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Perspectives on mating–system evolution: comparing concepts in plants and animals

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Abstract

The study of mating systems, defined as the distribution of who mates with whom and how often in a sexually reproducing population, forms a core pillar of evolution research due to their effects on many evolutionary phenomena. Historically, the "mating system" has either been used to refer to the rate of self-fertilization or to the formation of mating pairs between individuals of distinct sexes. Consequently, these two types of mating systems have tended to be studied separately rather than jointly. This separation often means that mating systems are not necessarily researched in a coherent manner that might apply to different types of organisms (e.g., plants versus animals, or hermaphrodites versus dioecious species), even if similar mechanisms may drive the evolution of self-fertilization and mating pair formation. Here, we review the evolution of both plant and animal mating systems, highlighting where similar concepts underlie both these fields and also where differing mechanisms are at play. We particularly focus on the effects of inbreeding, but also discuss the influence of spatial dynamics on mating–system evolution. We end with a synthesis of these different ideas and propose ideas for which concepts can be considered together to move towards a more cohesive approach to studying mating–system evolution.

Keywords: self-fertilization, polygyny, mating system, inbreeding, spatial evolution, Baker's law, transmission advantage

Introduction

A species' mating system, which can be described as the distribution of "who mates with whom and how often" in a sexually reproducing population (Barrett, 2013), has attracted the attention of evolutionary biologists since Darwin's (1877) seminal work. This is because a species' mating system is a major determinant of the distribution and maintenance of genetic diversity (Barrett et al., 2014; Ellegren & Galtier, 2016; Hartfield et al., 2017; Wright, 1951; Wright et al., 2013), and also modulates the strength and direction of sexual selection, generating much of the fascinating diversity in life, for instance, in the shapes of flowers or the courtship rituals of many animals (Barrett, 2002; Shuster & Wade, 2003). Strictly speaking, the term "mating" involves a direct sexual encounter (copulation) between a male and a female with the potential outcome of insemination and fertilization. This definition applies to sexually reproducing animals with distinct sexes (gonochorism), but not to plants, external spawners, or sessile animals such as marine invertebrates, where the pollen or sperm is released into the environment and fertilization is independent of a direct encounter between the sexes. If we broaden the definition of the term "mating system" to describe patterns of fertilization, we can apply this framework across taxa and to species that do not require copulation for insemination. Through the lens of these definitions, we aim to shed light on the key differences and commonalities in the evolutionary drivers that shape mating–system evolution across taxa.

In plant biology, the mating system usually refers to the selfing rate (Neal & Anderson, 2005), i.e., the proportion of self-fertilized progeny produced by self-compatible hermaphrodites. This also holds for some hermaphroditic animals such as snails (Jarne & Charlesworth, 1993) or nematodes (Picard et al., 2021), but hermaphroditism is much more phylogenetically constrained in animals compared to angiosperms (Jarne & Auld, 2006). Plant mating systems are categorized as outcrossing (cross-fertilization), autogamous (self-fertilizing), or mixed mating, where both strategies are employed (Richards, 1997). Immobile plants, with their modular structure and widespread overwhelming hermaphroditism, are primarily

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faced with the problem of whether to self or not. Notably, around 50% of angiosperms self-fertilize to some degree, with between 10-15% being predominantly selfing (Goodwillie et al., 2005; Igic & Kohn, 2006), including several important food crops (Zohary et al., 2012). Because of the frequency of self-fertilization in hermaphroditic plants, research on plant mating systems has tended to be framed in terms of the costs and benefits of inbreeding and how natural selection acts to either allow, promote or prevent inbreeding (Takebayashi & Morrell, 2001). The relationship between inbreeding depression and the "transmission advantage" of self-fertilization (Fisher, 1941) has therefore largely shaped theoretical models of mating–system evolution in plants (e.g., Lande & Schemske, 1985).

In contrast with plants, the theory of mating–system evolution in animals has been largely focussed on gonochoric organisms, where the mating system typically describes how individuals form mating pairs over time and the type of pair bond formed, such as monogamy, polygyny, polyandry, and promiscuity (Emlen & Oring, 1977). Hermaphroditic species are estimated to represent 5%–6% of animal species, though this figure increases to 33% when insects are excluded. The distribution of selfing rates in animals is similar to plants, although estimates are based on fewer species (Avise, 2011; Escobar et al., 2011; Felmy et al., 2023; Jarne & Auld, 2006; Pannell & Jordan, 2022). In animals, however, there has been much less consideration of inbreeding as a driver of "who mates with whom," although considerable attention has been dedicated to whether and when animals should inbreed or not (Jarne & Auld, 2006; Kokko et al., 2014). Indeed, separate sexes and the evolution of pre-mating dispersal due to drivers such as kin competition and environmental variability (Clobert, 2012) mean there is a lower risk of inbreeding compared to plants (de Boer et al., 2021). Instead, theoretical work on the evolution of animal mating system strategies has focussed on competition for access to mates (usually for males), resource availability (usually for females), and the resulting operational sex ratio, together with sexual selection and parental care (Emlen & Oring, 1977; Kokko et al., 2014; Royle et al., 2012; Shuster & Wade, 2003; Trivers, 1972).

Thus, studies of mating systems of plants and animals have differed markedly in the types of questions addressed and in the theoretical frameworks developed (cf. Goodwillie et al., 2005; Kokko et al., 2014). This is despite the conceptual similarity of some of the concepts that each field has focussed on. Our goal in this review is to compare and, where possible, align evolutionary concepts and the terminology used in plant and animal mating system research and to uncover where concepts that are more developed in one area of research can be usefully applied in the other. We argue that new insights can be gained by thinking about how these different categorizations differ from those provided in each "standard" body of literature, prompting more nuanced questions into why certain mating system traits evolve. For example, Cutter (2019) compared pollen and sperm production in plants and animals. Selfing plants tend not to be pollen-limited but might use fewer numbers for outcrossing after self-fertilization, a phenomenon known as "pollen discounting." In contrast, the selfing nematode *Caenorhabditis elegans* is inherently sperm-limited; as it produces sperm before oocytes, there is a trade-off between increasing fecundity through higher sperm numbers and growth rate through earlier fertilization (Cutter, 2004). This comparison hence raises the more fundamental question of how selfing organisms regulate pollen or sperm numbers following a shift to inbreeding and whether the outcomes differ depending on whether the species is a plant or an animal.

In this review, we primarily focus on the role of inbreeding as a driver of mating–system evolution. We thus compare the advantages and costs of inbreeding and mechanisms of inbreeding avoidance across plants and animals. We also focus attention on the role of spatial dynamics, which have been given comparatively less emphasis than inbreeding, and how these dynamics affect mating–system evolution in both systems. We explain how these key factors can be influenced by ecological, environmental, or demographic factors that affect how mating–system evolution acts out in nature. Figure 1 summarizes the different concepts we compare in this review. It highlights comparisons between ideas developed with plants in mind, with a focus on the contrast between selfing and outcrossing, and animals, with a focus on mating under gonochoric reproduction or biparental inbreeding. In some cases there are no obvious similarities, such as with parental care in animals. However, there are several potentially useful links, including the reasons for and implications of avoiding selfing in plants and avoiding biparental inbreeding in animals. A key aim of our review is to encourage the application of the concepts and ideas generated by zoologists to plants and vice versa, to allow researchers to think more cohesively about the underlying causes of mating–system evolution in their chosen fields.

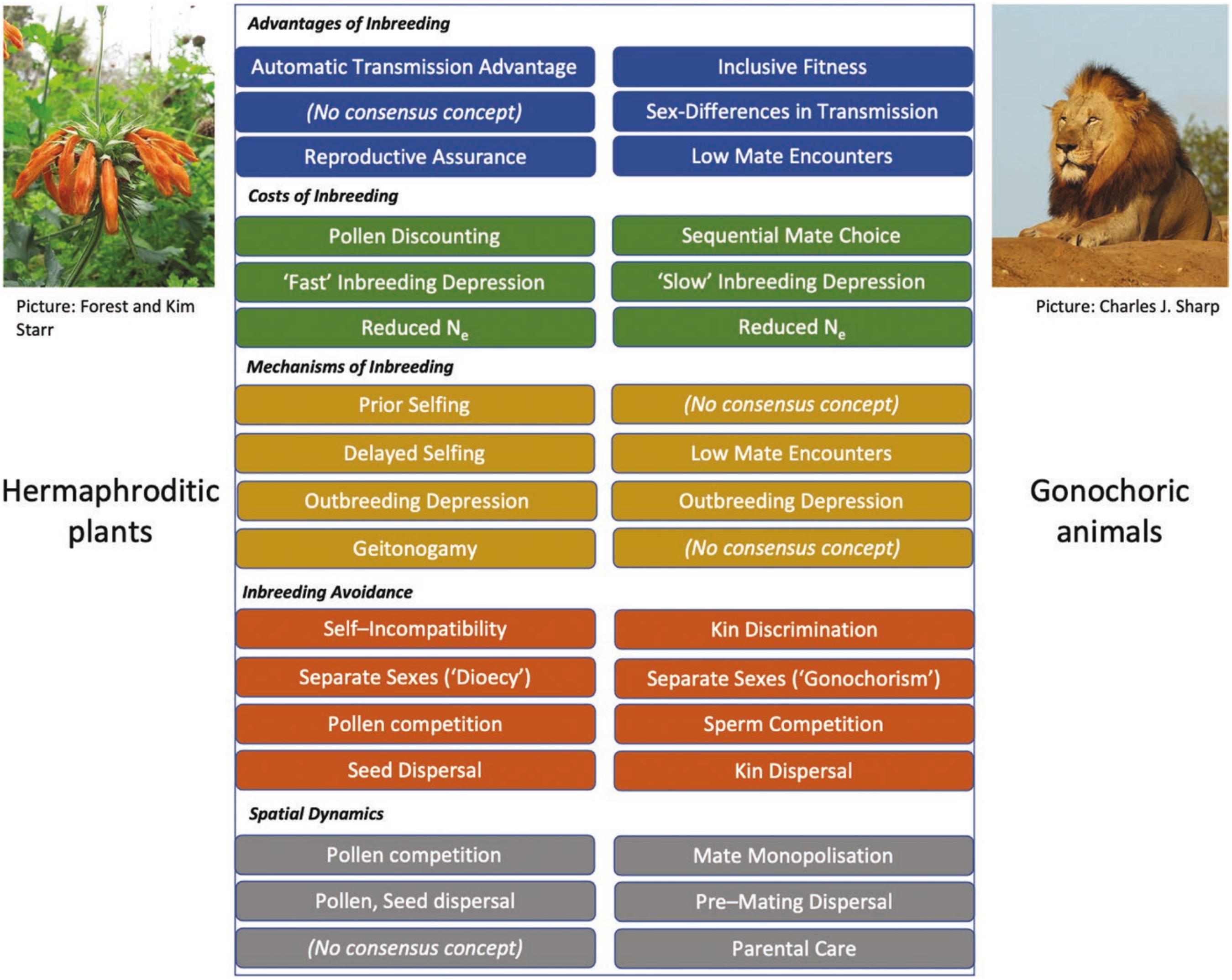
Advantages of inbreeding in plants and animals

The genetic advantage of inbreeding: automatic gene transmission

Any individual that reproduces by outcrossing contributes a single copy of its genes to its progeny, with the second copy coming from his or her partner. By contrast, progeny produced by selfing receive both copies of their genome from the same parent. As Fisher (1941) first noted, an allele causing a hermaphrodite in an otherwise outcrossing population to self-fertilize will have an immediate 50% transmission advantage compared to competing alleles at the same locus (Figure 2). This advantage arises because selfing hermaphrodites transmit genes to the next generation through both male and female gametes used to outcross, and also through male gametes used for selfing.

Fisher's insight forms the fundamental basis of much of the theoretical analysis of the evolution of selfing versus outcrossing in hermaphroditic populations, but the idea is generally applicable to autosomal loci that influence the rate of inbreeding (Kokko & Ots, 2006). In the latter case, the gene transmission benefits of inbreeding have been framed in terms of inclusive fitness in the sense that inbred progeny carry two copies of the same gene that are identical by descent (Kokko & Ots, 2006; Szulkin et al., 2013). While there have been some attempts to bridge the concept of automatic gene transmission advantage through selfing and biparental inbreeding (e.g., Olsen et al., 2021), a systematic comparison and contrast of these different concepts is missing.

Although models of biparental inbreeding predict evolution of inbreeding preference under restricted circumstances, such as low inbreeding depression and female choice (Duthie et al. 2016; Kokko & Ots, 2006; Puurtinen, 2011), inbreeding



Hermaphroditic plants	Gonochoric animals
Advantages of Inbreeding	
Automatic Transmission Advantage	Inclusive Fitness
(No consensus concept)	Sex-Differences in Transmission
Reproductive Assurance	Low Mate Encounters
Costs of Inbreeding	
Pollen Discounting	Sequential Mate Choice
'Fast' Inbreeding Depression	'Slow' Inbreeding Depression
Reduced N_e	Reduced N_e
Mechanisms of Inbreeding	
Prior Selfing	*(No consensus concept)*
Delayed Selfing	Low Mate Encounters
Outbreeding Depression	Outbreeding Depression
Geitonogamy	*(No consensus concept)*
Inbreeding Avoidance	
Self–Incompatibility	Kin Discrimination
Separate Sexes ('Dioecy')	Separate Sexes ('Gonochorism')
Pollen competition	Sperm Competition
Seed Dispersal	Kin Dispersal
Spatial Dynamics	
Pollen competition	Mate Monopolisation
Pollen, Seed dispersal	Pre–Mating Dispersal
(No consensus concept)	Parental Care

Figure 1. An overview of the concepts present and being compared in this review. Different colors denote the different major themes discussed here. Ideas on the left-hand side are those that are normally applied to hermaphrodite plants, while those on the right apply to gonochoristic (i.e., separate sex) animals. Concepts on the same line denote ideas that seem to be equivalent between the two groups but are considered in different ways (e.g., self-fertilization in plants compared to biparental inbreeding in animals).

preference is rarely seen (or at least reported) in animals (de Boer et al., 2021; Kokko & Ots, 2006). There are key differences between species that are able to self-fertilize and species with obligate biparental reproduction, which may complicate predictions of allele dynamics under biparental inbreeding (Duthie & Reid, 2016). These complications may lead to the transmission advantage of inbreeding being comparatively weaker through biparental inbreeding than through selfing. Most gonochoric animals display pre-mating dispersal, where offspring disperse as juveniles or before reproduction, from the place of birth to the place of reproduction (Bowler & Benton, 2005). Among several factors, kin competition and stochasticity in the environment are key drivers of juvenile dispersal (Bowler & Benton, 2005; Clobert, 2001, 2012). In most animals, pre-mating dispersal coupled with separate sexes means that individuals are fundamentally less likely to reproduce with relatives, and thus selection on inbreeding strategies (either preference or avoidance) will be weaker than in hermaphroditic organisms. This expectation is supported by the absence of active inbreeding preference and inbreeding avoidance mechanisms in many species (de Boer et al., 2021; Pike et al., 2021).

Another factor pertaining to systems with separate sexes, which can change predictions on the transmission advantage of biparental inbreeding compared to selfing, is the extent to which conflict arises over whether to mate with a related individual or not. The reason is that, under polygyny (i.e., males mate with multiple females), the transmission advantage typically differs between sexes, with males usually tolerating higher levels of inbreeding depression because they typically forgo fewer outbreeding opportunities per inbred mating than females (Waser et al. 1986; Parker 2006; Puurtinen 2011; Szulkin et al. 2013; Duthie & Reid 2016). The sex differences disappear when relatedness between mates is 1 (as under self-fertilization) because both partners achieve the same fitness from their own and from their partner's reproduction (i.e., they are genetically identical).

Despite the potential gene transmission advantages of biparental inbreeding through inclusive fitness, the above arguments lead to the general expectation that these advantages

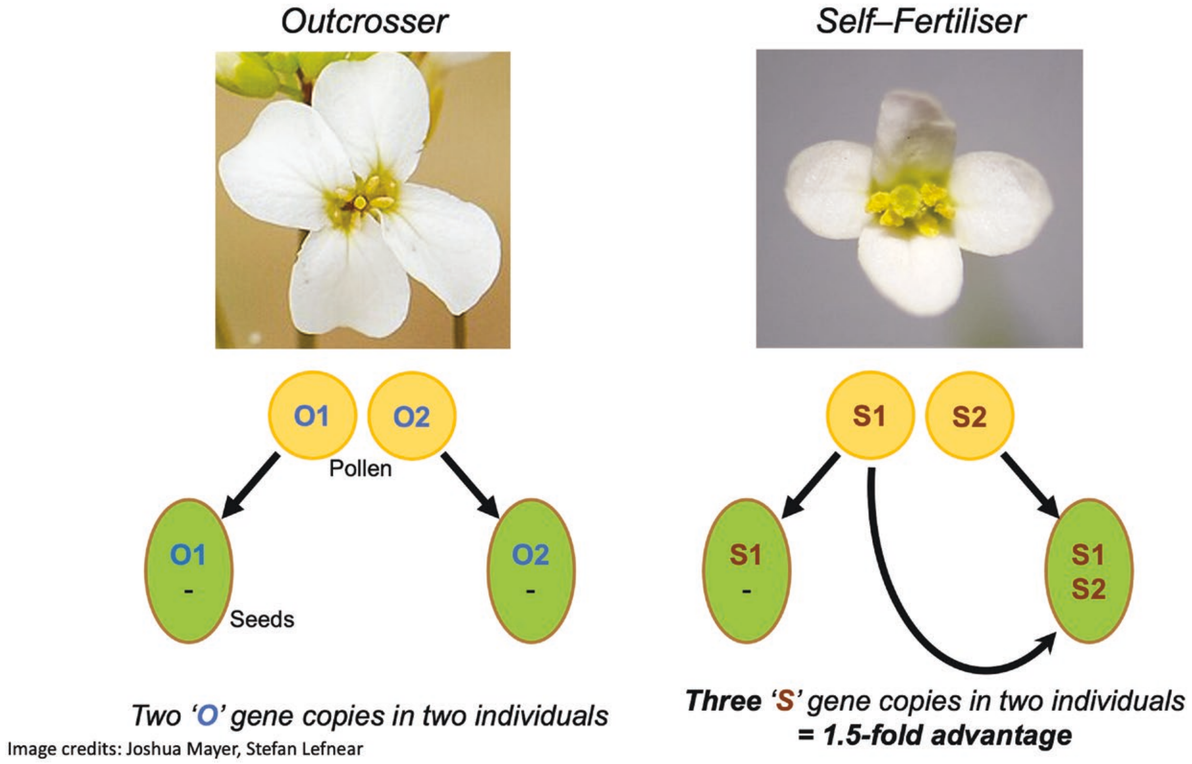


Figure 2. Illustration of the 1.5-fold transmission advantage of selfing. Arrows show transmission of pollen from each individual. "O" indicates pollen from outcrossed individuals, "S" indicates pollen from selfing individuals.

should be comparably small and rarely lead to inbreeding preference. Even when obligate inbreeding occurs as a reproductive strategy in animals somewhat similar to self-fertilization in plants (Avilés & Purcell, 2012), this is hypothesized to result from constraints on pre-mating dispersal rather than driven by the transmission advantage (Settepani et al., 2017). Transmission advantages via inclusive fitness benefits may then come into play during and after the evolution of an inbreeding mating system (Lubin & Bilde, 2007), but it seems unlikely that they would drive the evolution of inbreeding preference.

The demographic advantage of inbreeding: reproductive assurance

Alongside the advantages of inbreeding in propagating an individual's own genotype, inbreeding also confers reproductive assurance against mate limitation. If mate limitation is sufficiently strong, selfing can be selected for even when inbreeding depression is high (Cheptou, 2004). This is especially recognized in the plant literature, where there is a well-known demographic advantage of selfing in hermaphroditic organisms (Goodwillie & Weber, 2018; Opedal et al., 2016). This is common following (re-)colonization of empty habitat patches, range expansions, and at the margins of a species' range (reviewed in Pannell, 2016; Pannell et al., 2015). The association between increased capacity for uniparental reproduction and (long distance) dispersal ability is at the heart of "Baker's law," which was initially formulated for the colonization of oceanic islands and subsequently developed regarding extinction-colonization dynamics in metapopulations and colonisations during invasions, range expansions (Baker, 1955, 1967; Pannell & Barrett, 1998; Pannell et al., 2015). Pannell et al. (2015) pointed out that Baker's law describes the demographic sieve on preexisting variation in the mating system that is present during long-distance dispersal, leading to colonization of new patches. For example, within some plant species with mating system variation among populations, autogamous populations are more frequent at range margins (although this pattern may have alternative explanations, including selection under reduced pollinator or mate availability in marginal populations; Pujol et al., 2009; Griffin & Willi, 2014; Matos Paggi et al., 2015; but see Herlihy & Eckert, 2005). Consequently, selfing lineages are expected to be better colonizers than their outcrossing counterparts (Baker, 1955; Grossenbacher et al., 2017), which could facilitate the expansion of species' ranges into environments where pollinators or conspecifics are scarce (Grossenbacher et al., 2015). In line with these ideas, selfing species may have larger areas of distribution than outcrossing species (Lowry & Lester, 2006) and are more frequently found at high latitudes (Grossenbacher et al., 2015).

Reproductive assurance as a supposed advantage of selfing also occurs in hermaphroditic animals. For instance, hermaphroditic populations (compared to separate sex populations) are found at range margins in shrimps inhabiting ephemeral ponds (Longhurst, 1955), the observation that apparently inspired Baker's law (Pannell et al., 2015). Other forms of reproductive assurance occur in hermaphroditic animals, for instance, in the form of delayed selfing (e.g., in freshwater snails, Noël et al., 2016) or in the form of hypodermic self-insemination (Ramm et al., 2015).

Reproductive assurance plays out differently in gonochoric animals, and the notion that mating with close relatives may be an adaptation to mate limitation has received relatively little attention, although models predict higher inbreeding tolerance (yet not preference) when mate encountering rates are low (e.g., Kokko & Ots, 2006). Males, as the mate-limited sex, are under strong selection to compete for females. Furthermore, as a general rule, since a male can fertilize multiple females (e.g., through polygynous or promiscuous mating systems), there is high variation in reproductive success among males. This reinforces sexual selection on traits to monopolize females (harem polygyny) or to combat other males pre- or post-mating (e.g., sperm competition) if females mate with multiple males (i.e., polyandry, which is very common, especially when there is no male care or resource provisioning; Taylor et al. (2014)). In the context of mate limitation, the evolution of female mating with multiple males can help overcome reproductive failure (Greenway et al., 2015). However, it also enables fertilization with unrelated or more genetically compatible sperm, which is proposed to facilitate the successful colonization of new habitats and promote adaptation to environmental change (Candolin & Heuschele, 2008; Lewis et al., 2020; Parrett & Knell, 2018), and protect against extinction in small populations (Yasui & Garcia-Gonzalez, 2016). Female multiple mating may also reduce the cost of inbreeding (explained further below in the section "Consequences of mating system for genetic diversity and evolution"). In the context of range expansion, the combined effects of spatial sorting for dispersal traits and spatial selection on life histories, whereby traits that enhance dispersal ability and reproductive rate are "sorted" along density clines (Alex Perkins et al., 2013; Phillips et al., 2010; Shine et al., 2011; Van Petegem et al., 2016), describe a process very similar to Baker's law. Although attention has been given mainly to the spatial sorting and selection of dispersal and reproductive rate, these processes may also affect traits that allow individuals at the expanding margin to overcome mate limitation and ensure reproduction, such as traits enhancing mate finding (Tschol et al., 2024), female multiple mating, or inbreeding tolerance.

In contrast, the study of dioecy in flowering plants focuses less on its consequences with regards to sex-specific mating and sexual selection. Dioecy is rare at the species level but common at the family level, implying that while hermaphroditism is generally favoured there may be common ecological or environmental conditions that underlie it. Hence, research has instead tended to focus on uncovering which traits correlate with dioecy to test hypotheses regarding its appearance (Renner, 2014; Renner & Ricklefs, 1995; Vamosi et al., 2003). Specifically, dioecy is observed to be more common in wind-pollinated species than animal-pollinated species. An early hypothesis for this association is that wind-pollinated species do not need to have both male- and female functions within the same flower (Grant, 1951), unlike with animal pollination where flowers benefit from donating and receiving pollen per visit (Charlesworth, 1993). Furthermore, wind pollination of cosexual plants has been posited to lead to "pollen clogging" where self-pollen lands on the stigmas and prevents efficient cross-fertilization (Charlesworth, 1993; Lloyd & Webb, 1986). Dioecy is also associated with longevity, as long-lived species are better able to withstand a poor breeding season and are less in need of reproductive assurance (Baker, 1955; Renner, 2014). Longer-lived plants are also larger and hence more prone to geitonogamy (selfing from the same pollinator visiting multiple flowers on a plant), which can cause inbreeding depression (Barrett et al., 1996). An additional complicating factor is that dioecious plants can sometimes exhibit "leaky" sex expression and create mating-structures associated with the opposite sex (Pannell, 2017). This can also be seen as a reproductive assurance mechanism; for example, an experiment with *Mercurialis annua* systematically removed males from a dioecious population, which led to females evolving male function and reproducing by self-fertilization (Cossard et al., 2021).

Costs of inbreeding in plants and animals

The cost of inbreeding due to "pollen discounting" and its animal cognates

Various factors can modulate the balance between transmission advantage and inbreeding depression (Charlesworth & Charlesworth, 1987a; Charlesworth et al., 1990; Lloyd, 1979, 1992; Lloyd & Schoen, 1992). In selfing species (especially plants), an important question concerns how many outcrossing opportunities males forego due to selfing, referred to under the term "pollen discounting" (Holsinger, 1991; Porcher & Lande, 2005; Jordan & Otto, 2012; see Figure 3). This constraint has the potential to impede the evolution to high selfing rates in the absence of an inbreeding cost, as pollen discounting reduces the transmission advantage by limiting the amount of pollen carrying the selfing allele to other individuals (Nagylaki, 1976). Conversely, if selfers show higher siring success than self-incompatible individuals (i.e., negative pollen discounting), then selfing can be favoured even if there is no transmission advantage (Stone et al., 2014).

In animals, the term "opportunity cost" refers to the cost paid by inbreeding individuals when mating with relatives reduces mating opportunities, including outbreeding opportunities (Parker, 2006; Waser et al., 1986). Kokko and Ots' (2006) model predicts that when the choice between a related or an unrelated mating partner occurs sequentially, and especially in combination with low mate availability, mating with relatives should be tolerated compared to when the choice is simultaneous (Kokko & Ots, 2006). Moreover, choice mechanisms such as pre-mating discrimination against related mates (Pusey & Wolf, 1996) or post-mating mechanisms of preferential fertilization with sperm from unrelated males (Jennions & Petrie, 2000), are somewhat comparable to hermaphrodites rejecting self-pollen in plants. One explanation for the evolution of female multiple mating is protection against fertilizing the eggs with sperm from related males (Bretman et al., 2004; Jennions & Petrie, 2000). If there is a risk of mating with a close relative but also a risk of remaining unmated, then female multiple mating would ensure reproduction and facilitate post-mating mate choice, e.g., against related males.

The immediate genetic costs of inbreeding: inbreeding depression

Any genetic advantage conferred by inbreeding must be set against the potential disadvantage of reduced progeny fitness due to inbreeding depression caused by the expression of deleterious recessive mutations in the homozygous state or loss of heterozygote advantage (Charlesworth & Charlesworth, 1987a; Charlesworth & Willis, 2009). Inbreeding depression is considered the key factor counteracting the evolution to high rates of inbreeding (Charlesworth & Charlesworth, 1987a). The transition to inbreeding mating systems and selfing should only be possible if the benefits of various reproductive strategies (e.g., the automatic transmission advantage, reproductive assurance, or reduced dispersal costs) outweigh the cost of inbreeding depression (Goodwillie et al., 2005;

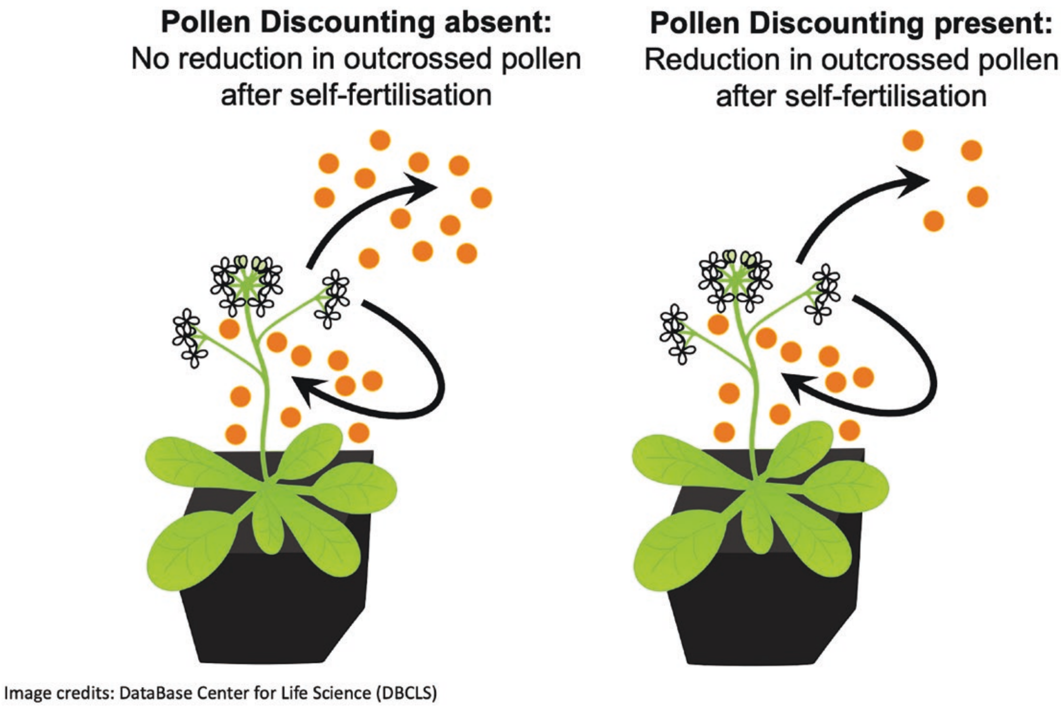


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Figure 3. A cartoon demonstrating "Pollen discounting." Note that while plants (and pollen) are shown here, the same general ideas also apply to self-fertilizing animals and limited sperm for outcrossed matings after selfing.

Settepani et al., 2017). A value of zero implies an absence of inbreeding depression, while a value of one indicates that inbreeding is lethal. Negative values are indicative of outbreeding depression, where inbreeding actually yields higher fitness. Negative values are generally found in predominantly selfing species due to, e.g., accumulation of genetic incompatibilities (including Dobzhansky–Müller incompatibilities or chromosomal rearrangements) that can be fixed within inbred lines at local geographic regions, which are exposed during rare outcrossing events between those lines (Clo et al., 2021; Soto et al., 2023).

Because the automatic transmission advantage of self-fertilization amounts to a fitness benefit of 50%, inbreeding depression must exceed 0.5 for selection to favour outcrossing, otherwise complete selfing is favoured (Lande & Schemske, 1985; Charlesworth & Charlesworth, 2010, Box 9.3). Comparisons of inbreeding depression in plant populations found that selfing species have lower median inbreeding depression (measured around 0.3) than mixed mating and outcrossing species (measured median values of 0.5–0.6; Winn et al., 2011). These observations are consistent with the prediction that strong inbreeding only evolves when inbreeding depression is relatively low. Yet, it could also be the case that selfing species have purged deleterious alleles that would reduce fitness (see below). Under biparental inbreeding, since it is less severe than selfing and hence the gene transmission advantages are weaker, then the evolution of inbreeding will be disfavoured by selection at lower levels of inbreeding depression, with the threshold inbreeding level differing between the sexes (Duthie & Reid 2015, 2016a, Parker, 2006).

Despite theoretical expectations that only obligate outcrossing or selfing are stable states, a large proportion of angiosperms (around 35%–40%) are mixed mating (Goodwillie et al. 2005). Hermaphroditic animals, such as flatworms or snails, are often predominantly outcrossing, with occasional selfing when mating partners are absent (Jarne & Auld, 2006). Nonetheless, there is variation in selfing in these animals with the selfing rate being negatively correlated with the level of inbreeding depression (Escobar et al., 2011). Similarly, hermaphroditic marine invertebrates show widely distributed inbreeding values, suggesting variable selfing rates with a distribution similar to that of plants (Olsen et al., 2021). Again, some species with intermediate values occur, suggestive of mixed mating.

Inbreeding and the purging of inbreeding depression

Inbreeding increases population-level homozygosity above Hardy–Weinburg equilibrium. For "regular" systems of inbreeding, where the extent of inbred matings is fixed and known, there are equations that relate the degree of inbreeding to the elevation in homozygosity (see Box 1 for details). In particular, selfing causes the most drastic effects of inbreeding compared to biparental inbred matings. Increasing homozygosity within a population means that inbreeding depression will decrease, as inbred and outbred offspring will have similar fitness if all individuals carry the same deleterious mutations at the homozygous state (Bataillon & Kirkpatrick, 2000). This effect makes a reversion to a more outcrossing reproductive strategy unlikely (Abu Awad & Billiard, 2017; Charlesworth et al., 1990; Harkness et al., 2019; Kamran-Disfani & Agrawal, 2014; Lande & Porcher, 2015).

The level of homozygosity at equilibrium in a population will depend on how inbreeding occurs (compare expressions in Box 1). The resulting homozygosity is proposed to lead to "purging" of deleterious mutations, where recessive variants are exposed to selection and subsequently removed (Crnokrak & Barrett, 2002). It has been hypothesized that "slow" rates of inbreeding (i.e., low elevated homozygosity and half-sib

Box 1: Inbreeding coefficients and effective population sizes

Nonrandom mating, in whatever form it occurs, will inevitably have consequences on the effective population size N_e. The effective size is a measure of the amplitude of genetic drift both due to demographic processes (i.e., fluctuations in population size, population structure) and inbreeding, a concept first introduced by Wright (1931). In the case of the effect of inbreeding on N_e, an important parameter is the coefficient of inbreeding, F_{IS} (hereafter denoted F). The inbreeding coefficient concretely represents the departure from Hardy–Weinberg (H-W) frequencies and is part of a set of measures developed for subdivided populations (F-statistics; Wright (1951)). In the simplest case of a single bi-allelic locus, with alleles A and a, present at frequencies p and q respectively (with $p = 1 - q$), the expected genotypic frequencies in a population of fixed size, with no selection or mutation, are:

Genotype	AA	Aa	aa
Frequencies	$p^2 + Fpq$	$2pq(1 - F)$	$q^2 + Fpq$

In panmictic populations, $F = 0$, and genotypic frequencies are at H-W equilibrium. Deviations from panmixia (i.e., random breeding pairs) can take many forms and include reproductive strategies such as self-fertilization, sib mating, assortative mating, polyandry, or polygyny. Most forms of nonrandom mating result in inbreeding, meaning that $0 \leq F \leq 1$. In this case, it is obvious from the expressions above that the main consequence of inbreeding will be the reduction of the proportion of heterozygotes (respectively, increase of the proportion of homozygotes). However, this is not always the case, with, for example, polyandry due to male-biased dispersal seems to lead to $F \leq 0$ (Sugg et al., 1996) and simulations show that such multiple mating among females can result in a higher expected N_e (at least temporarily; Lotterhos, 2011).

The inbreeding coefficient is likely to change with every generation of nonrandom mating. For situations where the reproductive mode is considered stable, expressions for this quantity have been proposed (Caballero & Hill, 1992b) and a few simple cases can be found (Table I). How F is calculated depends on the type of inbreeding exhibited in a population, as does the consequent rescaling of N_e. Caballero and Hill (1992a) proposed the following general expression to describe the relationship between N_e and F for a population of fixed size N, where there are equal sexes and inbreeding is due to mating with relatives (e.g., sib mating):

$$N_e = \frac{4N}{2(1-F) + S^2(1+3F)} \tag{i}$$

Here, S^2 is the corrected variance of the number of gametes contributed per parent to the next generation given by $\sigma^2 N/(N-1)$, where σ^2 is the true variance. If inbreeding is due to selfing, the equation for N_e is instead given by:

$$N_e = \frac{4N}{2(1-F) + (S_g)^2(1+F)} \tag{ii}$$

where S_g is the variance in the number of successful gametes (and is not necessarily equal to S in *Equation i*, as explained below). From these general expressions, one can see that the variance in the number of offspring alone has a significant effect on N_e, with very high variance resulting in very small effective size (Gillespie, 1974). If the number of gametes contributed follows a Poisson distribution of family size, as is the case in the Wright-Fisher model, this gives $S^2 = 2$ for biparental inbreeding and $(S_g)^2 = 2 + 2\alpha$ under selfing (forα the selfing rate), and we obtain the often-used expression for $N_e = N/(1+F)$.

Table 1. Expressions for the coefficient of inbreeding F at equilibrium for specific breeding strategies, where α is the rate of inbreeding, considered fixed. These expressions are valid in the simplest scenario, not accounting for selection, fluctuating population size or linkage as presented in (Caballero & Hill, 1992a). Sex ratios are considered equal and population size is infinite.

Type of inbreeding	Coefficient of inbreeding, ***F***
Self-fertilization	$\frac{\alpha}{2-\alpha}$
Partial full-sib mating	$\frac{\alpha}{4-3\alpha}$
Partial half-sib mating	$\frac{\alpha}{8-7\alpha}$

The qualitative relationship between F and N_e is unchanged for different values of S^2 as can be seen in Figure A1. As F increases, N_e decreases, whatever the mechanism behind an increased inbreeding coefficient. However, to obtain these expressions, several simplifying assumptions have to be made, such as discrete generations, autosomal inheritance (not sex-chromosome linked) and the absence of selection, i.e., there is no correlation between the fertility of a parent and that of its offspring. Accounting for more complex genetic structures (i.e., selection, interactions between loci) can cause N_e to be decreased even further, with the expression for F becoming more complex. This is in great part due to increased linkage and identity disequilibria (Roze, 2016; Uyenoyama & Waller, 1991). Most works have examined these genetic effects when inbreeding is due to selfing, but it is quite probable that similar effects would be observed for other forms of inbreeding.

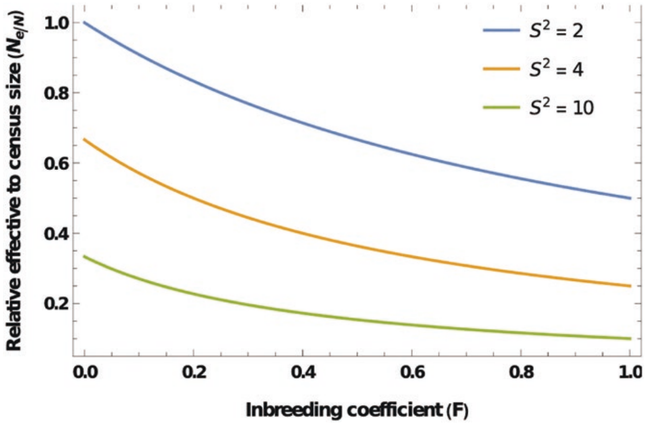

Figure A1. The relative effective-to-census population size (N_e/N) as a function of the inbreeding coefficient *F*, calculated using *Equation i*. The different coloured lines represent different variances in gamete or progeny number S^2.

mating) can reduce the magnitude of expressed inbreeding depression compared to "fast" rates of inbreeding (i.e., high elevated homozygosity and full-sib mating, or self-fertilization; Demontis et al., 2009; Porcher & Lande, 2016; Swindell & Bouzat, 2006). This is because selection is more effective under slow inbreeding due to more efficient purging of deleterious mutations due to a higher effective population size, N_e, and selection for heterozygous individuals (Wang et al. 1999). There is some empirical support for the effect of slow inbreeding influencing the magnitude of inbreeding depression using different rates of experimental inbreeding in *Drosophila* lines (Demontis et al., 2009; Pekkala et al., 2014), with a recent experiment showing that inbreeding load is removed after around 100 generations under slow inbreeding (Pérez-Pereira et al., 2021). One caveat that has been raised with measuring mutation purging is that if one observes increased fitness over time in an experiment, this could actually reflect adaptation to experimental conditions rather than active purging (Crnokrak & Barrett, 2002; Willis, 1999).

The evolution of sociality in spiders is accompanied by a transition to full-sib mating and obligatory inbreeding (Lubin & Bilde, 2007). A history of slow inbreeding due to philopatry in ancestral subsocial species might lead to purging and inbreeding tolerance (Bilde et al., 2005), which then facilitates the transition to an obligatory inbreeding (full-sib mating) mating system and permanent sociality (Berger-Tal et al., 2014). Because inbreeding depression amounts to active selection against deleterious mutations, understanding mating–system evolution must ultimately account for the joint evolution of inbreeding depression otherwise theoretical models may fail to predict equilibrium conditions (Duthie & Reid, 2016a; Porcher & Lande, 2013). This is also the case when considering the evolution of self-fertilization (as reviewed by Charlesworth & Charlesworth, 1998).

Inbreeding also reduces N_e (Box 1), exacerbating the effects of genetic drift and reducing the efficacy of selection (Charlesworth, 2003; Glémin, 2003). These processes theoretically lead to elevated accumulation of deleterious mutations in the genome, especially in predominantly inbred or selfing populations. Empirical support has been found in *Arabidopsis lyrata* (Willi, 2013) and in the genus *Stegodyphus* (Settepani et al., 2017), but not in the *Triticeae* clade (Escobar et al., 2010). In animal populations, inbreeding can be used to refer to any process that elevates homozygosity, even if there is no active mate choice with related individuals. In particular, small population sizes will lead to genetic drift creating elevated homozygosity in a population, which can superficially resemble inbreeding. However, the dynamics of deleterious mutation purging are different; only highly recessive mutations are purged by drift, whereas deleterious mutations with any dominance level can be removed by active inbreeding. One reason for this difference is that the efficacy of selection is reduced in small populations, weakening the potential to purge deleterious mutations (Glémin, 2003). These drift effects can alter the steady-state level of self-fertilization; the presence of restricted gene flow and density-dependent regulation in spatial populations, leading to increased genetic relatedness (and hence "biparental inbreeding"), can lead to intermediate levels of self-fertilization being maintained (Ronfort & Couvet, 1995; Uyenoyama, 1986).

Purging of inbreeding depression can also change the realized level of inbreeding in a population. For example, in a mixed-mating selfing species, if selfed offspring exhibit high inbreeding depression then they will not persist, so the remaining population is effectively outbred (Kelly, 1999). A similar mechanism was also observed in song sparrows, where following a population crash caused by severe winter weather, the individuals that survived were less inbred than those that died (Keller et al., 1994).

Consequences of the mating system for genetic diversity and evolution

In species with separate sexes (both plants and animals), an imbalance in the variance in mating success between sexes can affect genetic diversity. N_e will decrease in cases where females are limited in mating opportunities compared to males (Balloux & Lehmann, 2003), due to an elevation of drift that accelerates loss of genetic diversity. Female multiple mating can counteract this effect by reducing variance in reproductive success among males, meaning that a greater proportion of the population contributes to reproduction, resulting in an increase in N_e over monandry (Lotterhos, 2011). Similarly, self-fertilization is expected to decrease the amount of genetic diversity for several reasons. First, N_e of self-fertilizing populations should be smaller than that of their outcrossing counterparts (Box 1). Consequently, due to increased genetic drift causing loss of variants, selfing populations should exhibit a decrease in neutral diversity. The same logic should also apply under full-sib mating in gonochorous organisms. Empirical data on molecular markers strongly support this prediction; intraspecific (see, for example, Barrett & Husband, 1990) and interspecific (Charlesworth, 2003; Glémin et al., 2006; Hamrick & Godt, 1996; Settepani et al., 2017) comparisons have confirmed that selfing (and inbred biparental populations) have less neutral molecular genetic diversity than outcrossing ones. However, when looking at quantitative genetics data, selfing was not observed to affect heritable variance of quantitative traits (Clo & Opedal, 2021; Clo et al., 2019; Opedal et al., 2017).

Because of the inevitable unidirectional evolution towards high self-fertilization, coupled with the genetic consequences associated with it (including potentially reduced adaptive potential and decreased selection against deleterious mutations; Barrett et al., 2014; Hartfield, 2016; Hartfield et al., 2017), it is expected that lineages that transition from outcrossing to selfing will lead to extinction at a faster rate than those that do not (the “dead-end hypothesis”; Igic & Busch, 2013; Takebayashi & Morrell, 2001). Phylogenetic data supporting this idea is found in plants (Goldberg et al., 2010; Goodwillie, 1999) and in the nematode genus *Caenorhabditis* (Cutter et al., 2019). A similar signal is observed with biparental inbreeding, where it has appeared relatively recently in spiders and other arthropods (Settepani et al., 2017).

Mechanisms of inbreeding and inbreeding avoidance

In plants and hermaphroditic animals

As most angiosperms are hermaphroditic, the evolution of pollen recognition systems (gametophytic or sporophytic self-incompatibility) and separate sexes (dioecy, gyno- or androdioecy), are studied from the angle of inbreeding avoidance (Charlesworth & Charlesworth, 1978, 1987b; Freeman et al., 1997). While it has been customary in many modelling studies to consider the rate of inbreeding as a simple variable, it is, in reality, the outcome of a complex process (Whitehead et al., 2018). In plants, the selfing rate depends on the actual mechanism of selfing, and, how much and when self-pollen versus outcross pollen grains are deposited on a stigma, and the pistil’s physiological response to the pollen mix presented to it (Eckert et al., 2010).

Prior, competing and delayed selfing constitute modes that differ in terms of the relative timing of self- versus outcross pollen deposition on stigmas (Eckert et al., 2010). Traits that may reduce selfing in these animals are an asynchronous release of male and female gametes by a given individual (Lotterhos et al., 2010), but many of these species are understudied and their possible mechanisms of inbreeding avoidance are unknown. Prior selfing corresponds to the context-independent situation, often implicit in mathematical models, where a given proportion of ovules is destined for self-fertilization by the individual genotype (Davis & Delph, 2005; Tian-Bi et al., 2008). In many natural populations, however, the selfing rate is the outcome of competition between self-pollen and outcross pollen grains simultaneously deposited on a stigma, a phenomenon called competing selfing (Goodwillie & Weber, 2018). The realized mating system then depends on the proportion of self- versus outcross pollen grains deposited on the stigma, as well as on the extent to which the stigma differentially promotes their passage in the race to fertilize ovules (Sakai, 1995). The rate of competing selfing is context-dependent because the mix of self and outcross pollen deposited on a stigma depends on the identity and behaviour of the pollen vector, and on the number, density, and size of outcross pollen donors in the mating neighbourhood (Elle et al., 2010). Analogous to the competition between self and non-self-pollen in plants, sperm competition has been shown to strongly favour outrossed over self sperm in *C. elegans* (Ward & Carrel, 1979).

Self-fertilization can also be delayed. Here, plants may have mechanisms that limit and/or avoid the deposition of their pollen on their own stigmas when flowers first open, and self-fertilizing occurs after outcrossing opportunities have been exhausted (Eckert et al., 2010). In situations in which outcross pollen is not deposited on the stigma early in the flowering period, selfing may be allowed or promoted by the late breakdown of a self-incompatibility system, or as a result of the movement of anthers towards and onto the stigma (see for example Kalisz et al., 1999). Alternatively, protogyny can also promote delayed selfing, with stigmas becoming receptive to outcross pollen before the flower’s anthers open but remaining receptive to the later arrival of self-pollen and thus allowing self-fertilization if all ovules have not already been fertilized (Lloyd & Webb, 1986). In populations in which individuals only have one chance to mate, such as annuals or monocarpic perennials, delayed selfing would seem to represent a particularly promising strategy that both promotes outcrossing and assures reproductive success when outcrossing is ultimately not possible (Aarssen, 2000). Delayed selfing is much more permissible and is expected to always be favoured unless inbreeding depression is lethal (Goodwillie & Weber, 2018; Lloyd, 1979, 1992). Delayed selfing for reproductive assurance is also commonly observed in usually outcrossing hermaphroditic snails (e.g., Auld & Henkel, 2014; Tsitrone et al., 2003) and flatworms (Ramm, 2017). Conceptually, this is similar to the prediction that dioecious animals should have an increased propensity to mate with relatives if individuals can reproduce several times in their life, but there are long wait times between matings due to, e.g., low mate encounters or long time-outs after matings (Kokko & Ots, 2006).

Selfing may also result from pollen transfer between different flowers of the same individual (geitonogamy), at rates that can be context-dependent (Jong et al., 1993). Geitonogamy is a particularly deleterious outcome of mating because it implies (1) the production of potentially low-quality selfed offspring and (2) pollen discounting (Holsinger, 1991; Jordan & Otto, 2012; Porcher & Lande, 2005). Geitonogamous selfing should be context-dependent in several ways. First, as for competing selfing, the selfing rate through geitonogamy should depend on the relative abundance of open flowers on the target plant relative to those on other individuals (Eckert, 2000). Plants with relatively large floral displays are expected to experience higher levels of geitonogamy because pollinators will tend to stay on the plant for longer, transferring pollen among its flowers, compared to those with smaller displays (Eckert, 2000). Second, the geitonogamous selfing rate may depend on which pollinators are abundant at the time of mating (Snow et al., 1996). Third, the geitonogamous selfing rate experienced by individual flowers can depend on their position in the floral display in some species. For example, flowers have been found to have greater selfing rates at the top of vertical inflorescences than at the bottom because bumblebees tend to probe flowers in succession from bottom to top (Barrett et al., 1994). We do not know of any strict analogy of geitonogamy in animals. However, within-clone mating in facultatively asexual species, which is genetically equivalent to self-fertilization, may be regarded as conceptually similar.

Due to the potentially negative effects of inbreeding in plants, various adaptations have arisen that prevent it. These include the presence of self-incompatibility loci, which detect if incoming pollen is from a related individual and reject the mating if so (De Nettancourt, 2013). There can also be floral modifications that prevent inbreeding by pollinators (reviewed by Barrett, 2002). These include heterostyly where the presence of different stamen-style configurations minimize self-pollination, and enantiostyly where flowers have mirror-image configurations. Dichogamy is another mechanism, where flowers activate their male, female functions at different periods so only one is principally functional at a given time.

In gonochoric species, especially animals

As mentioned above, the theory of dispersal evolution in animals suggests that several factors, such as kin competition and environmental stochasticity drive evolution of natal pre-mating dispersal, which facilitates outcrossing (Bowler & Benton, 2005; Clobert, 2001). Furthermore, in small populations or group-living species where the risk of mating with relatives is high, inbreeding depression may also drive the evolution of pre-mating dispersal as a means of inbreeding avoidance, which is often sex-biased (Bocedi, 2021; Guillaume & Perrin, 2009; Pusey & Wolf, 1996; Ronce, 2007; Roze & Rousset, 2009; Szulkin & Sheldon, 2008). Selection on mechanisms to recognize related individuals and avoid consanguineous matings should then be relaxed in species with effective juvenile dispersal or when animals do not live in structured groups of relatives. Perhaps because many gonochoric animals do not frequently face a high risk of inbreeding, the prevalence and magnitude of inbreeding and inbreeding depression in wild animal populations are not well understood. Most data comes from small island populations or threatened species, mostly vertebrates (Crnokrak & Roff, 1999; Hasselgren & Norén, 2019; Huisman et al., 2016; Reid et al., 2007; Stoffel et al., 2021). These studies, however, report inbreeding depression of a magnitude that is likely to be of ecological significance in natural populations. Therefore, although the risk of inbreeding might be low in many species, the costs of inbreeding depression in species with a high risk of reproduction among consanguineous mates should favour mechanisms of inbreeding avoidance.

However, two recent meta-analyses suggest that the evidence for inbreeding avoidance in animals is highly variable, with a high prevalence of non-biased mating with respect to relatedness. That is, there is neither inbreeding avoidance nor preference (de Boer et al., 2021; Pike et al., 2021). Factors that contribute to the strength of selection for inbreeding avoidance include the magnitude of inbreeding depression (Berger-Tal et al., 2014; Pike et al., 2021), the frequency of interactions with relatives, and potential for causing outbreeding depression by mating with unrelated partners (Berger-Tal et al., 2014; Dorsey & Rosenthal, 2023). Both pre- and post-mating adaptations to reduce the possibility of inbreeding have been documented in cases where there is a chance of mating with relatives, for example, in small populations or in social groups (Jennions & Petrie, 2000; Pusey & Wolf, 1996). Pre-mating adaptations include kin discrimination (which can be seen as similar to self-incompatibility in plants) and sex-biased dispersal, which are predominantly found in group-living animals where philopatry increases the risk of inbreeding (Facon et al., 2006). Post-mating adaptations include polyandry, as female multiple mating can act as means of inbreeding avoidance via multiple mechanisms. Female multiple mating increases the proportion of half-sibs relative to full-sibs in the population, thereby reducing the level of close inbreeding (Bocedi, 2021; Germain et al. 2018). It also opens the possibility for sperm competition and cryptic female choice, potentially facilitating fertilization with sperm from unrelated males (Bilde et al., 2007; Bretman et al., 2004; Tregenza & Wedell, 2002).

Spatial dynamics and mating–system evolution

Spatial dynamics and mating–system evolution in animals

Spatial dynamics include processes that shape selection on mating system strategies in different ways. Some of these processes arise as a consequence of evolution in small and potentially isolated populations. These outcomes include founder effects, increased genetic drift and the subsequent risk of inbreeding, mate limitation and spatial sorting and selection of "colonizer" traits during range expansions. The specific spatial structure, connectivity among sub-populations and extinction-colonization dynamics, shape the level of gene flow among populations and the relatedness structure within populations. As such, spatial dynamics can create multiple and sometimes contrasting selection pressures on mating system traits but also, importantly, on dispersal traits. Evolution of mating systems and dispersal have therefore the potential to affect each other; however, we still know very little about their joint evolution (Auld & Rubio de Casas, 2013).

In the now classic theory of evolution of animal mating systems, spatial dynamics are considered not so much in terms of mate availability and reproductive assurance but rather in terms of mate monopolization (Shuster & Wade, 2003). While males are limited by access to females, females are limited by resources; therefore, females disperse according to resources and males according to females. This can lead to males holding territory with many females or males monopolizing a harem of females, both leading to a single male fertilizing many females, termed polygyny. This results in high variance among males in fertilization success and reduces N_e. This effect is particularly strong when males provide no offspring care. Female polyandry can counteract this effect (see above). In some systems, the degree of spatial aggregation (or spatial crowding) of receptive females, together with temporal crowding (or synchronization), is one of the key drivers determining who mates with whom and the intensity of sexual selection. Whether only females or also males provide parental care (see below) is also key for the evolution of different mating systems (e.g., from monogamy to polygyny, polyandry, or promiscuity; Trivers (1972)).

In addition, and contrary to plants, many animals display pre-mating dispersal. The main factors driving dispersal are reducing competition with kin over resources, inbreeding avoidance, heterosis, and variation in resources over time and space (Clobert 2001; Bowler & Benton 2005; Ebert et al., 2002; Guillaume & Perrin, 2006; Ronce, 2007; Rosa & Saastamoinen, 2017; Roze & Rousset, 2009). If kin competition leads to pre-mating dispersal as a common pattern, it follows that the risk of reproducing among relatives is reduced, and would suggest that the former is a stronger driver as it occurs earlier in the life cycle. However, separating kin competition from inbreeding avoidance as drivers of pre-mating dispersal is inherently difficult (Bowler & Benton, 2006). Some species display sex-biased dispersal (though these observations are still not theoretically or empirically resolved; Li & Kokko, 2019), notably some mammals and birds, with male-biased dispersal sometimes reported to be more common in mammals (expected to be largely polygynous) and female-biased dispersal more common in birds (expected to be largely monogamous, at least socially; Greenwood, 1980). A meta-analysis provides support for the resource competition hypothesis (Greenwood, 1980), identifying parental care and sexual dimorphism as major drivers of sex-biased dispersal (Trochet et al., 2016). The role of social systems emerges as an important factor in shaping sex-biased dispersal in birds and mammals but also sex differences in the acquisition of mates and other resources influence asymmetry and direction of dispersal among the sexes. There are, however, only a few reports of sex-biased dispersal in other major taxonomic groups (arthropods, amphibians, reptiles, fish; Trochet et al., 2016). Eusocial insects are typically characterized by monogamy or secondary polyandry (see, for example, Boomsma & Ratnieks, 1997), and outcrossing is maintained by pre-mating dispersal of sexuals (both males and females).

In contrast to social species with outcrossing mating systems, the joint evolution of sociality and obligate inbreeding (which could present a parallel to selfing) has evolved in different arthropod taxa (Chapman et al., 2000; Keller et al., 2011; Settepani et al., 2017). The prevailing hypothesis for this transition is that constraints on pre-mating dispersal coupled with inbreeding tolerance and benefits of social living leads to strict inbreeding (Settepani et al., 2017), rather than transmission benefits or reproductive assurance. Dispersal occurs post-mating by fertilized females or by fission of groups, which implies a complete lack of gene flow among breeding groups.

Spatial dynamics and mating–system evolution in plants

The evolution of mating systems over spatial scales underlie some of the earliest hypotheses regarding the evolution of self-fertilization, most notably Baker's law and reproductive assurance as explained in preceding sections. One of the few models that consider the joint evolution of dispersal and mating systems has been developed under conditions of pollen limitation (Cheptou & Massol, 2009; Massol & Cheptou 2011a). Based on observations that some inbred weeds can evolve selfing in the face of heterogeneous environmental and pollinator effects (Grant, 1967), they considered the joint evolution of dispersal and self-fertilization where pollination is stochastic. They find that two different syndromes evolve; one of highly dispersing outcrossers, and another of selfers with low dispersal rate. The reason for these different syndromes evolving is that, if pollination is erratic, then outcrossing individuals with higher dispersal rates would be selected for in case there is a lack of pollination, avoiding extinction at the local scale. Conversely, selfers suffer from inbreeding depression and are poor competitors with outcrossers, hence limit dispersal in order to avoid others. These predictions seem to contradict the initial predictions made by Baker's law and triggered debates as to how Baker's law should be defined and whether it is due to just mate limitation or also pollinator limitation (Busch, 2011; Cheptou, 2012; Massol & Cheptou, 2011b; Pannell et al., 2015). Pannell et al. (2015) concluded that while both these effects can be considered by Baker's law, mate limitation is a more relevant mechanism driving it. Recently, Weissman et al. (2024) showed that cleistogamy (closed flowers on a plant that promotes self-fertilization) is more prevalent in seemingly less stable biomes, in line with the idea that unpredictable environments can promote increased selfing locally. However, this was an observational study; it remains to be tested if environmental unpredictability is the cause behind increased cleistogamy, and whether such species also have lower dispersal in line with the models of Cheptou & Massol (2009) and Massol & Cheptou (2011a).

It has been shown in animals that pre-mating dispersal can evolve to limit competition among kin for local resources. This pattern can theoretically be found in plants too; following Cheptou and Massol (2009) and Massol & Cheptou (2011a), the presence of any limiting resource (e.g., pollinators, nutrients) might lead to the evolution of dispersal and outcrossing mating strategies. To our knowledge, no studies yet exist in linking competition for local resources with the mating system in plant species at large taxonomic scale (File et al., 2011). In the mixed-mating species, *Impatiens capensis*, Schmitt and Ehrhardt (1987) tested the sib-competition hypothesis and found no evidence that sibling competition for local resources should enhance outcrossing in controlled conditions for their model species. A similar trend has been found in the plant species *Anthoxanthum odoratum* (Kelley et al., 1988). Testing the hypothesis of pre-mating dispersal could either be done by replicating studies at the species level, or by working at a larger taxonomic scale. One can think about looking at the proportion of outcrossing and selfing species at a metapopulation scale, and the variation of the mating system within-species in the same design, as a function of an estimator of resource competition (as measured by, e.g., plant density or species diversity).

Selection for capacity for self-fertilization in otherwise outcrossing colonizing species can evolve to avoid local competition. For example, many studies found a prevalence of self-compatible species on islands (Bernardello et al., 2001; Chamorro et al., 2012), even if others found a high proportion of self-incompatible and/or dioecious plant species in oceanic islands (Bawa, 1982; Carlquist, 1966; Sakai et al., 1995). More recently, Grossenbacher et al. (2017) found a greater proportion of self-compatible species in islands compared to mainland regions, at a large taxonomic scale (>1,500 species). This variation in outcomes among studies could be attributed to the evolution of self-incompatibility systems and/or reproduction traits after colonization and establishment (Pannell et al., 2015). However, the association between self-compatibility and island colonization seems to be the rule, even if the forces (e.g., avoiding local competition or lack of compatible pollinators) driving the association still need to be elucidated.

Additional mechanisms

In Box 2, we outline two additional cases where there are ideas specific to one kingdom but with few analogous mechanisms in the other and discuss whether the plant-animal divide can be bridged accordingly. First, we outline how parental care in animals affects mating–system evolution, especially with regards to how the contribution from each parent influences which mating system is favoured. Second, we describe "promiscuity" and reproductive variance in selfing and outcrossing plants, explaining mechanisms that could conceptually be similar to promiscuity in animal mating systems.

Box 2: Parental care, plant promiscuity, and mating–system evolution

Parental care

There is remarkable variation in patterns of parental care across the animal kingdom. In mammals, offspring care is predominantly provided by females; in some fish and birds, care is provided only by males; and in birds there is often biparental care. Many species, mostly invertebrates, have no parental care. Whether males contribute to care or not has major implications for the mating system (Emlen & Oring, 1977). In the absence of male parental care, the ability to monopolize females or resource holding territories promotes polygyny. Polygyny also arises following lek formation, where males gather to display in a single spot. Conversely, if single females hold large territories and males need to search for females, the distribution of matings becomes less biased and promotes monogamy. Monogamy is generally selected against and is only stable when biparental care is required for offspring to survive; this is seen in some bird species and fish. Many birds show social monogamy but have a genetically promiscuous mating system (Griffith et al., 2002), as both sexes seek extra-pair matings; males to directly increase reproductive success, and females to acquire indirect genetic benefits (Jennions & Petrie, 2000). Only when both parents are constrained in their ability to seek mates outside their social bond do we expect to see genetic monogamy. Finally, when males provide exclusive care, as seen in some birds and fish species, we expect to see sex-role reversal with females competing for access to male parental care. This can lead to sequential polyandry with the female leaving each male to care for the eggs, while she seeks a new male to care for the next batch of eggs.

In contrast, these notions of parental care are hardly transposable to plants. One main difference is that most angiosperms are monoecious having the two sexes on the same individual. This weakens some sexual selection concepts and theoretical expectations for such organisms (Morgan, 1994). However, one parallel is possible when looking at resource allocation. In plants, similar to polyandrous animal species, females generally mate with several males in outcrossing and mixed-mating species (Barrett & Harder, 2017). This can potentially lead to inter-sexual conflict for the allocation of maternal resources in the different fertilized ovules (Haig, 2000). Indeed, while mothers are theoretically expected to maximize their fitness by allocating resources equally among offspring, fathers increase their fitness by forcing more maternal resources to be invested in their progeny at the expense of ovules fertilized by other males (Smith & Fretwell, 1974; Trivers, 1974). These conflicts are supposed to be greater in outcrossing populations because the probability of multiple siring is high, while kin-based cooperation should decrease conflict in inbreeding populations. Therefore, maternal genomes should evolve countermeasures against unbalanced resource allocation among offspring in outcrossing populations. In selfing populations, resource allocation conflicts should theoretically be weaker, leading to balanced allocation to offspring. Consequently, crosses between plants with different selfing histories (i.e., between a predominantly selfing plant and a predominantly outcrossing one) can lead to unbalanced resource allocation among offspring. These expectations have received strong empirical support (see Brandvain & Haig, 2005; Raunsgard et al., 2018 for reviews).

Plant promiscuity

In similar ways that are found in the animal kingdom, several mechanisms can modify the variance of reproduction in plants. Delayed stigma receptivity, where outcross pollen arrives before stigmas become receptive and stays there until fertilization occurs, should favour outcrossing and increase genetic diversity (Lankinen et al., 2007). Delayed stigma receptivity should also favour pollen competition (Galen et al., 1986; Herrero, 2003) as it increases the probability of receiving compatible or superior pollen donors (Willson, 1994). It potentially also prevents fertilization by self-pollen of low quality (Armbruster & Gobeille Rogers, 2004). Similarly, it has been found that higher pollen density can increase the probability of germination and promote pollen competition, as shown in the tree *Betula pubescens* (Holm, 1994). These temporal dynamics in female receptivity, leading to male (pollen) competition, potentially share similarities to lek competition in (co) sexual animal populations where multiple males compete among themselves for reproduction (Fiske et al., 1998). It remains to be seen if theory from animal ecology regarding the spatial distribution of resources and temporal activity of mates (Emlen & Oring, 1977) can be used to understand the evolution of these mechanisms in plant evolution.

On the other hand, other processes could limit the number of offspring. Some species have evolved stigma closure (e.g., when stigma lobes close together, either temporarily or permanently; Waser & Fugate, 1986) after mechanical stimulation (Newcombe, 1922). This process limits the variance of pollen donors and favour monogamy and/or limit polyandry in plants, which could have positive or negative consequences on individuals' fitness depending on the selfing rate of the species. In predominantly selfing species where outbreeding depression is observed even at limited geographical scales among inbred lines (Clo et al., 2021; Le Rouzic et al., 2024; Soto et al., 2023), stigma closure after self-pollination may limit outbreeding events and hence negative consequences on reproductive success due to outbreeding depression caused by genetic incompatibilities. Conversely, in self-incompatible species (e.g., those in the *Bignoniaceae* family) where flowers bloom en mass and hence there is a high potential for geitonogamy, stigma closure can occur after incompatible self-pollen disposition from pollinators, impeding compatible pollen deposition from other plants and leading to reduce fitness and fruit set (Milet-Pinheiro et al., 2009).

Perspective and future directions

In this review, we have aimed to provide a broad overview of "mating system" scholarship when considered in animals and plants. Our goal was to see whether these research strands, that historically have tended to occur in isolation, have any commonalities in the concepts they consider and where their ideas diverge. We aimed to focus on potential similarities, including the advantages of inbreeding via "transmission advantages" and reproductive assurance; costs of inbreeding via pollen or sperm discounting and inbreeding depression; how inbreeding can be avoided; and how spatial structure interacts with the mating system. However, even in these areas where it seems that there are similarities, there are important differences between the two fields. For example, while inbreeding can be advantageous in animals due to increasing kin selection, the advantages may not be as great due to the timing of mating for each sex, and pre-mating dispersal driving individuals away from relatives. The dynamics of inbreeding depression also play out differently between selfers and biparental species, with the latter more likely to exhibit "slow" inbreeding due to the persistence of weakly recessive deleterious alleles.

There are key differences between the study of animal and plant mating systems that require clarification. From a (selfing) plant perspective, the presence of self-fertilization tends to be seen as advantageous when present due to, for example, its transmission advantage (Fisher, 1941) or reproductive assurance (Baker, 1955). However, this is often not the case in animal populations, where the assumption is that inbreeding is primarily negative and is hence avoided (Keller, 2002). For example, empirical studies have shown that mechanisms such as pre-mating dispersal act as a means to avoid kin mating and reduce the risk of inbreeding (e.g., Dolotovskaya et al., 2020; Lebigre et al., 2010; Nelson-Flower et al., 2012; Pusey 1987; Szulkin & Sheldon, 2008). However, there also exist theoretical scenarios where inbreeding can be advantageous (Kokko & Ots, 2006; Szulkin et al., 2013; Waser et al., 1986), and recent meta-analytic studies find a prevalence of inbreeding tolerance in animals (de Boer et al., 2021; Pike et al., 2021). Yet even in highly inbred species such as social spiders, the observed inbreeding is driven not by an adaptive mechanism but indirectly through other means (e.g., selection against pre-mating dispersal; Bilde et al., 2005; Lubin & Bilde, 2007). In general, highly related biparental animal populations are exceptional, as opposed to selfing plants where high relatedness is the norm. This example demonstrates that discussing these separate ideas and looking for potential commonalities and differences can help researchers in both fields better understand and investigate the evolution of mating systems more generally. We are also mindful that there are many other concepts we could have discussed in this review, and some of our comparisons are imperfect. We hence present it as an initial aim at bridging these fields, with future research and discussions needed to refine the comparisons made here, and resolve if there are any other overlapping concepts.

Given the ideas in this review, we present several ideas on how we can better compare the existing mating-system concepts, and for future research with regards to either selfing plants and hermaphroditic animals, or gonochoric animals and dioecious plants.

Explicit theoretical comparison between selfing and biparental mating systems

In order to truly consider the commonalities and differences between plant and animal mating systems, there needs to be more investigations that simultaneously compare the two, both theoretically and empirically. A good starting point is the development of theoretical work that explicitly compares the evolution of self-fertilization and biparental inbreeding to predict potential similarities and differences that can be tested empirically. Classic examples include early work by Wright (1951) and Ghai (1969) that compared inbreeding effects due to selfing and biparental inbreeding (see also Box 1). More recent theoretical studies are starting to develop a theory of evolution of inbreeding preference and avoidance in systems with biparental reproduction and self-fertilization, which explicitly takes into account evolution of inbreeding depression (Duthie & Reid, 2016a; Duthie et al., 2016; Porcher & Lande, 2016). Another example is the study of Scott et al. (2024) that compares the effect of both monandry-polyandry and outcrossing-selfing on gametic selection and their differential effects on deleterious mutations and those subject to balancing selection. This study demonstrates the contrasting effects of different mating systems on mutation load. The degree of monandry-polyandry only affects load if gametic selection is present, while selfing can actually increase load if gametic selection operates, in contrast to classic theoretical expectations. A knock-on effect here is that gametic selection can decrease inbreeding depression in outcrossing species, making it more permissible for selfing to subsequently evolve.

Developing this theory can be used to address open questions, including: how does the spread of a modifier for increased inbreeding differ between selfing and biparental inbreeding, and are the two mechanisms vastly different? How does pre-mating dispersal, inbreeding and mating systems interact in biparental animals, and do equivalent mechanisms act in selfers? Are the drivers of inbreeding avoidance in biparental species similar to those that cause outcrossing to be maintained in hermaphrodite species?

Better experimental quantification of different concepts

In addition to the development of new theory, there also needs to be better quantification of evolutionary concepts to determine if similar processes do act between plants and animals. First, this means better testing of classic mating system ideas that may have been well-developed theoretically but seldom tested empirically. Even today, there are few direct tests of the transmission advantage in selfers, and those that have been undertaken do not necessarily find outcomes that match classic assumptions (e.g., Stone et al. (2014) reported negative pollen discounting). Second, this also means developing experiments that directly compare similar concepts under selfing and biparental inbreeding. For example, we extensively discuss the trade-off between genetic transmission and inbreeding depression, but to our knowledge no quantitative comparisons exist comparing this effect under different inbreeding levels. One idea would be to use self-compatible species that can be selfed or inbred to different degrees as experimental systems to test these ideas.

Is selfing tolerated rather than adaptive?

Work on the evolution of self-fertilization has highlighted how the field predominantly views selfing as an adaptive trait. That is, if self-fertilization is present, then it is due to a transmission advantage that outweighs any inbreeding depression. However, this is not the general view with regards to inbred animal mating systems, where inbreeding is generally seen as a maladaptive outcome due to other factors, such as small population size. This comparison hence raises the question as to what extent selfing in natural populations is truly adaptive, rather than arising as a by-product of other factors? The latter question was posed by Winn et al. (2011) in addressing why mixed-mating plants exhibit the same levels of inbreeding depression as outcrossing plants; mixed-mating could be stable but could also be short-lived and evolve towards outcrossing if selfed offspring have reduced fitness. Similarly, many hermaphroditic animal species predominantly outcross due to costs of inbreeding depression in selfers (Ramm, 2017).

It is difficult to disentangle inbreeding tolerance from preference. Inbreeding tolerance should increase in plants and animals with mate limitation (Kokko & Ots, 2006). Due to the sessile nature of plants (and some animals), mate limitation is more likely, which should favour inbreeding tolerance. In some gonochoric animals, philopatry leads to kin-structured neighbourhoods and low levels of inbreeding, which promotes partial purging of inbreeding depression and inbreeding tolerance (Bilde et al., 2005). Inbreeding tolerance can be observed in self-incompatible species that are capable of delayed selfing following a temporal breakdown in or transient self-incompatibility (Goodwillie & Weber, 2018). Whether this inbreeding tolerance leads to obligate inbreeding more often in plants than animals has yet to be addressed. Three mechanisms could nonetheless support a less hindered transition to preferential inbreeding: more efficient purging under selfing (Glémin, 2003), a strong automatic advantage, and a history of slow inbreeding and purging (Bilde et al., 2005).

One future research direction could be to use theories arising from animal mating systems as hypotheses to test whether selfing is tolerated in natural species and develop both novel theory and experiments to determine under what conditions such inbreeding could be tolerated rather than selected for or against.

How do feedbacks affect mating system evolution across spatial scales?

This review has also highlighted the importance of feedbacks affecting mating system evolution in both plants and animals, especially across spatial scales. In animals, inbreeding avoidance to prevent inbreeding depression has been theoretically proposed to drive sex-biased dispersal, although theoretical and empirical results paint a much more complex scenario (Li & Kokko, 2019). Inbreeding depression can also drive the evolution of pre-mating dispersal, with either no sex bias or a bistable scenario predicted (only one sex disperses and the other is completely philopatric), but cannot alone predict the direction of the bias and the main patterns observed in nature. For example, the most common association between polygyny and male-biased dispersal does not emerge from models only considering inbreeding load (Guillaume & Perrin, 2009), but it depends on the interplay between inbreeding avoidance, demographic and environmental stochasticity (Henry et al., 2016). Selection against pre-mating dispersal is hypothesized to contribute to transitions to sociality and inbreeding in a range of gonochoric animals (Settepani et al., 2017). The role of social systems also emerges as an important factor in shaping sex-biased dispersal in birds and mammals (Perrin & Goudet, 2001), but also sex differences in mate acquisition and other resources influence asymmetry and direction of dispersal among the sexes (Bowler & Benton, 2006). Critically, however, the feedback of evolution of sex-biased or loss of pre-mating dispersal on evolution of inbreeding depression, level of inbreeding and mating system has yet to be investigated.

In plants, there has been little modelling on the interplay between dispersal and inbreeding strategies. A couple of models have shown how feedback between dispersal and selfing can lead to different dispersal-mating syndromes occurring (Cheptou & Massol, 2009; Massol & Cheptou 2011a), which go against classic predictions arising from Baker's Law. One recent model further showed that evolution of inbreeding depression during range expansion promotes loss of self-incompatibility (Encinas-Viso et al., 2020).

Overall, these examples show how, in both fields, explicitly considering the role of spatial dynamics and investigating the feedbacks between evolution of inbreeding depression and mating system, both theoretically and empirically, represent rich avenues for future research.

Data availability

No new data were generated or analysed in support of this research.

Author contributions

Josselin Clo (Conceptualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Diala Abu Awad (Writing—original draft [supporting], Writing—review & editing [supporting]), Trine Bilde (Writing—original draft [supporting], Writing—review & editing [supporting]), Greta Bocedi (Writing—original draft [supporting], Writing—review & editing [supporting]), Christoph Haag (Writing—original draft [supporting], Writing—review & editing [supporting]), John Pannell (Writing—original draft [supporting], Writing—review & editing [supporting]), and Matthew Hartfield (Conceptualization [equal], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

None declared.

References

Aarssen, L. W. (2000). Why are most selfers annuals? A new hypothesis for the fitness benefit of selfing. *Oikos*, *89*(3), 606–612. https://doi.org/10.1034/j.1600-0706.2000.890321.x

Abu Awad, D., & Billiard, S. (2017). The double edged sword: The demographic consequences of the evolution of self-fertilization. *Evolution*, *71*(5), 1178–1190. https://doi.org/10.1111/evo.13222

Alex Perkins, T., Phillips, B. L., Baskett, M. L., & Hastings, A. (2013). Evolution of dispersal and life history interact to drive accelerating spread of an invasive species. *Ecology Letters*, *16*, 1079–1087.

Armbruster, W. S., & Gobeille Rogers, D. (2004). Does pollen competition reduce the cost of inbreeding? *American Journal of Botany*, *91*(11), 1939–1943. https://doi.org/10.3732/ajb.91.11.1939

Auld, J. R., & Henkel, J. F. (2014). Diet alters delayed selfing, inbreeding depression, and reproductive senescence in a freshwater snail. *Ecology and Evolution*, *4*(14), 2968–2977. https://doi.org/10.1002/ece3.1146

Auld, J. R., & Rubio de Casas, R. (2013). The correlated evolution of dispersal and mating-system traits. *Evolutionary Biology*, *40*, 185–193.

Avilés, L. & Purcell, J. (2012). Chapter 3 – The evolution of inbred social systems in spiders and other organisms: From short-term gains to long-term evolutionary dead ends? In H. J. Brockmann, T. J. Roper, M. Naguib, … L. W. Simmons (Eds.), *Advances in the study of behavior* (pp. 99–133). Academic Press.

Avise, J. (2011). *Hermaphroditism: A primer on the biology, ecology, and evolution of dual sexuality*. Columbia University Press.

Baker, H. G. (1955). Self-compatibility and establishment after ‘long-distance’ dispersal. *Evolution*, *9*(3), 347–349. https://doi.org/10.2307/2405656

Baker, H. G. (1967). Support for Baker’s law—As a rule. *Evolution*, *21*(4), 853–856. https://doi.org/10.1111/j.1558-5646.1967.tb03440.x

Balloux, F., & Lehmann, L. (2003). Random mating with a finite number of matings. *Genetics*, *165*(4), 2313–2315. https://doi.org/10.1093/genetics/165.4.2313

Barrett, S. C. H. (2002). The evolution of plant sexual diversity. *Nature Reviews Genetics*, *3*(4), 274–284. https://doi.org/10.1038/nrg776

Barrett, S. C. (2013). IV.8. Evolution of mating systems: Outcrossing versus selfing. In S. C. Barrett (Ed.), *IV.8. Evolution of mating systems: Outcrossing versus selfing* (pp. 356–362). Princeton University Press.

Barrett, S. C. H., Arunkumar, R., & Wright, S. I. (2014). The demography and population genomics of evolutionary transitions to self-fertilization in plants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *369*(1648), 20130344. https://doi.org/10.1098/rstb.2013.0344

Barrett, S. C. H., & Harder, L. D. (2017). The ecology of mating and its evolutionary consequences in seed plants. *Annual Review of Ecology, Evolution, and Systematics*, *48*, 135–157.

Barrett, S. C. H., Harder, L. D., & Cole, W. W. (1994). Effects of flower number and position on self-fertilization in experimental populations of Eichhornia paniculata (Pontederiaceae). *Functional Ecology*, *8*, 526–535.

Barrett, S. C. H., Harder, L. D., & Worley, A. C. (1996). The comparative biology of pollination and mating in flowering plants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *351*, 1271–1280.

Barrett, S. C. H., & Husband, B. C. (1990). Variation in outcrossing rates in *Eichhornia paniculata*: The role of demographic and reproductive factors*. *Plant Species Biology*, *5*(1), 41–55. https://doi.org/10.1111/j.1442-1984.1990.tb00191.x

Bataillon, T., & Kirkpatrick, M. (2000). Inbreeding depression due to mildly deleterious mutations in finite populations: Size does matter. *Genetical Research*, *75*(1), 75–81. https://doi.org/10.1017/s0016672399004048

Bawa, K. S. (1982). Outcrossing and the incidence of dioecism in island floras. *American Naturalist*, *119*(6), 866–871. https://doi.org/10.1086/283960

Berger-Tal, R., Tuni, C., Lubin, Y., … Bilde, T. (2014). Fitness consequences of outcrossing in a social spider with an inbreeding mating system. *Evolution*, *68*(2), 343–351. https://doi.org/10.1111/evo.12264

Bernardello, G., Anderson, G. J., Stuessy, T. F., & Crawford, D. J. (2001). A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernández islands (Chile). *Botanical Review*, *67*, 255–308.

Bilde, T., Lubin, Y., Smith, D., … Maklakov, A. A. (2005). The transition to social inbred mating systems in spiders: Role of inbreeding tolerance in a subsocial predecessor. *Evolution*, *59*(1), 160–174.

Bilde, T., Maklakov, A. A., & Schilling, N. (2007). Inbreeding avoidance in spiders: Evidence for rescue effect in fecundity of female spiders with outbreeding opportunity. *Journal of Evolutionary Biology*, *20*(3), 1237–1242. https://doi.org/10.1111/j.1420-9101.2006.01280.x

Bocedi, G. (2021). Dispersal and polyandry evolve as competing inbreeding avoidance strategies. *bioRxiv* 2021–10.

Boomsma, J. J., & Ratnieks, F. L. W. (1997). Paternity in eusocial hymenoptera. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *351*, 947–975.

Bowler, D. E., & Benton, T. G. (2005). Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biological Reviews of the Cambridge Philosophical Society*, *80*(2), 205–225. https://doi.org/10.1017/s1464793104006645

Brandvain, Y., & Haig, D. (2005). Divergent mating systems and parental conflict as a barrier to hybridization in flowering plants. *American Naturalist*, *166*(3), 330–338. https://doi.org/10.1086/432036

Bretman, A., Wedell, N., & Tregenza, T. (2004). Molecular evidence of post–copulatory inbreeding avoidance in the field cricket *Gryllus bimaculatus*. *Proceedings of the Royal Society B: Biological Sciences*, *271*, 159–164.

Busch, J. W. (2011). Demography, pollination, and Baker’s law. *Evolution*, *65*(5), 1511–1513. https://doi.org/10.1111/j.1558-5646.2011.01224.x

Caballero, A., & Hill, W. G. (1992a). Effective size of nonrandom mating populations. *Genetics*, *130*(4), 909–916. https://doi.org/10.1093/genetics/130.4.909

Caballero, A., & Hill, W. G. (1992b). Effects of partial inbreeding on fixation rates and variation of mutant genes. *Genetics*, *131*(2), 493–507. https://doi.org/10.1093/genetics/131.2.493

Candolin, U., & Heuschele, J. (2008). Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology and Evolution*, *23*(8), 446–452. https://doi.org/10.1016/j.tree.2008.04.008

Carlquist, S. (1966). The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution*, *20*(4), 433–455. https://doi.org/10.1111/j.1558-5646.1966.tb03379.x

Chamorro, S., Heleno, R., Olesen, J. M., … Traveset, A. (2012). Pollination patterns and plant breeding systems in the Galápagos: A review. *Annals of Botany*, *110*(7), 1489–1501. https://doi.org/10.1093/aob/mcs132

Chapman, T. W., Crespi, B. J., Kranz, B. D., & Schwarz, M. P. (2000). High relatedness and inbreeding at the origin of eusociality in gall-inducing thrips. *Proceedings of the National Academy of Sciences of the United States of America*, *97*(4), 1648–1650. https://doi.org/10.1073/pnas.020510097

Charlesworth, B., & Charlesworth, D. (1978). A model for the evolution of Dioecy and Gynodioecy. *American Naturalist*, *112*, 975–997.

Charlesworth, B., & Charlesworth, D. (1998). Some evolutionary consequences of deleterious mutations. *Genetica*, *102–103*(1–6), 3–19.

Charlesworth, B., & Charlesworth, D. (2010). *Elements of evolutionary genetics*. Roberts & Company Publishers.

Charlesworth, D. (1993). Why are unisexual flowers associated with wind pollination and unspecialized pollinators? *American Naturalist*, *141*(3), 481–490. https://doi.org/10.1086/285485

Charlesworth, D. (2003). Effects of inbreeding on the genetic diversity of populations. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *358*(1434), 1051–1070. https://doi.org/10.1098/rstb.2003.1296

Charlesworth, D., & Charlesworth, B. (1987b). The effect of investment in attractive structures on allocation to male and female functions in plants. *Evolution*, *41*(5), 948–968. https://doi.org/10.1111/j.1558-5646.1987.tb05869.x

Charlesworth, D., & Charlesworth, B. (1987a). Inbreeding depression and its evolutionary consequences. *Annual Review of Ecology, Evolution, and Systematics*, *18*, 237–268.

Charlesworth, D., Morgan, M. T., & Charlesworth, B. (1990). Inbreeding depression, genetic load, and the evolution of outcrossing rates in a multilocus system with no linkage. *Evolution*, *44*(6), 1469–1489. https://doi.org/10.1111/j.1558-5646.1990.tb03839.x

Charlesworth, D., & Willis, J. H. (2009). The genetics of inbreeding depression. *Nature Reviews Genetics*, *10*(11), 783–796. https://doi.org/10.1038/nrg2664

Cheptou, P. -O. (2004). Allee effect and self-fertilization in hermaphrodites: Reproductive assurance in demographically stable populations. *Evolution*, *58*(12), 2613–2621. https://doi.org/10.1111/j.0014-3820.2004.tb01615.x

Cheptou, P. -O. (2012). Clarifying Baker's law. *Annals of Botany*, *109*(3), 633–641. https://doi.org/10.1093/aob/mcr127

Cheptou, P. O., & Massol, F. (2009). Pollination fluctuations drive evolutionary syndromes linking dispersal and mating system. *American Naturalist*, *174*(1), 46–55. https://doi.org/10.1086/599303

Clo, J., Gay, L., & Ronfort, J. (2019). How does selfing affect the genetic variance of quantitative traits? An updated meta-analysis on empirical results in angiosperm species. *Evolution*, *73*(8), 1578–1590. https://doi.org/10.1111/evo.13789

Clo, J., & Opedal, O. H. (2021). Genetics of quantitative traits with dominance under stabilizing and directional selection in partially selfing species. *Evolution*, *75*(8), 1920–1935. https://doi.org/10.1111/evo.14304

Clo, J., Ronfort, J., & Gay, L. (2021). Fitness consequences of hybridization in a predominantly selfing species: Insights into the role of dominance and epistatic incompatibilities. *Heredity*, *127*(4), 393–400. https://doi.org/10.1038/s41437-021-00465-2

Clobert, J. (2001). *Dispersal*. OUP Oxford.

Clobert, J. (2012). *Dispersal ecology and evolution*. Oxford University Press.

Cossard, G. G., Gerchen, J. F., Li, X., … Pannell, J. R. (2021). The rapid dissolution of dioecy by experimental evolution. *Current Biology*, *31*(6), 1277–1283.e5. https://doi.org/10.1016/j.cub.2020.12.028

Crnokrak, P., & Barrett, S. C. H. (2002). Perspective: Purging the genetic load: A review of the experimental evidence. *Evolution*, *56*(12), 2347–2358. https://doi.org/10.1111/j.0014-3820.2002.tb00160.x

Crnokrak, P., & Roff, D. A. (1999). Inbreeding depression in the wild. *Heredity*, *83 (Pt 3)*, 260–270. https://doi.org/10.1038/sj.hdy.6885530

Cutter, A. D. (2004). Sperm-limited fecundity in nematodes: how many sperm are enough? *Evolution*, *58*(3),651–655, https://doi.org/10.1111/j.0014-3820.2004.tb01687.x

Cutter, A. D. (2019), Reproductive transitions in plants and animals: selfing syndrome, sexual selection and speciation. *New Phytol, 224*, 1080–1094. https://doi.org/10.1111/nph.16075

Cutter, A. D., Morran, L. T., & Phillips, P. C. (2019). Males, outcrossing, and sexual selection in *Caenorhabditis nematodes*. *Genetics*, *213*(1), 27–57. https://doi.org/10.1534/genetics.119.300244

Darwin, C. (1877). *The effects of cross and self fertilisation in the vegetable kingdom*. D. Appleton.

Davis, S. L., & Delph, L. F. (2005). Prior selfing and gynomonoecy in *Silene noctiflora* L. (Caryophyllaceae): Opportunities for enhanced outcrossing and reproductive assurance. *International Journal of Plant Sciences*, *166*(3), 475–480. https://doi.org/10.1086/428630

de Boer, R. A., Vega-Trejo, R., Kotrschal, A., & Fitzpatrick, J. L. (2021). Meta-analytic evidence that animals rarely avoid inbreeding. *Nature Ecology and Evolution*, *5*(7), 949–964. https://doi.org/10.1038/s41559-021-01453-9

De Nettancourt, D. (2013). *Incompatibility and incongruity in wild and cultivated plants*. Springer Science & Business Media.

Demontis, D., Pertoldi, C., Loeschcke, V., … Kristensen, T. N. (2009). Efficiency of selection, as measured by single nucleotide polymorphism variation, is dependent on inbreeding rate in *Drosophila melanogaster*. *Molecular Ecology*, *18*(22), 4551–4563. https://doi.org/10.1111/j.1365-294X.2009.04366.x

Dolotovskaya, S., Roos, C., & Heymann, E. W. (2020). Genetic monogamy and mate choice in a pair-living primate. *Scientific Reports*, *10*(1), 20328. https://doi.org/10.1038/s41598-020-77132-9

Dorsey, O. C., & Rosenthal, G. G. (2023). A taste for the familiar: Explaining the inbreeding paradox. *Trends in Ecology and Evolution*, *38*(2), 132–142. https://doi.org/10.1016/j.tree.2022.09.007

Duthie, A. B., Bocedi, G., & Reid, J. M. (2016). When does female multiple mating evolve to adjust inbreeding? Effects of inbreeding depression, direct costs, mating constraints, and polyandry as a threshold trait. *Evolution*, *70*(9), 1927–1943. https://doi.org/10.1111/evo.13005

Duthie, A. B., & Reid, J. M. (2015). What happens after inbreeding avoidance? Inbreeding by rejected relatives and the inclusive fitness benefit of inbreeding avoidance. *PLoS One*, *10*(4), e0125140. https://doi.org/10.1371/journal.pone.0125140

Duthie, A. B., & Reid, J. M. (2016). Evolution of inbreeding avoidance and inbreeding preference through mate choice among interacting relatives. *American Naturalist*, *188*(6), 651–667. https://doi.org/10.1086/688919

Ebert, D., Haag, C., Kirkpatrick, M., … Pajunen, V. I. (2002). A selective advantage to immigrant genes in a daphnia metapopulation. *Science*, *295*(5554), 485–488. https://doi.org/10.1126/science.1067485

Eckert, C. G. (2000). Contributions of autogamy and geitonogamy to self-fertilization in a mass-flowering, clonal plant. *Ecology*, *81*(2), 532–542. https://doi.org/10.2307/177446

Eckert, C. G., Kalisz, S., Geber, M. A., … Winn, A. A. (2010). Plant mating systems in a changing world. *Trends in Ecology and Evolution*, *25*(1), 35–43. https://doi.org/10.1016/j.tree.2009.06.013

Elle, E., Gillespie, S., Guindre-Parker, S., & Parachnowitsch, A. L. (2010). Variation in the timing of autonomous selfing among populations that differ in flower size, time to reproductive maturity, and climate. *American Journal of Botany*, *97*(11), 1894–1902. https://doi.org/10.3732/ajb.1000223

Ellegren, H., & Galtier, N. (2016). Determinants of genetic diversity. *Nature Reviews Genetics*, *17*, 422–433.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223. https://doi.org/10.1126/science.327542

Encinas-Viso, F., Young, A. G., & Pannell, J. R. (2020). The loss of self-incompatibility in a range expansion. *Journal of Evolutionary Biology*, *33*(9), 1235–1244. https://doi.org/10.1111/jeb.13665

Escobar, J. S., Auld, J. R., Correa, A. C., … David, P. (2011). Patterns of mating-system evolution in hermaphroditic animals: Correlations among selfing rate, inbreeding depression, and the timing of reproduction. *Evolution*, *65*(5), 1233–1253. https://doi.org/10.1111/j.1558-5646.2011.01218.x

Escobar, J. S., Cenci, A., Bolognini, J., … Glémin, S. (2010). An integrative test of the dead-end hypothesis of selfing evolution in *Triticeae* (Poaceae). *Evolution*, *64*(10), 2855–2872. https://doi.org/10.1111/j.1558-5646.2010.01045.x

Facon, B., Ravigné, V., & Goudet, J. (2006). Experimental evidence of inbreeding avoidance in the hermaphroditic snail *Physa acuta*. *Evolutionary Ecology*, *20*, 395–406.

Felmy, A., Streiff, A. B., & Jokela, J. (2023). Propensity for selfing varies within a population of hermaphroditic snails: Coexistence of selfers, outcrossers and mixed-mating individuals. *Royal Society Open Science*, *10*(10), 230532. https://doi.org/10.1098/rsos.230532

File, A. L., Murphy, G. P., & Dudley, S. A. (2011). Fitness consequences of plants growing with siblings: Reconciling kin selection, niche partitioning and competitive ability. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1727), 209–218. https://doi.org/10.1098/rspb.2011.1995

Fisher, R. A. (1941). Average excess and average effect of a gene substitution. *Annals of Eugenics*, *11*(1), 53–63. https://doi.org/10.1111/j.1469-1809.1941.tb02272.x

Fiske, P., Rintamäki, P. T., & Karvonen, E. (1998). Mating success in lekking males: A meta-analysis. *Behavioral Ecology*, *9*, 328–338.

Freeman, D. C., Doust, J. L., El-Keblawy, A., … McArthur, E. D. (1997). Sexual specialization and inbreeding avoidance in the evolution of dioecy. *Botanical Review*, *63*, 65–92.

Galen, C., Shykoff, J. A., & Plowright, R. C. (1986). Consequences of stigma receptivity schedules for sexual selection in flowering plants. *American Naturalist*, *127*, 462–476.

Glémin, S. (2003). How are deleterious mutations purged? Drift versus nonrandom mating. *Evolution*, *57*(12), 2678–2687. https://doi.org/10.1111/j.0014-3820.2003.tb01512.x

Ghai, G. L. (1969). Structure of populations under mixed random and sib mating. *Theoretical and Applied Genetics*, *39*(4), 179–182. https://doi.org/10.1007/BF00272526

Gillespie, J. H. (1974). Natural selection for within-generation variance in offspring number. *Genetics*, *76*(3), 601–606. https://doi.org/10.1093/genetics/76.3.601

Germain, R. R., Arcese, P., & Reid, J. M. (2018). The consequences of polyandry for sibship structures, distributions of relationships and relatedness, and potential for inbreeding in a wild population. *The American Naturalist*, *191*(5), 638–657

Glémin, S., Bazin, E., & Charlesworth, D. (2006). Impact of mating systems on patterns of sequence polymorphism in flowering plants. *Proceedings Biological Sciences*, *273*(1604), 3011–3019. https://doi.org/10.1098/rspb.2006.3657

Goldberg, E. E., Kohn, J. R., Lande, R., … Igić, B. (2010). Species selection maintains self-incompatibility. *Science*, *330*(6003), 493–495. https://doi.org/10.1126/science.1194513

Goodwillie, C. (1999). Multiple origins of self-compatibility in *Linanthus* section *Leptosiphon* (polemoniaceae): Phylogenetic evidence from internal-transcribed-spacer sequence data. *Evolution*, *53*(5), 1387–1395. https://doi.org/10.1111/j.1558-5646.1999.tb05403.x

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

Goodwillie, C., & Weber, J. J. (2018). The best of both worlds? A review of delayed selfing in flowering plants. *American Journal of Botany*, *105*(4), 641–655. https://doi.org/10.1002/ajb2.1045

Grant, V. (1951). The fertilization of flowers. *Scientific American*, *184*(6), 52–56. https://doi.org/10.1038/scientificamerican0651-52

Grant, W. F. (1967). Cytogenetic factors associated with the evolution of weeds. *Taxon*, *16*(4), 283–293. https://doi.org/10.2307/1216376

Greenway, E. V., Dougherty, L. R., & Shuker, D. M. (2015). Mating failure. *Current Biology*, *25*, R534–R536.

Greenwood, P. J. (1980). Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour*, *28*(4), 1140–1162. https://doi.org/10.1016/s0003-3472(80)80103-5

Griffin, P. C., & Willi, Y. (2014). Evolutionary shifts to self-fertilisation restricted to geographic range margins in North American Arabidopsis lyrata. *Ecology Letters*, *17*(4), 484–490. https://doi.org/10.1111/ele.12248

Griffith, S. C., Owens, I. P. F., & Thuman, K. A. (2002). Extra pair paternity in birds: A review of interspecific variation and adaptive function. *Molecular Ecology*, *11*(11), 2195–2212. https://doi.org/10.1046/j.1365-294x.2002.01613.x

Grossenbacher, D., Briscoe Runquist, R., Goldberg, E. E., & Brandvain, Y. (2015). Geographic range size is predicted by plant mating system. *Ecology Letters*, *18*(7), 706–713. https://doi.org/10.1111/ele.12449

Grossenbacher, D. L., Brandvain, Y., Auld, J. R., … Goldberg, E. E. (2017). Self-compatibility is over-represented on islands. *New Phytologist*, *215*(1), 469–478. https://doi.org/10.1111/nph.14534

Guillaume, F., & Perrin, N. (2006). Joint evolution of dispersal and inbreeding load. *Genetics*, *173*(1), 497–509. https://doi.org/10.1534/genetics.105.046847

Guillaume, F., & Perrin, N. (2009). Inbreeding load, bet hedging, and the evolution of sex-biased dispersal. *American Naturalist*, *173*(4), 536–541. https://doi.org/10.1086/597218

Haig, D. (2000). The kinship theory of genomic imprinting. *Annual Review of Ecology and Systematics*, *31*(1), 9–32. https://doi.org/10.1146/annurev.ecolsys.31.1.9

Hamrick, J. L., & Godt, M. J. W. (1996). Effects of life history traits on genetic diversity in plant species. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *351*, 1291–1298.

Harkness, A., Brandvain, Y., & Goldberg, E. E. (2019). The evolutionary response of mating system to heterosis. *Journal of Evolutionary Biology*, *32*(5), 476–490. https://doi.org/10.1111/jeb.13430

Hartfield, M. (2016). Evolutionary genetic consequences of facultative sex and outcrossing. *Journal of Evolutionary Biology*, *29*(1), 5–22. https://doi.org/10.1111/jeb.12770

Hartfield, M., Bataillon, T., & Glémin, S. (2017). The evolutionary interplay between adaptation and self-fertilization. *Trends in Genetics*, *33*(6), 420–431. https://doi.org/10.1016/j.tig.2017.04.002

Hasselgren, M., & Norén, K. (2019). Inbreeding in natural mammal populations: Historical perspectives and future challenges. *Mammal Review*, *49*(4), 369–383. https://doi.org/10.1111/mam.12169

Henry, R. C., Coulon, A., & Travis, J. M. J. (2016). The evolution of male-biased dispersal under the joint selective forces of inbreeding load and demographic and environmental stochasticity. *American Naturalist*, *188*(4), 423–433. https://doi.org/10.1086/688170

Herlihy, C. R., & Eckert, C. G. (2005). Evolution of self-fertilization at geographical range margins? A comparison of demographic, floral, and mating system variables in central vs. peripheral populations of *Aquilegia canadensis* (Ranunculaceae). *American Journal of Botany*, *92*(4), 744–751. https://doi.org/10.3732/ajb.92.4.744

Herrero, M. (2003). Male and female synchrony and the regulation of mating in flowering plants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *358*(1434), 1019–1024. https://doi.org/10.1098/rstb.2003.1285

Holm, S. O. (1994). Pollination density – Effects on pollen germination and pollen tube growth in *Betula pubescens* Ehrh. in northern Sweden. *New Phytologist*, *126*(3), 541–547. https://doi.org/10.1111/j.1469-8137.1994.tb04253.x

Holsinger, K. E. (1991). Mass-action models of plant mating systems: The evolutionary stability of mixed mating systems. *American Naturalist*, *138*(3), 606–622. https://doi.org/10.1086/285237

Huisman, J., Kruuk, L. E. B., Ellis, P. A., … Pemberton, J. M. (2016). Inbreeding depression across the lifespan in a wild mammal population. *Proceedings of the National Academy of Sciences of the United States of America*, *113*(13), 3585–3590. https://doi.org/10.1073/pnas.1518046113

Igic, B., & Busch, J. W. (2013). Is self-fertilization an evolutionary dead end? *New Phytologist*, *198*(2), 386–397. https://doi.org/10.1111/nph.12182

Igic, B., & Kohn, J. R. (2006). The distribution of plant mating systems: Study bias against obligately outcrossing species. *Evolution*, *60*(5), 1098–1103.

Jarne, P., & Auld, J. R. (2006). Animals mix it up too: The distribution of self-fertilization among hermaphroditic animals. *Evolution*, *60*(9), 1816–1824. https://doi.org/10.1554/06-246.1

Jarne, P., & Charlesworth, D. (1993). The evolution of the selfing rate in functionally hermaphrodite plants and animals. *Annual Review of Ecology and Systematics*, *24*, 441–466.

Jennions, M. D., & Petrie, M. (2000). Why do females mate multiply? A review of the genetic benefits. *Biological Reviews of the Cambridge Philosophical Society*, *75*(1), 21–64. https://doi.org/10.1017/s0006323199005423

Jong, T.J. de, Waser, N. M., & Klinkhamer, P. G. L. (1993). Geitonogamy: The neglected side of selfing. *Trends in Ecology and Evolution*, *8*, 321–325.

Jordan, C. Y., & Otto, S. P. (2012). Functional pleiotropy and mating system evolution in plants: Frequency-independent mating. *Evolution*, *66*(4), 957–972. https://doi.org/10.1111/j.1558-5646.2011.01513.x

Kalisz, S., Vogler, D., Fails, B., … Gonzales, R. (1999). The mechanism of delayed selfing in *Collinsia verna* (Scrophulariaceae). *American Journal of Botany*, *86*(9), 1239–1247.

Kamran-Disfani, A., & Agrawal, A. F. (2014). Selfing, adaptation and background selection in finite populations. *Journal of Evolutionary Biology*, *27*(7), 1360–1371. https://doi.org/10.1111/jeb.12343

Keller, L. (2002). Inbreeding effects in wild populations. *Trends in Ecology and Evolution*, *17*(5), 230–241. https://doi.org/10.1016/s0169-5347(02)02489-8

Keller, L., Peer, K., Bernasconi, C., … Shuker, D. M. (2011). Inbreeding and selection on sex ratio in the bark beetle *Xylosandrus germanus*. *BMC Evolutionary Biology*, *11*, 359. https://doi.org/10.1186/1471-2148-11-359

Keller, L. F., Arcese, P., Smith, J. N. M., … Stearns, S. C. (1994). Selection against inbred song sparrows during a natural population bottleneck. *Nature*, *372*(6504), 356–357. https://doi.org/10.1038/372356a0

Kelley, S. E., Antonovics, J., & Schmitt, J. (1988). A test of the short-term advantage of sexual reproduction. *Nature*, *331*(6158), 714–716. https://doi.org/10.1038/331714a0

Kelly, J. K. (1999). Response to selection in partially self-fertilizing populations. I. selection on a single trait. *Evolution*, *53*(2), 336–349. https://doi.org/10.1111/j.1558-5646.1999.tb03770.x

Kokko, H., Klug, H., Jennions, M. D., … Simmons, L. W. (2014). Mating systems. *The Evolution of Insect Mating Systems*, *42*.

Kokko, H., & Ots, I. (2006). When not to avoid inbreeding. *Evolution*, *60*(3), 467–475.

Lande, R., & Porcher, E. (2015). Maintenance of quantitative genetic variance under partial self-fertilization, with implications for evolution of selfing. *Genetics*, *200*(3), 891–906. https://doi.org/10.1534/genetics.115.176693

Lande, R., & Schemske, D. W. (1985). The evolution of self-fertilization and inbreeding depression in plants. I. Genetic models. *Evolution*, *39*(1), 24–40. https://doi.org/10.1111/j.1558-5646.1985.tb04077.x

Lankinen, A., Armbruster, W. S., & Antonsen, L. (2007). Delayed stigma receptivity in *Collinsia heterophylla* (Plantaginaceae): Genetic variation and adaptive significance in relation to pollen competition, delayed self-pollination, and mating-system evolution. *American Journal of Botany*, *94*(7), 1183–1192. https://doi.org/10.3732/ajb.94.7.1183

Le Rouzic, A., Roumet, M., Widmer, A., & Clo, J. (2024). Detecting directional epistasis and dominance from cross-line analyses in alpine populations of Arabidopsis thaliana. *Journal of Evolutionary Biology*, *37*, 839–847.

Lebigre, C., Alatalo, R. V., & Siitari, H. (2010). Female-biased dispersal alone can reduce the occurrence of inbreeding in black grouse (*Tetrao tetrix*). *Molecular Ecology*, *19*(9), 1929–1939. https://doi.org/10.1111/j.1365-294X.2010.04614.x

Lewis, R. C., Pointer, M. D., Friend, L. A., … Spurgin, L. G. (2020). Polyandry provides reproductive and genetic benefits in colonising populations. *Ecology and Evolution*, *10*(19), 10851–10857. https://doi.org/10.1002/ece3.6742

Li, X. -Y., & Kokko, H. (2019). Sex-biased dispersal: A review of the theory. *Biological Reviews of the Cambridge Philosophical Society*, *94*(2), 721–736. https://doi.org/10.1111/brv.12475

Lloyd, D. G. (1979). Some reproductive factors affecting the selection of self-fertilization in plants. *American Naturalist*, *113*(1), 67–79. https://doi.org/10.1086/283365

Lloyd, D. G. (1992). Self- and cross-fertilization in plants. II. The selection of self- fertilization. *International Journal of Plant Sciences*, *153*(3, Part 1), 370–380. https://doi.org/10.1086/297041

Lloyd, D. G., & Schoen, D. J. (1992). Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Sciences*, *153*(3, Part 1), 358–369. https://doi.org/10.1086/297040

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

Longhurst, A. R. (1955). Evolution in the Notostraca. *Evolution*, *9*(1), 84–86. https://doi.org/10.2307/2405360

Lotterhos, K. E. (2011). The context-dependent effect of multiple paternity on effective population size. *Evolution*, *65*(6), 1693–1706. https://doi.org/10.1111/j.1558-5646.2011.01249.x

Lotterhos, K. E., Levitan, D. R., & Traits, G. (2010). Gamete release and spawning behavior in broadcast spawning marine invertebrates. *The Evolution of Primary Sexual Characters in Animals*, *99*, 120.

Lowry, E., & Lester, S. E. (2006). The biogeography of plant reproduction: Potential determinants of species' range sizes. *Journal of Biogeography*, *33*, 1975–1982.

Lubin, Y., & Bilde, T. (2007). The evolution of sociality in spiders. *Advances in the Study of Behavior*, *37*, 83–145.

Massol, F., & Cheptou, P. -O. (2011a). Evolutionary syndromes linking dispersal and mating system: The effect of autocorrelation in pollination conditions. *Evolution*, *65*(2), 591–598. https://doi.org/10.1111/j.1558-5646.2010.01134.x

Massol, F., & Cheptou, P. -O. (2011b). When should we expect the evolutionary association of self-fertilization and dispersal? *Evolution*, *65*(5), 1217–1220. https://doi.org/10.1111/j.1558-5646.2011.01225.x

Matos Paggi, G., Palma-Silva, C., Bodanese-Zanettini, M. H., … Bered, F. (2015). Limited pollen flow and high selfing rates toward geographic range limit in an Atlantic forest bromeliad. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *211*, 1–10. https://doi.org/10.1016/j.flora.2015.01.001

Milet-Pinheiro, P., Carvalho, A. T., Kevan, P. G., & Schlindwein, C. (2009). Permanent stigma closure in Bignoniaceae: Mechanism and implications for fruit set in self-incompatible species. *Flora - Morphology, Distribution, Functional Ecology of Plants*, *204*(1), 82–88. https://doi.org/10.1016/j.flora.2007.11.006

Morgan, M. T. (1994). Models of sexual selection in hermaphrodites, especially plants. *American Naturalist*, *144*, S100–S125.

Nagylaki, T. (1976). A model for the evolution of self-fertilization and vegetative reproduction. *Journal of Theoretical Biology*, *58*(1), 55–58. https://doi.org/10.1016/0022-5193(76)90138-7

Neal, P. R., & Anderson, G. J. (2005). Are "mating systems" 'breeding systems' of inconsistent and confusing terminology in plant reproductive biology? or is it the other way around? *Plant Systematics and Evolution*, *250*(3–4), 173–185. https://doi.org/10.1007/s00606-004-0229-9

Nelson-Flower, M. J., Hockey, P. A. R., O'Ryan, C., & Ridley, A. R. (2012). Inbreeding avoidance mechanisms: Dispersal dynamics in cooperatively breeding southern pied babblers. *Journal of Animal Ecology*, *81*, 876–883.

Newcombe, F. C. (1922). Significance of the behavior of sensitive stigmas. *American Journal of Botany*, *9*(3), 99–120. https://doi.org/10.1002/j.1537-2197.1922.tb05659.x

Noël, E., Chemtob, Y., Janicke, T., … David, P. (2016). Reduced mate availability leads to evolution of self-fertilization and purging of inbreeding depression in a hermaphrodite. *Evolution*, *70*(3), 625–640. https://doi.org/10.1111/evo.12886

Olsen, K. C., Ryan, W. H., Kosman, E. T., … Winn, A. A. (2021). Lessons from the study of plant mating systems for exploring the causes and consequences of inbreeding in marine invertebrates. *Marine Biology*, *168*, 1–12.

Opedal, O. H., Albertsen, E., Armbruster, W. S., … Pélabon, C. (2016). Evolutionary consequences of ecological factors: Pollinator reliability predicts mating-system traits of a perennial plant. *Ecology Letters*, *19*(12), 1486–1495. https://doi.org/10.1111/ele.12701

Opedal, O. H., Bolstad, G. H., Hansen, T. F., … Pélabon, C. (2017). The evolvability of herkogamy: Quantifying the evolutionary potential of a composite trait. *Evolution*, *71*(6), 1572–1586. https://doi.org/10.1111/evo.13258

Pannell, J. R. (2016). Evolution of the mating system in colonizing plants. In S. C. H. Barrett, R. I. Colautti, K. M. Dlugosch, & L. H. Rieseberg (Eds.), *Invasion genetics* (pp. 57–80). Wiley.

Pannell, J. R. (2017). Plant sex determination. *Current Biology*, *27*(5), R191–R197. https://doi.org/10.1016/j.cub.2017.01.052

Pannell, J. R., Auld, J. R., Brandvain, Y., … Winn, A. A. (2015). The scope of Baker's law. *New Phytologist*, *208*(3), 656–667. https://doi.org/10.1111/nph.13539

Pannell, J. R., & Barrett, S. C. H. (1998). Baker's law revisited: Reproductive assurance in a metapopulation. *Evolution*, *52*(3), 657–668. https://doi.org/10.1111/j.1558-5646.1998.tb03691.x

Pannell, J. R., & Jordan, C. Y. (2022). Evolutionary transitions between hermaphroditism and dioecy in animals and plants. *Annual Review of Ecology, Evolution, and Systematics*, *53*, 183–201.

Parker, G. A. (2006). Sexual conflict over mating and fertilization: An overview. *Philosophical Transactions of the Royal Society of London, Series B: Biological Sciences*, *361*(1466), 235–259. https://doi.org/10.1098/rstb.2005.1785

Parrett, J. M., & Knell, R. J. (2018). The effect of sexual selection on adaptation and extinction under increasing temperatures. *Proceedings Biological Sciences*, *285*(1877), 20180303. https://doi.org/10.1098/rspb.2018.0303

Pekkala, N., Knott, K. E., Kotiaho, J. S., … Puurtinen, M. (2014). The effect of inbreeding rate on fitness, inbreeding depression and heterosis over a range of inbreeding coefficients. *Evolutionary Applications*, *7*(9), 1107–1119. https://doi.org/10.1111/eva.12145

Pérez-Pereira, N., Pouso, R., Rus, A., … Caballero, A. (2021). Long-term exhaustion of the inbreeding load in *Drosophila melanogaster*. *Heredity*, *127*(4), 373–383. https://doi.org/10.1038/s41437-021-00464-3

Perrin, N., & Goudet, J. (2001). Inbreeding, kinship, and the evolution of natal dispersal. In J. Clobert, E. Danchin, A. A. Dhondt, & J. D. Nichols (Eds.), *Dispersal* (pp. 123–142). Oxford University Press.

Phillips, B. L., Brown, G. P., & Shine, R. (2010). Life-history evolution in range-shifting populations. *Ecology*, *91*(6), 1617–1627. https://doi.org/10.1890/09-0910.1

Picard, M. A. L., Vicoso, B., Bertrand, S., & Escriva, H. (2021). Diversity of modes of reproduction and sex determination systems in invertebrates, and the putative contribution of genetic conflict. *Genes*, *12*(8), 1136. https://doi.org/10.3390/genes12081136

Pike, V. L., Cornwallis, C. K., & Griffin, A. S. (2021). Why don't all animals avoid inbreeding? *Proceedings Biological Sciences*, *288*(1956), 20211045. https://doi.org/10.1098/rspb.2021.1045

Porcher, E., & Lande, R. (2005). The evolution of self-fertilization and inbreeding depression under pollen discounting and pollen limitation. *Journal of Evolutionary Biology*, *18*(3), 497–508. https://doi.org/10.1111/j.1420-9101.2005.00905.x

Porcher, E., & Lande, R. (2013). Evaluating a simple approximation to modeling the joint evolution of self-fertilization and inbreeding depression. *Evolution*, *67*(12), 3628–3635. https://doi.org/10.1111/evo.12216

Porcher, E., & Lande, R. (2016). Inbreeding depression under mixed outcrossing, self-fertilization and sib-mating. *BMC Evolutionary Biology*, *16*, 105. https://doi.org/10.1186/s12862-016-0668-2

Pujol, B., Zhou, S. -R., Sanchez Vilas, J., & Pannell, J. R. (2009). Reduced inbreeding depression after species range expansion. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(36), 15379–15383. https://doi.org/10.1073/pnas.0902257106

Pusey, A. E. (1987). Sex-biased dispersal and inbreeding avoidance in birds and mammals. *Trends in Ecology & Evolution*, *2*(10), 295–299.

Pusey, A., & Wolf, M. (1996). Inbreeding avoidance in animals. *Trends in Ecology and Evolution*, *11*(5), 201–206. https://doi.org/10.1016/0169-5347(96)10028-8

Puurtinen, M. (2011). Mate choice for optimal (K)Inbreeding. *Evolution*, *65*(5), 1501–1505. https://doi.org/10.1111/j.1558-5646.2010.01217.x

Ramm, S. A. (2017). Exploring the sexual diversity of flatworms: Ecology, evolution, and the molecular biology of reproduction. *Molecular Reproduction and Development*, *84*(2), 120–131. https://doi.org/10.1002/mrd.22669

Ramm, S. A., Schlatter, A., Poirier, M., & Schärer, L. (2015). Hypodermic self-insemination as a reproductive assurance strategy. *Proceedings Biological Sciences*, *282*(1811), 20150660. https://doi.org/10.1098/rspb.2015.0660

Raunsgard, A., Opedal, O. H., Ekrem, R. K., … Pélabon, C. (2018). Intersexual conflict over seed size is stronger in more outcrossed populations of a mixed-mating plant. *Proceedings of the National Academy of Sciences of the United States of America*, *115*(45), 11561–11566. https://doi.org/10.1073/pnas.1810979115

Reid, J. M., Arcese, P., Keller, L. F., … Hasselquist, D. (2007). Inbreeding effects on immune response in free-living song sparrows (Melospiza melodia). *Proceedings Biological Sciences*, *274*(1610), 697–706. https://doi.org/10.1098/rspb.2006.0092

Renner, S. S. (2014). The relative and absolute frequencies of angiosperm sexual systems: Dioecy, monoecy, gynodioecy, and an updated online database. *American Journal of Botany*, *101*(10), 1588–1596. https://doi.org/10.3732/ajb.1400196

Renner, S. S., & Ricklefs, R. E. (1995). Dioecy and its correlates in the flowering plants. *American Journal of Botany*, *82*, 596–606.

Richards, A. J. (1997). *Plant breeding systems*. Garland Science.

Ronce, O. (2007). How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 231–253. https://doi.org/10.1146/annurev.ecolsys.38.091206.095611

Ronfort, J., & Couvet, D. (1995). A stochastic model of selection on selfing rates in structured populations. *Genetical Research*, *65*, 209–222.

Rosa, E., & Saastamoinen, M. (2017). Sex-dependent effects of larval food stress on adult performance under semi-natural conditions: only a matter of size? *Oecologia*, *184*(3), 633–642. https://doi.org/10.1007/s00442-017-3903-7

Royle, N. J., Smiseth, P. T. & Kölliker, M. (2012). *The evolution of parental care*. Oxford University Press.

Roze, D. (2016). Background selection in partially selfing populations. *Genetics*, *203*(2), 937–957. https://doi.org/10.1534/genetics.116.187955

Roze, D., & Rousset, F. (2009). Strong effects of heterosis on the evolution of dispersal rates. *Journal of Evolutionary Biology*, *22*(6), 1221–1233. https://doi.org/10.1111/j.1420-9101.2009.01735.x

Sakai, A. K., Wagner, W. L., Ferguson, D. M., & Herbst, D. R. (1995). Origins of dioecy in the Hawaiian flora. *Ecology*, *76*(8), 2517–2529. https://doi.org/10.2307/2265825

Sakai, S. (1995). Evolutionarily stable selfing rates of hermaphroditic plants in competing and delayed selfing modes with allocation to attractive structures. *Evolution*, *49*(3), 557–564. https://doi.org/10.1111/j.1558-5646.1995.tb02287.x

Schmitt, J., & Ehrhardt, D. W. (1987). A test of the sib-competition hypothesis for outcrossing advantage in impatiens capensis. *Evolution*, *41*(3), 579–590. https://doi.org/10.1111/j.1558-5646.1987.tb05828.x

Scott, M. F., Mackintosh, C., & Immler, S. (2024). Gametic selection favours polyandry and selfing. *PLoS Genetics*, *20*(2), e1010660. https://doi.org/10.1371/journal.pgen.1010660

Settepani, V., Schou, M. F., Greve, M., … Bilde, T. (2017). Evolution of sociality in spiders leads to depleted genomic diversity at both population and species levels. *Molecular Ecology*, *26*(16), 4197–4210. https://doi.org/10.1111/mec.14196

Shine, R., Brown, G. P., & Phillips, B. L. (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(14), 5708–5711. https://doi.org/10.1073/pnas.1018989108

Shuster, S. M., & Wade, M. J. (2003). *Mating systems and strategies*. Princeton University Press.

Smith, C. C., & Fretwell, S. D. (1974). The optimal balance between size and number of offspring. *American Naturalist*, *108*, 499–506.

Snow, A. A., Spira, T. P., Simpson, R., & Klips, R. A. 1996. The ecology of geitonogamous pollination. In D. G. Lloyd, & S. C. H. Barrett (Eds.), *Floral biology: Studies on floral evolution in animal-pollinated plants* (pp. 191–216). Springer US.

Soto, T. Y., Rojas-Gutierrez, J. D., & Oakley, C. G. (2023). Can heterosis and inbreeding depression explain the maintenance of outcrossing in a cleistogamous perennial? *American Journal of Botany*, *110*(10), e16240. https://doi.org/10.1002/ajb2.16240

Stoffel, M. A., Johnston, S. E., Pilkington, J. G., & Pemberton, J. M. (2021). Genetic architecture and lifetime dynamics of inbreeding depression in a wild mammal. *Nature Communications*, *12*(1), 2972. https://doi.org/10.1038/s41467-021-23222-9.

Stone, J. L., VanWyk, E. J., & Hale, J. R. (2014). Transmission advantage favours selfing allele in experimental populations of self-incompatible *Witheringia solanacea* (Solanaceae). *Evolution*, *68*(7), 1845–1855. https://doi.org/10.1111/evo.12419

Sugg, D. W., Chesser, R. K., Dobson, F. S., & Hoogland, J. L. (1996). Population genetics meets behavioral ecology. *Trends in Ecology and Evolution*, *11*, 338–342.

Swindell, W. R., & Bouzat, J. L. (2006). Ancestral inbreeding reduces the magnitude of inbreeding depression in *Drosophila melanogaster*. *Evolution*, *60*(4), 762–767.

Szulkin, M., & Sheldon, B. C. (2008). Dispersal as a means of inbreeding avoidance in a wild bird population. *Proceedings Biological Sciences*, *275*(1635), 703–711. https://doi.org/10.1098/rspb.2007.0989

Szulkin, M., Stopher, K. V., Pemberton, J. M., & Reid, J. M. (2013). Inbreeding avoidance, tolerance, or preference in animals? *Trends in Ecology and Evolution*, *28*(4), 205–211. https://doi.org/10.1016/j.tree.2012.10.016

Takebayashi, N., & Morrell, P. L. (2001). Is self-fertilization an evolutionary dead end? Revisiting an old hypothesis with genetic theories and a macroevolutionary approach. *American Journal of Botany*, *88*(7), 1143–1150.

Taylor, M. L., Price, T. A. R., & Wedell, N. (2014). Polyandry in nature: A global analysis. *Trends in Ecology and Evolution*, *29*(7), 376–383. https://doi.org/10.1016/j.tree.2014.04.005

Tian-Bi, Y. -N. T., N'goran, E. K., N'guetta, S. -P., … Jarne, P. (2008). Prior selfing and the selfing syndrome in animals: An experimental approach in the freshwater snail Biomphalaria pfeifferi. *Genetics Research*, *90*(1), 61–72. https://doi.org/10.1017/S0016672307008919

Tregenza, T., & Wedell, N. (2002). Polyandrous females avoid costs of inbreeding. *Nature*, *415*(6867), 71–73. https://doi.org/10.1038/415071a

Trivers, R. L. (1972). Parental investment and sexual selection. In B. Campbell (Ed.), *Sexual selection and the descent of man* (pp. 136–179). Aldine-Atherton.

Trivers, R. L. (1974). Parent-offspring conflict. *American Zoologist*, *14*(1), 249–264. https://doi.org/10.1093/icb/14.1.249

Trochet, A., Courtois, E. A., Stevens, V. M., … Clobert, J. (2016). Evolution of sex-biased dispersal. *Quarterly Review of Biology*, *91*(3), 297–230. https://doi.org/10.1086/688097

Tschol, M., Reid, J. M., & Bocedi, G. (2024). Sexual selection and mate limitation shape evolution of species' range limits. *Evolution*, *78*(5), 951–963. https://doi.org/10.1093/evolut/qpae031

Tsitrone, A., Jarne, P., & David, P. (2003). Delayed selfing and resource reallocations in relation to mate availability in the freshwater snail *Physa acuta*. *American Naturalist*, *162*(4), 474–488. https://doi.org/10.1086/376889

Uyenoyama, M. K. (1986). Inbreeding and the cost of meiosis: The evolution of selfing in populations practicing biparental inbreeding. *Evolution*, *40*(2), 388–404. https://doi.org/10.1111/j.1558-5646.1986.tb00479.x

Uyenoyama, M. K., & Waller, D. M. (1991). Coevolution of self-fertilization and inbreeding depression I. Mutation-selection balance at one and two loci. *Theoretical Population Biology*, *40*(1), 14–46. https://doi.org/10.1016/0040-5809(91)90045-h

Vamosi, J. C., Otto, S. P., & Barrett, S. C. H. (2003). Phylogenetic analysis of the ecological correlates of dioecy in angiosperms. *Journal of Evolutionary Biology*, *16*(5), 1006–1018. https://doi.org/10.1046/j.1420-9101.2003.00559.x

Van Petegem, K. H. P., Boeye, J., Stoks, R., & Bonte, D. (2016). Spatial selection and local adaptation jointly shape life-history evolution during range expansion. *American Naturalist*, *188*(5), 485–498. https://doi.org/10.1086/688666

Wang, J., Hill, W. G., Charlesworth, D., & Charlesworth, B. (1999). Dynamics of inbreeding depression due to deleterious mutations in small populations: mutation parameters and inbreeding rate. *Genetics Research*, *74*(2), 165–178.

Ward, S., & Carrel, J. S. (1979). Fertilization and sperm competition in the nematode *Caenorhabditis elegans*. *Developmental Biology*, *73*(2), 304–321. https://doi.org/10.1016/0012-1606(79)90069-1

Waser, N. M., & Fugate, M. L. (1986). Pollen precedence and stigma closure: A mechanism of competition for pollination between *Delphinium nelsonii* and *Ipomopsis aggregata*. *Oecologia*, *70*(4), 573–577. https://doi.org/10.1007/BF00379906

Waser, P. M., Austad, S. N., & Keane, B. (1986). When should animals tolerate inbreeding? *American Naturalist*, *128*, 529–537.

Weissman, M., Zhang, D., Kartzinel, R., & Weinreich, D. (2024). *Balancing the risks of mating: Biogeographic evidence of cleistogamy as a bet hedging strategy*.

Whitehead, M. R., Lanfear, R., Mitchell, R. J., & Karron, J. D. (2018). Plant mating systems often vary widely among populations. *Frontiers in Ecology and Evolution*, *6*.

Willi, Y. (2013). Mutational meltdown in selfing *Arabidopsis lyrata*. *Evolution*, *67*(3), 806–815. https://doi.org/10.1111/j.1558-5646.2012.01818.x

Willis, J. H. (1999). The role of genes of large effect on inbreeding depression in *Mimulus guttatus*. *Evolution*, *53*(6), 1678–1691. https://doi.org/10.1111/j.1558-5646.1999.tb04553.x

Willson, M. F. (1994). Sexual selection in plants: Perspective and overview. *American Naturalist*, *144*, S13–S39. https://doi.org/10.1086/285651

Winn, A. A., Elle, E., Kalisz, S., … Vallejo-Marín, M. (2011). Analysis of inbreeding depression in mixed-mating plants provides evidence for selective interference and stable mixed mating. *Evolution*, *65*(12), 3339–3359. https://doi.org/10.1111/j.1558-5646.2011.01462.x

Wright, S. (1931). Evolution in mendelian populations. *Genetics*, *16*(2), 97–159. https://doi.org/10.1093/genetics/16.2.97

Wright, S. (1951). The genetical structure of populations. *Ann Eugen*, *15*(4), 323–354. https://doi.org/10.1111/j.1469-1809.1949.tb02451.x

Wright, S. I., Kalisz, S., & Slotte, T. (2013). Evolutionary consequences of self-fertilization in plants. *Proceedings Biological Sciences*, *280*(1760), 20130133. https://doi.org/10.1098/rspb.2013.0133

Yasui, Y., & Garcia-Gonzalez, F. (2016). Bet-hedging as a mechanism for the evolution of polyandry, revisited. *Evolution*, *70*(2), 385–397. https://doi.org/10.1111/evo.12847

Zohary, D., Hopf, M., & Weiss, E. (2012). *Domestication of plants in the old world: The origin and spread of domesticated plants in Southwest Asia, Europe, and the Mediterranean Basin*. Oxford University Press.