectively. Squares with the same color and shading, other than purple, represent the same outcross mate (e.g., the dark gold plant sired seeds with Plant A and served as both a female and a male mate for Plant B). For the hermaphrodites, purple areas identify the incidence of self-mating, including autogamy (light purple) and geitonogamy (dark purple). Both plants engaged equally in self-mating, although Plant A experienced more geitonogamy and less autogamy than Plant B. For the hermaphrodites, Plant A realized more mating success overall (combined areas of the red- and blue-outlined squares) and as a female (total area of the red-outlined square), whereas Plant B was more successful as a male (total area of the blue-outlined square). Plant A had a relatively low female selfing rate (proportion of the red-outlined box colored purple) and a relatively high male selfing rate (proportion of the blue-outlined box colored purple) compared with Plant B. Similar interpretations are evident for the portfolio variation among plants of the dioecious species (Plants C–F), except for the absence of self-mating.
siring success despite pollen discounting (Harder & Wilson 1998). Third, mating-system studies typically involve samples collected on a single date, providing a snapshot of mating outcomes rather than revealing insights into short- and long-term mating-system dynamics for individuals and populations. Finally, few studies consider cross-mate diversity and its influences, especially that via male function.

Standard mating-system metrics include the proportion of selfed (female selfing rate, $s$) or outcrossed (female outcrossing rate, $t = 1 - s$) seeds and the proportion of all possible pairs of seeds produced by a plant represented by outcrossed full siblings (correlated paternity, $r_p$; Ritland 1989). Dorken & Perry (2017) argued that, given a particular size of mating neighborhood, the siring of seeds on plants with large $r_p$ had been monopolized by a subset of possible paternal mates. As a result, the traits of these mates should be promoted by sexual selection. The inverse of correlated paternity provides a measure of average female mate diversity. Specifically, $m_e = 1/r_p$, or the effective mate number, represents the average number of mates per female if all males contributed pollen independently and equally. Note that both $t$ and $r_p$ estimated from seed or seedling tissue provide biased estimates of mating (i.e., zygote) outcomes if seeds develop differentially according to genotype (Maki 1993).

Consideration of existing estimates identifies various generalities about mating-system variation. Approximately 50% of angiosperms (Igic & Kohn 2006) and 40% of conifers (Leslie et al. 2013) obligately outcross, although their measured outcrossing rates are often somewhat less than 1, usually because of biparental inbreeding. In contrast, 5–6% of angiosperm species predominantly self-fertilize ($t < 0.1$; Igic & Kohn 2006). These extremes are probably consequences of the accumulation of mutational load under predominant outcrossing and the purging of load under predominant selfing, respectively (Lande & Schemske 1985). Nevertheless, pure selfing is unlikely because of counteracting selection to maintain some recombination (Kamran-Disfani & Agrawal 2014). Less understood are the many cases with mixtures of selfed and outcrossed offspring (mixed mating; Goodwillie et al. 2005). Three nonexclusive classes of explanation for mixed mating have been proposed: Geitonogamy is an unavoidable cost of outcrossing for self-compatible species that display multiple flowers simultaneously; autonomous selfing provides reproductive assurance for outcrossing species, thus making the best of a bad situation when pollination is limited; and mixed mating is adaptive. Theoretical analysis has identified diverse factors that favor adaptive mixed mating, including interseason variation in pollination (Morgan & Wilson 2005), joint effects of reproductive traits on different components of self- and cross-mating success (Harder et al. 2008, Johnston et al. 2009), and pleiotropy of the outcrossing rate with pollen export and viability or both (Jordan & Otto 2012). These hypotheses have rarely been tested empirically; however, clear examples of adaptive mixed mating are evident in the few species that produce both closed, selfing flowers and open flowers capable of outcrossing (cleistogamy; Oakley et al. 2007). A relevant question awaiting detailed assessment is the extent to which selfed offspring of mixed-mating species survive to become reproductive adults.

Unlike the female outcrossing-rate continuum, variation in the diversity of a female’s mates and its ecological associations and evolutionary implications has received limited analysis. Correlated paternity is reported frequently (e.g., Figure 3), as it is provided by the most commonly used software package for estimating outcrossing rates (MLTR). However, these estimates have been subject to limited meta-analysis. A plot of estimates of effective mate number, $m_e$, and correlation of paternity, $r_p$, versus $t$ for 66 species, ranging from annuals to trees (Figure 3A), suggests interesting generalities beyond the pervasive promiscuity of seed plants. Among mixed-mating species, the

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$2r_p$ is also an unbiased estimator of Simpson’s (1949) diversity index.
female outcrossing rate, $t$, for (A) 66 species of seed plants and (B) individual plants of hermaphroditic Myrtus communis and dioecious Pistacia lentiscus. In panel A, observations represent medians for species represented by multiple sites or years. References to data sources are provided in the Supplemental Material. Observations depicted in panel B are drawn from Nora et al. (2016).

effective mate number generally increases slowly in association with increasing female outcrossing rate and varies relatively little around this trend. In contrast, the effective mate number varies extensively among predominantly outcrossing species (Figure 3A), and even within species, depending on the type of pollinator (Rhodes et al. 2017). These contrasting patterns are also evident among individuals of a mixed-mating hermaphrodite species, Myrtus communis, and an obligately outcrossing dioecious species, Pistacia lentiscus (Figure 3B), (Nora et al. 2016). As mate number should vary positively with the extent of pollen dispersal (Mitchell et al. 2013, Dorken & Perry 2017), this contrast suggests that highly mobile pollen vectors or extensive pollen carryover are more characteristic of pollen dispersal of predominant outcrossers than of mixed-mating species.

3. PLANT TRAITS THAT AFFECT MATING

Two classes of plant characteristics govern mating opportunities and influence mating portfolios. The most fundamental class comprises essential qualitative aspects of being a plant, including immobility, a metameric body plan, and, for angiosperms, closed carpels. These traits are largely immutable. The second class of mating-related traits is subject to environmental modification and/or varies genetically among individuals and species. These traits range from overarching allocation strategies (e.g., extent of clonality, reproductive investment, and variation in gender) to specific features of reproductive organs (e.g., structure, deployment, and phenology). We now consider key features of both classes and identify their diverse influences on mating.

3.1. General Plant Traits

Distinctive features of mating by plants arise from being immobile, with multiple exposed sex organs, commonly hermaphroditic and long-lived, and possibly clonal. Although none of these attributes are unique to plants, together they shape the mating environment, mating outcomes, and their consequences for individuals, populations, and species. As various aspects of hermaphroditism have already been illustrated in Section 2, here we focus on the fundamental mating implications of immobility, characteristic life-history traits, modularity and clonality.
3.1.1. Immobility. Plant immobility has two key mating consequences: Outcrossing requires pollen vectors, and the neighborhood of potential mates is largely fixed, at least during reproductive seasons. Reliance on pollen vectors introduces several complications. Vector behavior is governed by fluid dynamics (wind- and water-pollination) or animal self-interest, which need not promote mating. Indeed, for most angiosperms less than 1% of the pollen removed from anthers eventually reaches stigmas, on average. Such poor pollen-transport efficiency universally favors improved pollen export (Harder & Wilson 1994) and can favor improved pollen import if pollination limits seed production (Harder & Aizen 2010). In addition, reliance on vectors causes highly stochastic pollen dispersal owing to variability in both pollen transport and vector abundance. Thus, even if enough pollen arrives to fertilize all ovules, on average, some flowers can receive insufficient pollen, limiting female mating success, whereas others receive excess pollen, limiting male success (Richards et al. 2009). Such variation promotes traits that increase average pollination (see Section 3.3), reduce variation (Richards et al. 2009), allow capitalization on pollination windfalls (Schreiber et al. 2015), or a combination thereof.

The fixed locations of neighbors influence the number and variety of a plant’s mating opportunities. Pollen generally disperses locally, so variance in plant density can lead to mate limitation, generating mating variance among plants. Such variance is compounded for species with distinct mating types (e.g., heterostyly and dioecy), because of heterogeneity in mating-type frequency within mating neighborhoods (Van Drunen & Dorken 2014), which in dioecious species can affect progeny sex ratios (Stehlik et al. 2008). Coupled with local seed dispersal, limited pollen dispersal generates spatial genetic structure within populations. In structured populations, neighbors tend to be relatives, increasing the chance of biparental inbreeding. In general, population structure increases with inbreeding and is more prevalent among herbaceous species than woody species (Vekemans & Hardy 2004).

3.1.2. Life-history characteristics. Correlations between habitat characteristics and plant life histories generate further associations with mating systems. For plants with annual life cycles, poor conditions during reproductive seasons severely impact lifetime fitness, favoring autonomous selfing. Consequently, selfing is much more prevalent among annuals than perennials (Munoz et al. 2016). Furthermore, among annuals, selfing is particularly common for species that occupy habitats with brief periods for growth and reproduction. As predominant selfing is viable only with weak inbreeding depression, the history of selfing populations includes a period of purging during their divergence from outcrossing populations (Dart & Eckert 2013). Furthermore, most annuals are small, so their growth involves relatively few mitotic divisions, reducing lifetime mutation rate and mutational load (Scofield & Schultz 2006, but see Otto & Orive 1995). Collectively, these influences reduce the severity of inbreeding depression in annuals compared with perennials (Angeloni et al. 2011). Increased selfing should also select for increased allocation to female function (Zhang 2006). Thus, the evolution of selfing in annuals involves synergistic selection that creates independence from pollen vectors, increases investment in seed production, and reduces mutational load, thereby enabling full realization of the genetic transmission advantage of selfing and reproductive assurance. Overall, this selection promotes mating success in environments with ephemeral growing conditions.

In contrast, perennials more frequently occupy saturated, often competitive environments in which offspring quality is particularly beneficial. Species in such environments predominantly outcross, and most facultative or obligate outcrossers are perennials (Munoz et al. 2016). Among perennials, woody species generally have higher outcrossing rates than herbaceous species (Duminil et al. 2009). Furthermore, perennials that obligately outcross generally live much longer than self-compatible species with bisexual flowers, even after accounting for differences in growth
Iteroparity: a life-history strategy in which a plant engages in multiple reproductive episodes during its lifetime

Genet: a genetic individual (clone)

Ramet: vegetative or reproductive shoots of a genet, sometimes growing independently

habit (Ehrlén & Lehtilä 2002). These associations reflect various consequences of perenniality for mutational load and inbreeding depression. First, because of more lifetime cell divisions, perennials tend to accumulate more mutations than do annuals (Scofield & Schultz 2006). Second, with longer generations mutational load becomes increasingly due to recessive, rather than partially dominant, mutations (Morgan 2001). Last, longevity compounds the effects of inbreeding depression on survival (Morgan et al. 1997). These consequences expose many perennials to severe lifetime inbreeding depression. Indeed, mutational loads may often allow selective interference to resist purging (Lande et al. 1994), because even when self-fertilization occurs, most or all selfed offspring fail (Delmas et al. 2014). Therefore, the inbreeding coefficients of perennials, especially woody species, are generally lower than expected from their outcrossing rates, indicating strong selection against inbred individuals (Duminil et al. 2009).

Perenniarity also introduces various nongenetic consequences to mating that promote its association with outcrossing and influence mate diversity. Because of modularity (Section 3.1.3), perennials grow continuously during their lives, increasing flower production, often in association with clonal propagation (Section 3.1.4). In addition to generally increasing fertility with age/size, larger whole-plant floral displays can affect mating outcomes (see Section 3.3). Most perennials also reproduce iteroparously, which reduces the lifetime fitness effects of environmental variance, including annual variation in pollination success, eroding benefits of reproductive assurance during unpredictable poor years (Morgan & Wilson 2005). Iteroparity requires resource storage between years, so that reproductive outcomes during one year can affect future survival or reproduction. On the one hand, if selfed seeds fail owing to poor quality, they represent squandered resources, which could accentuate interyear costs of reproduction, generating interyear seed discounting (Morgan et al. 1997). On the other hand, resource continuity between reproductive seasons allows plants to draw on past savings or borrow from the future to capitalize on a season of unusually good mating success (Ida et al. 2013). Together, the many genetic and nongenetic consequences of perenniality shape the life histories of gymnosperms and most angiosperms and explain why outcrossing is the predominant mating system among seed plants.

3.1.3. Modularity. Metameric growth and the modular body plan of plants have diverse mating consequences. Most obviously, plants typically produce multiple flowers simultaneously, often arrayed in one or more inflorescences. For animal-pollinated species, attraction increases with the number of flowers displayed simultaneously (display size). However, for hermaphroditic species, large displays also increase the chance of geitonogamy and associated mating costs (Harder & Barrett 1995). Geitonogamy often constitutes a major component of overall self-pollination for both abiotically (Friedman & Barrett 2009) and biotically (Hobbhahn et al. 2017) pollinated species. Production of multiple flowers also introduces within-individual variation as a feature of the sexual phenotype that is subject to selection (Herrera 2009). Such variation can reflect phenotypic plasticity, often mediated by internal resource dynamics, or vary independently of resource dynamics according to flower position (Diggle 2003). The latter architectural effects commonly occur for species that produce bisexual flowers, and underlie sexual systems that involve different combinations of bisexual, female, and male flowers. Such effects represent adaptation to specific pollination and mating environments (see Section 3.3). Production of multiple reproductive organs also allows flexible resource allocation to developing fruits in response to seed quantity and quality (Ida et al. 2013), modifying the representation of paternal alleles among seeds.

3.1.4. Clonality. Clonal growth has several mating consequences, depending on genet size and the spatial arrangement of ramets (clonal architecture). Subdivision of genets into ramets is advantageous if vegetative or reproductive performance decelerates with increasing body size.
Subdivision counteracts diminishing returns associated with pollen dispersal, favoring increased male allocation (Dorken & Van Drunen 2010). Offsetting these benefits, clonality exposes opportunities for among-ramet geitonogamy, which should generally increase with clone size (Vallejo-Marín et al. 2010). The severity of this problem depends on two factors. First, subdivision of a genet’s flowers among ramets increases the chance of pollen vectors moving to neighboring plants rather than among ramets within individual genets (Liao & Harder 2014). Second, the incidence of geitonogamy within and among ramets (Hu et al. 2015) should provide insights into floral strategies that limit the mating costs of large floral displays. A further mating consequence arises for species with distinct mating types (e.g., dioecy and heterostyly) if clonality reduces disassortative mating (Barrett 2015). By interfering with negative frequency-dependent selection, clonality fosters persistence of nonequilibrium morph ratios, exacerbating historical contingency.

3.2. Design and Display of Reproductive Organs

Seed-plant reproductive organs shape mating outcomes by influencing pollination and progamic processes. These processes include aspects of flowering phenology that determine interactions with pollen vectors and access to mates; diverse morphological and physiological features of reproductive organs that influence pollen removal, transport, and deposition; and features of male gametophytes and female organs that control postpollination processes. In addition to shaping these largely ecological interactions, these traits are fundamental to mating-system evolution. Mating-system evolution minimally requires a change in these traits that modifies the processes they regulate. Detailed consideration of how these traits individually affect mating is beyond the scope of this review. Instead, we consider them generically with respect to their roles promoting beneficial autogamy, discouraging detrimental selfing and sexual interference, and enhancing outcrossing and mate diversity.

3.2.1. Self-promotion. Autonomous selfing requires self-compatible flowers with primary sex organs that contact each other. Such flowers need not open or possess devices for manipulating pollen vectors. However, flowers of species with moderate to high selfing tend to be diminutive versions of flowers of the outcrossing relatives from which they evolved. Mixed-mating species often possess features that facilitate beneficial autogamy (Goodwillie et al. 2005). These traits cause vector-assisted pollen discounting and so are beneficial only if associated with delayed autogamy.

3.2.2. Anti-selfing. Sexual interference and discounting costs associated with prior, facilitated or competing selfing select for anti-autogamy traits. The most effective mechanism is production of separate female and male flowers (monoecy and dioecy). For species with bisexual flowers, temporal separation (Kalisz et al. 2012) and spatial segregation (Takebayashi et al. 2006) of pollen release and receptive stigmas (dichogamy and herkogamy, respectively) limit within-flower self-pollination. Regardless of how self-pollination occurs, self-fertilization is averted by self-incompatibility mechanisms that interfere with pollen germination, pollen-tube growth, or ovule function (Franklin-Tong 2008). Even in self-compatible species, self-pollen tubes can grow more slowly than cross-pollen tubes, with self-fertilization occurring only in the absence of cross-pollen tubes (cryptic self-incompatibility; Cruzan & Barrett 2016).
3.2.3. Cross-promotion. Most aspects of the reproductive phenology, morphology, and physiology of plants promote outcrossing, in general, and mate diversity, in particular. To the extent that variation in these aspects of reproductive biology affects individual mating success rather than fertility, they will be subject to sexual selection. Rather than detail the mating roles of specific traits, we identify features that generally promote outcrossing.

Pollen vectors do not inherently act in the interest of plant fertility or mating, so selection favors exploiting characteristic vector behavior or manipulating undesirable behavior to promote pollination. Pollinator exploitation is evident in the segregation of sex roles within inflorescences. For example, large-bodied bees characteristically move upward on vertical inflorescences, so presentation of male-functioning flowers above female-functioning flowers limits geitonogamy and associated pollen discounting, promoting pollen export (Harder et al. 2000). Obvious manipulation traits include features of animal-pollinated plants that attract pollinators (showy corollas, scent, and display size) and reinforce continued visitation (floral rewards). Also relevant are traits that control pollinator position and pollen exchange or modify fluid flows around flowers of abiotically pollinated species.

Both the fertility and the mating components of reproductive success represent the aggregate performance of all flowers on a plant. The preceding example of the benefits of sexual segregation within inflorescences illustrates this feature during individual pollinator visits, but it applies more generally to within-individual variation (e.g., sex-allocation gradients within inflorescences; Brunet & Charlesworth 1995), aspects of flowering phenology (Devaux et al. 2014), and lifetime phenotype dynamics (e.g., size-dependent sex allocation; Zhang 2006).

Cross-promotion traits often represent adaptive compromises between mating quality and quantity, between competing mating functions, or both. Quality-quantity compromises are evident in pollen production, pollen presentation strategies, and floral display size. In addition to promoting outcrossing generally, the last two features directly affect mate diversity by affecting the number of pollinators transporting pollen from a plant. Quality-quantity compromises are evident for traits such as herkogamy and dichogamy, which reciprocally affect autogamy and outcrossing (Medrano et al. 2012). Compromises between competing functions are especially evident for hermaphrodites in all aspects of sex allocation, sexual interference, and sexual conflict. They also arise when traits serve multiple functions in interaction with vectors (Hobbhahn et al. 2017).

Rather than being fixed, many mating traits vary adaptively within individual plants, depending on ecological circumstance. This flexibility is evident among reproductive seasons in size-dependent sex allocation (Zhang 2006). Within-season examples include facultative responses to variation in pollinator visits that adjust floral sex-phase duration (Vranken et al. 2014), pollen removal (Harder & Wilson 1994), and floral display size (Harder & Johnson 2005). Together, these cross-promotion traits illustrate key features underlying the diversity of reproductive phenotypes and mating systems among seed plants.

Less clear is the extent to which traits that affect mate diversity evolve because they promote this feature of mating portfolios. Pannell & Labouche (2013) proposed that mate diversity evolves as a by-product of selection that enhances overall siring success. However, synergy between increased fertility and benefits of mate diversity should accentuate the evolution of the underlying traits, complicating differentiation between their influences.

4. ECOLOGICAL AND DEMOGRAPHIC CONTEXT FOR MATING

Mating patterns arise from interactions between plant traits and the environmental and demographic milieu in which plants live, but the specific ecological mechanisms causing variation in mating-system evolution are often poorly understood. This knowledge gap is surprising because
several parameters central to theoretical models of mating-system diversity (see Goodwillie et al. 2005), such as inbreeding depression (Cheptou & Donohue 2011), pollen limitation (Harder & Aizen 2010), reproductive assurance (Kalisz et al. 2004), and pollen discounting (Kohn & Barrett 1994), depend on environmental conditions. We now examine the role of this context dependence in modulating mating patterns and their evolution, which can vary at different spatial and temporal scales.

4.1. Local Influences

The specific abiotic and biotic conditions experienced by individual plants establish the mating opportunities that plant traits modify to determine realized mating outcomes (Figure 1). Environmental factors act most extensively during pollination; however, they also impinge on progamic processes, as the style creates the environment in which male gametophytes vie for access to ovules. Environmental effects also influence seed development, which, despite being a postmating process, significantly influences the representation of parental alleles prior to offspring independence.

Mating opportunities during pollination depend on the abundance and quality of potential mates within the pollen-dispersal neighborhood and the abundance and behavior of pollen vectors, which establish that neighborhood. Unsurprisingly, outcrossing generally varies positively with local mate density (Ghazoul 2005) and pollinator abundance (Kalisz et al. 2004, Yin et al. 2016). At least for animal-pollinated plants, these effects do not arise independently, because dense aggregations tend to attract more pollinators (Ghazoul 2005). In contrast, mate diversity and biparental inbreeding can decline with increasing density (González-Varo et al. 2009), suggesting that the variety of routes along which pollen vectors move among plants increases with interplant separation. The composition of local mating neighborhoods (e.g., presence of relatives and alternative mating types) can also affect mating opportunities and outcomes, in some cases imposing negative frequency-dependent selection (Dorken & Pannell 2009). These influences can vary within and among flowering seasons, depending on a plant’s phenology and that of its neighbors and pollen vectors (Kameyama & Kudo 2015). Variation in weather conditions influencing pollinator abundance contributes to this phenological effect and the benefits of reproductive assurance (Vaughton & Ramsey 2010).

Although both mate and pollinator limitation diminishes fertility, they can have contrasting effects on mating-system evolution if they occur chronically. In particular, mate limitation should generally favor increased self-fertilization, whereas pollinator limitation could provoke shifts to alternative pollen vectors, maintaining or enhancing outcrossing (Harder & Aizen 2010). The abundance, diversity, and variety of floral traits of coflowering species that compete for the same pollinators can also influence mating outcomes, perhaps even favoring increased selfing by less competitive species (Bell et al. 2005, Briscoe Runquist et al. 2016). Finally, changes in the types of available pollinators, including those resulting from range extensions, may also potentially promote correlated trait and mating-system evolution (Gervasi & Schiestl 2017).

Progamic conversion of pollen into zygotes depends on the conditions for pollen germination and tube growth (see Harder et al. 2016 for a review). Briefly, relevant influences can affect the success of male gametophytes in a density-independent or density-dependent manner. Density-independent features of the extrinsic and stylar environments include temperature, self-incompatibility, and the chemical and physical characteristics of pistils. These factors can directly modify mating outcomes if they affect pollen genotypes differently (Hedhly et al. 2005). Density dependence is manifest in gametophytic competition, as determined by the availability of stylar resources and the number of tube tips accessing resources simultaneously. Genotypic differences in pollen germination and tube growth determine competitive ability (Swanson et al. 2016), so
mating outcomes can depend on tube number and genetic diversity (Lankinen & Skogsmyr 2002). As mentioned in Section 2.2, features of the stylar environment that modulate gametophytic competition may implement mate choice in angiosperms.

Seed development can vary among embryo genotypes in association with the environment experienced by the maternal plant, individual ovaries, and embryos. Relevant extrinsic influences include environmental effects on early-acting inbreeding depression (Cheptou & Donohue 2011) and resource availability (Hove et al. 2016). Genotypic differences among developing seeds within ovaries can affect their development (Rigney 1995); however, the extent to which differential survival represents contrasting competitive ability or active maternal choice remains unclear (Korbecka et al. 2002). Whatever the cause, genotypic differences of developing seeds within and among fruits can affect a plant’s internal resource dynamics. For perennials, above-average seed quality can mobilize stored resources, whereas below-average seed quality can enhance storage, altering interyear reproductive patterns (Ida et al. 2013).

Factors that chronically limit seed production can influence mating-system evolution significantly. Harder & Aizen (2010) considered these effects in the absence of pollen or ovule discounting. They found that ovule limitation leads to the familiar result that lifetime inbreeding depression greater than 0.5 favors outcrossing; otherwise, selfing is favored. Resource limitation imposes more stringent conditions for the evolution of increased outcrossing, namely postdispersal inbreeding depression greater than 0.5. Finally, with pollen limitation, inbreeding depression becomes irrelevant to the evolution of selfing versus outcrossing. Instead, evolution of the mating system and the traits that control it proceeds in whatever direction increases maternal fitness, releasing the adaptive potential of natural selection.

4.2. Geographic Patterns

Mating systems are not randomly distributed with respect to geographic locale or biome. Beginning with the early naturalists, including John Henslow and Charles Darwin, the geographical distribution of species with contrasting mating systems has attracted attention (Lloyd 1980). More recently, it has been recognized that geographic gradients in precipitation, temperature, and growing season length often underlie variation in plant size, floral morphology, and phenology, with consequences for pollination and mating. Where these gradients include species range limits, they can provide an informative environmental and demographic context for studies of mating-system variation.

Populations at range margins are commonly more isolated, smaller, and at lower density than core populations owing to limited availability of suitable habitat and to visits by different pollinators. If these conditions cause pollinator or mate limitation, they can favor increased self-fertilization. This pattern is evident for some animal-pollinated herbs, in some cases as a response to selection for reproductive assurance (Hargreaves & Eckert 2014). However, increased self-mating at range margins is unlikely to apply generally to plant migration, especially for long-lived trees and shrubs that largely maintain outcrossing regardless of environmental context. Even herbaceous plants do not universally exhibit increased selfing at range margins (Moeller et al. 2012). The effects of geographical variation on mate diversity have not been considered. Small fragmented populations can experience sharp reductions in the number of effective pollen parents, resulting in a high correlation of outcrossed paternity and increased biparental inbreeding in subsequent generations (Young & Brown 1999). Such bottlenecks may occur frequently in peripheral populations at low density if they are subject to pollinator or mate limitation.

The evolution of selfing at range margins depends on the magnitude of inbreeding depression. To the extent that environmental stress intensifies inbreeding depression, stressful conditions in
peripheral populations may constrain the spread of selfing variants. However, inbreeding depression could be weak in such populations, particularly those that are small and inbred. Repeated population bottlenecks should reduce mutational load, with the magnitude of purging and fitness consequences depending on bottleneck severity and subsequent population growth (Kirkpatrick & Jarne 2000). The limited empirical evidence supports weaker inbreeding depression associated with reduced genetic load in geographically marginal versus core populations (Pujol et al. 2009). Whenever this pattern applies, selfing could be favored in marginal populations, even in the absence of selection for reproductive assurance, given genetic variation for traits that modify the selfing rate.

Colonization is commonly associated with low density, at least initially. In principle, a single plant capable of self-mating could found a new population following long-distance dispersal. Baker (1955) proposed that this capacity could explain the high incidence of self-compatible species on oceanic islands and the concomitant rarity of self-incompatibility (Baker’s law), which has been confirmed with an extensive survey (Grossenbacher et al. 2017). The scope of Baker’s law has been extended to establishment in other colonizing situations, including metapopulation dynamics (Pannell & Barrett 1998). Post-colonization population growth can alter selection on the mating system (Pannell 2015). In particular, increased density following successful establishment could favor increased outcrossing. Therefore, although selfing may be favored during the low-density colonization phase, as Baker envisioned, evolution of increased outcrossing in established populations may create opportunities for subsequent trait evolution and local adaptation.

Diverse physical factors (e.g., temperature and precipitation) determine variation in community composition globally, in turn affecting mutualistic and antagonistic interactions likely to influence plant reproduction. Latitudinal climatic gradients, including those influencing pollination success (Vamosi et al. 2006), alter species diversity, the intensity of biotic interactions, and specialization (Schemske et al. 2009). That outcrossing species are relatively more common in tropical communities than in temperate communities is commonly assumed (Lloyd 1980); however, latitude may be a surrogate for more relevant biological influences. In particular, a recent global analysis of outcrossing rates for 492 taxa found an overall decline toward higher latitudes and among some biomes (Moeller et al. 2017). However, phylogenetic analyses revealed no significant association of outcrossing rate with either latitude or biome after accounting for variation in life history and growth form. Thus, Moeller et al. (2017) concluded that observed latitudinal patterns in mating systems likely reflect variation in the representation of life forms rather than in the strength of plant-pollinator interactions. A recent detailed analysis of the latitudinal ranges of related selfing and outcrossing sister species found similar low-latitude range limits for both groups, but the ranges of selfers generally extend to higher latitudes (Grossenbacher et al. 2015).

### 4.3. Mating Systems and Global Environmental Change

The growth of global change biology has sparked interest in how the many facets of environmental change may influence plant reproduction. For example, habitat fragmentation is often associated with increased selfing, probably as a result of reduced density (Eckert et al. 2010, Harder & Aizen 2010). Such shifts in mating likely represent plasticity, rather than evolutionary change, especially in long-lived species. Plastic responses may also result from direct impact of environmental stress on traits that cause self-pollination. Stress induced by climate change may first increase selfing via plastic changes but then become fixed by genetic assimilation (Levin 2011); however, no evidence currently supports this mechanism for the evolution of selfing. Plastic shifts in mating patterns owing to novel conditions may have varied influences on niche evolution depending on the rates of selfing (Peterson & Kay 2015). Although plastic changes to mating are probably most common,
rapid short-term adaptive responses are possible when genetic variation and short life cycles permit (Bodbyl Roels & Kelly 2011).

Urbanization and environmental pollution can also influence mating patterns. Increased selfing is evident along gradients of urbanization (Cheptou & Avendaño 2006). Similarly, plants growing on heavy-metal-contaminated soils may self more, although evidence is mixed (Dubois et al. 2003). In agricultural ecosystems, herbicide spraying has caused contemporary evolution of herbicide resistance in numerous species. Recent evidence indicates that elevated selfing caused by reduced herkogamy has coevolved with increasing resistance, perhaps to reduce gene flow from nonresistant populations and maintain resistance in areas receiving regular sprays (Kuester et al. 2017).

5. CONCLUSIONS

The outcrossing-selfing paradigm has dominated research on plant mating systems since Darwin’s seminal work on floral mechanisms and the fitness consequences of cross- and self-fertilization. Considerable progress has been made, resulting in an extensive literature on mating-system evolution, including many marker-based estimates of maternal outcrossing rates at the population level (Goodwillie et al. 2005). Here, we have introduced a broader ecological perspective on plant mating that fully embraces the hermaphroditic condition of most seed plants. It recognizes that previous work in this area has largely neglected two key features: mate diversity and variation among individuals in mating success. To remedy these deficiencies, we apply the concept of mating portfolios. This expanded perspective acknowledges that an individual’s mating portfolio represents the range of offspring genetic combinations to which it contributes during its lifetime, which can vary greatly among plants. Two recent developments should enable future characterization of mating portfolios. First, recent analytical methods permit estimation of the maternal and paternal mating success of individuals within populations (Wang et al. 2012). Second, microsatellite and single nucleotide polymorphism markers are sufficiently powerful to facilitate parentage studies. These advances should allow researchers to investigate key ecological determinants of mating-system variation and their evolutionary consequences, refine many of Darwin’s original ideas on plant mating systems, and test current and future theories.

FUTURE DIRECTIONS

1. Characterize both female and male components of individual mating portfolios fully and determine the relative environment and genetic contributions to their variation.
2. Explore the abiotic and biotic causes of mating-system dynamics within and between reproductive seasons and the consequences of this variability for trait and mating-system evolution.
3. Use transplant experiments with clonal replicates to investigate the association of plasticity of floral traits and mating outcomes, and assess mating-system flexibility in the face of environmental heterogeneity.
4. Employ comparative methods to determine the ecological, life-history, and reproductive correlates of variation in mate diversity and its association with outcrossing rate for both sex roles.
5. Develop and use metagenomic approaches to screen the mate diversity of pollen on stigmas and pollen tubes in ovaries to assess progamic filtering of mating success.
6. Use families of different degrees of relatedness to investigate the extent to which inbreeding and outbreeding affect postpollination processes, including gametophytic competition and female mate choice.

7. Quantify sexual selection by decomposing the relation of reproductive success to floral traits into the covariances between trait values and mating success, and between mating success and fertility.

8. Using experimental evolution, investigate the short-term benefits of outcrossing and assess the relative importance of heterozygosity versus family genetic variation in maintaining outcrossing in heterogeneous environments.

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The Annual Review of Cancer Biology reviews a range of subjects representing important and emerging areas in the field of cancer research. The Annual Review of Cancer Biology includes three broad themes: Cancer Cell Biology, Tumorigenesis and Cancer Progression, and Translational Cancer Science.
# Contents

Ecological Responses to Habitat Fragmentation Per Se  
*Lenore Fahrig* ................................................................................. 1

Ecological Networks Across Environmental Gradients  
*Jason M. Tylianakis and Rebecca J. Morris* ...................................... 25

Impacts of Artificial Light at Night on Biological Timings  
*Kevin J. Gaston, Thomas W. Davies, Sophie L. Nedelec, and Lauren A. Holt* ........... 49

The Utility of Single Nucleotide Polymorphism (SNP) Data in Phylogenetics  
*Adam D. Leaché and Jamie R. Oaks* .................................................. 69

The Role of Sexual Selection in Local Adaptation and Speciation  
*Maria R. Servedio and Janette W. Boughman* ...................................... 85

The Potential Impacts of Climate Change on Biodiversity in Flowing Freshwater Systems  
*Jason H. Knouft and Darren L. Ficklin* .................................................... 111

The Ecology of Mating and Its Evolutionary Consequences in Seed Plants  
*Spencer C.H. Barrett and Lawrence D. Harder* ..................................... 135

Process-Based Models of Phenology for Plants and Animals  
*Isabelle Chuine and Jacques Régnière* ................................................. 159

Evolution of Ecological Niche Breadth  
*Jason P. Sexton, Jorge Montiel, Jackie E. Shay, Molly R. Stephens, and Rachel A. Slatyer* ................................................................................. 183

Analysis of Population Genomic Data from Hybrid Zones  
*Zachariah Gompert, Elizabeth G. Mandeville, and C. Alex Buerkle* ..................... 207

Biogeography and Biotic Assembly of Indo-Pacific Corvoid Passerine Birds  
*Kaustt Andreas Jonsson, Michael Krabbe Borregaard, Daniel Wisbech Carstensen, Louis A. Hansen, Jonathan D. Kennedy, Antonin Machac, Petter Zabi Marki, Jon Fjeldså, and Carsten Rubbek* .................................................. 231

Attached Algae: The Cryptic Base of Inverted Trophic Pyramids in Freshwaters  
*Yvonne Vadeboncoeur and Mary E. Power* ............................................. 255
Temporal Variation in Trophic Cascades
Jonah Piovia-Scott, Louie H. Yang, and Amber N. Wright ........................................... 281

Anthropogenic Extinction Dominates Holocene Declines of West Indian Mammals
Siobhán B. Cooke, Liliana M. Dávalos, Alexis M. Mychajliw, Samuel T. Turvey, and Nathan S. Upham ................................................................. 301

Spatially Explicit Metrics of Species Diversity, Functional Diversity, and Phylogenetic Diversity: Insights into Plant Community Assembly Processes
Thorsten Wiegand, María Uriarte, Nathan J.B. Kraft, Guochun Shen, Xugao Wang, and Fangliang He .............................................................. 329

Pollinator Diversity: Distribution, Ecological Function, and Conservation
Jeff Ollerton .................................................................................................................. 353

Evolution of Animal Neural Systems
Benjamin J. Liebeskind, Hans A. Hofmann, David M. Hillis, and Harold H. Zakon ................................................................. 377

Variability in Fitness Effects Can Preclude Selection of the Fittest
Christopher J. Graves and Daniel M. Weinreich .......................................................... 399

The Ecology of Soil Carbon: Pools, Vulnerabilities, and Biotic and Abiotic Controls
Robert B. Jackson, Kate Lajtha, Susan E. Crow, Gustaf Hugelius, Marc G. Kramer, and Gervasio Piñeiro ................................................................. 419

Apparent Competition
Robert D. Holt and Michael B. Bonsall ........................................................................ 447

Marine Infectious Disease Ecology
Kevin D. Lafferty ....................................................................................................... 473

Ecosystem Processes and Biogeochemical Cycles in Secondary Tropical Forest Succession
Jennifer S. Powers and Erika Marín-Spiotta .............................................................. 497

Interactions Among Invasive Plants: Lessons from Hawai‘i
Carla M. D’Antonio, Rebecca Ostertag, Susan Cordell, and Stephanie Yelenik .......... 521

Phylogenetics of Allopolyploids
Bengt Oxelman, Anne Krag Brysting, Graham R. Jones, Thomas Marcussen, Christoph Oberprieler, and Bernard E. Pfeil ................. 543

Identifying Causes of Patterns in Ecological Networks: Opportunities and Limitations
Carsten F. Dormann, Joehn Fründ, and H. Martin Schaefer .................................... 559
Innate Receiver Bias: Its Role in the Ecology and Evolution of Plant–Animal Interactions

*Florian P. Schiestl* ................................................................. 585

Evolutionary Rescue

*Graham Bell* ................................................................. 605

Indexes

Cumulative Index of Contributing Authors, Volumes 44–48 ......................... 629
Cumulative Index of Article Titles, Volumes 44–48 ................................. 633

Errata

An online log of corrections to *Annual Review of Ecology, Evolution, and Systematics* articles may be found at http://www.annualreviews.org/errata/ecolsys