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The Evolution of Plant Mating System: Is It Time for a Synthesis?

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1. Introduction

Diversity is the rule in living organisms. While this diversity is manifest at the various levels of the life tree, the diversity in the vegetable kingdom is probably the most apparent form, as revealed by the high diversity of plant morphologies and life histories even at small spatial scale. Since the first investigations in plant biology, botanists have always focused on the high variation of reproductive systems in plants and the floral diversity (forms and colors) in higher plants is one of the most obvious forms of variation. This has provided the basis for discriminating and classifying plants. In the 18th century, variation in sexual structures of plants has thus provided the basis for the Linnaean classification. Interestingly, such variation reveals variation and adaptation of the mating system and results from evolutionary processes in the phylogeny. Moreover, mating systems are central in population biology first because it ensures the maintenance (and eventually the growth) of populations and second because it shapes the transmission of phenotypic traits via the transmission of the hereditary material, thus conditioning evolutionary processes.

If the diversity of plant reproductive systems and floral morphologies have intrigued naturalists for a long time, botanic studies have long been only descriptive, without any evolutionary interpretation for the rise of such diversity. The first evolutionary interpretation has been proposed by Darwin who devoted three volumes on plants reproductive biology (Darwin, 1867; Darwin, 1876; Darwin, 1877). Pollination processes and the dependence to pollen vectors was the central selective force in Darwin's view. The rise of mendelian laws and more recently population genetics, particularly Sir Ronald Fisher's work in the 1940's, have laid the foundation for a solid theoretical framework, based on gene dynamics. In constrast, the botanical tradition has been developed in a more empirical way. These two historical traditions have given birth to two different approaches that have remained relatively separated until recently (Uyenoyama et al. 1993). In the last ten years, the rapprochement is however perceptible (Barrett, 2008). Interestingly, plant mating system studies is good example of fruitfull interaction between field data, theory and experiments. Field observations of flowering plants, interactions with pollinators have provided an important corpus of data. Also, mating system theory is an active field of research addressing major issues in evolutionary biology such as kin selection, the effect of deleterious mutations or mutual interactions. Finally, plant mating system is an area where

the experimental approach to test specific hypotheses has been succesful thanks to suitable tools and techniques. As a matter of example, self-fertilization can be precisely measured under natural conditions thanks to genetic markers, it can also be manipulated in laboratory thus allowing to test adaptive hypotheses.

In this review, I will present an overview of concepts, techniques and empirical data developed in plant mating system. Plant mating system encompasses various subfields such as the evolution of separate sexes, asexuality, the maintenance of sexual polymorphism in populations and the evolution in inbreeding regime. Because the evolution of self-fertilisation has been intensively studied and because hermaphroditism is widespread in plants, my chapter will focus mainly on the evolution of self-fertilisation in hermaphroditic plants.

2. Inbreeders and outbreeders in plants

2.1 The diversity of flowering plants

In higher plants, the flower is the fundamental unit for sexual reproduction. While the perfect flower is hermaphroditic, bearing both male (stamen) and female (pistil) functions, variations around the perfect type are theoretically possible. Some individuals may bear only female flower while other individuals bear male flower. Also, different type of flowers can coexist within individuals. These variations may be predicted by various combinations and it is important to note that most of them have been found in nature (Richard 1986). For example, dioecy corresponds to two types of individuals within populations: male bearing male flowers and female bearing female flowers. On this basis, up to seven types of sexual systems have been found in natural populations (see table 1). Among them, hermaphroditism where a single sexual type occurs in populations is by far the most widespread sexual types in higher plants representing more than 70% (Yampolsky and Yampolsky, 1922). It is worth noting that hermaphroditism also exists in many animal phyla (Jarne 1993) though it has mostly been studied in plants.

One sexual type	%	Two sexual types	%
Hermaphroditism (⚥)	72	Dioecy (♂ + ♀)	4
Monoecy (♂-♀)	5	Gynodioecy (♀ + ⚥)	7
Andromonoecy (♂-⚥)	1.7	Androdioecy (♂ + ⚥)	rare
Gynomonoecy (♀-⚥)	2.8		

Table 1. Classification of plant sexual types based (1) on the number of sexual types in the population and (2) on the number of sexes per sexual type. Hyphens in the first column symbolizes flower types in the same individual and the sign "plus" represents the occurrence of several sexual types in populations.

The evolution of separate sexes has often been considered as a way to avoid inbreeding (Bawa, 1980) but Charnov (1976) has provided another important argument based on resource allocation. Even in absence of self-fertilisation in hermaphrodites, Charnov (1976) showed that dioecy may be selectively advantageous depending on ressource trade-offs between male and female functions. The question of the maintenance of females in

gynodioecious plants or symmetrically males in androdioecious plants has been subject to important debate. Both theoretical models and empirical studies have shown that gynodiecy is evolutionary stable (e.g. *Thymus vulgaris*; Gouyon and Couvet, 1988). Interestingly, empirical data have revealed that the determinism of sexual types implies cytaplasmic genes coding for male sterility (favouring female transmission) and nuclear genes restoring male fertility. Theoretical studies have confirmed that nucleo-cytoplasmic allowed gynodioecy to evolve on a large range of parameters and models have revealed a male/female conflict. While androdioecy may seem similar, theoretical studies have shown that the conditions for its stability are narrow, which lead some authors to doubt about the existence of "true androdioecy" in plants (Charlesworth, 1984). A recent study by Saumitou-laprade et al. (2009) on *Phyllirea angustifolia* (Oleaceae) has demonstrated first that the species was functionally androdioecious and second, that self-incompatibility renders androdioecy evolutionary stable (Vassiliadis et al, 2000). In this species, Saumitou-Laprade et al (2009) demonstrated the existence of two groups of self-incompatibility in hermaphrodites while males were compatible with all the hermaphrodites.

2.2 Functional adaptation to selfing and outcrossing in hermaphrodites

In flowering plants, physiological and morphological adaptations promoting outcrossing or selfing have been described. Many functional adaptations favoring cross-pollination are designed to promote pollen transfer. Floral design such as structure, odour, scent and nectar production are important components involved in plant/pollinator interactions (Barrett and Harder 1996). Reduction in flower size (petals) is often associated with the increase of self-fertilization. This is illustrated in figure 1 in the genus *Amsinckia* (Baroaginaceae). The outcrosser *A. furcata* displays large flowers whereas its close relative selfer *A. vernicosa* exhibits a reduced corolla (Schoen et al. 1997). Also, temporal separation of male and female function within an individual (protoginy and protandry) and spatial separation (herkogamy) are phenological adaptations to outcrossing. A widespread mechanism promoting outcrossing is the physiological inability for self-pollen to germinate on the stigma of the same flower, i.e. self-incompatibility, which is known to have evolved in many families (Barrett 1988). There are also functional adaptations to self-fertilization. A widespread floral adaptation to self-fertilization that has evolved in many botanic families has been described: cleistogamy (Lord 1981). It corresponds to the production of flowers that do not open, which implies obligate self-fertilization. Individuals generally produce both cleistogamous flowers and chasmogamous flowers (open flowers) and the proportion of each type has been found to be influenced by both genetic and environmental factors (Lord 1981).

2.3 The evolutionary transition from outcrossing to selfing or selfing as "an evolutionary dead end"

The evolution of self-fertilisation from outcrossing ancestors is a frequent transition in plant kingdom (Stebbins 1950). In this context, self-fertilising taxa have been considered to go extinct at higher rate than outcrossing taxon, which suggests that selfing lineages have short lifetimes. Takebayshi and Morell (2001) qualify the evolution towards selfing as "an evolutionary dead end". The loss of adaptive potential and reduced genetic variation have been proposed to account for the higher extinction of selfers but none of these hypotheses have been investigated empirically. As an illustrative example, Schoen et al. (1997)

studied the evolutionary history of mating system in the genus *Amsinckia* (Boraginaceae). The authors mapped mating system characters (i.e. population selfing rates) on the phylogeny of the genus (fig. 1). Assuming that the ancestral taxon was an outcrosser, the phylogeny reveals that selfing lineages have evolved four times in the genus, in an irreversible way.
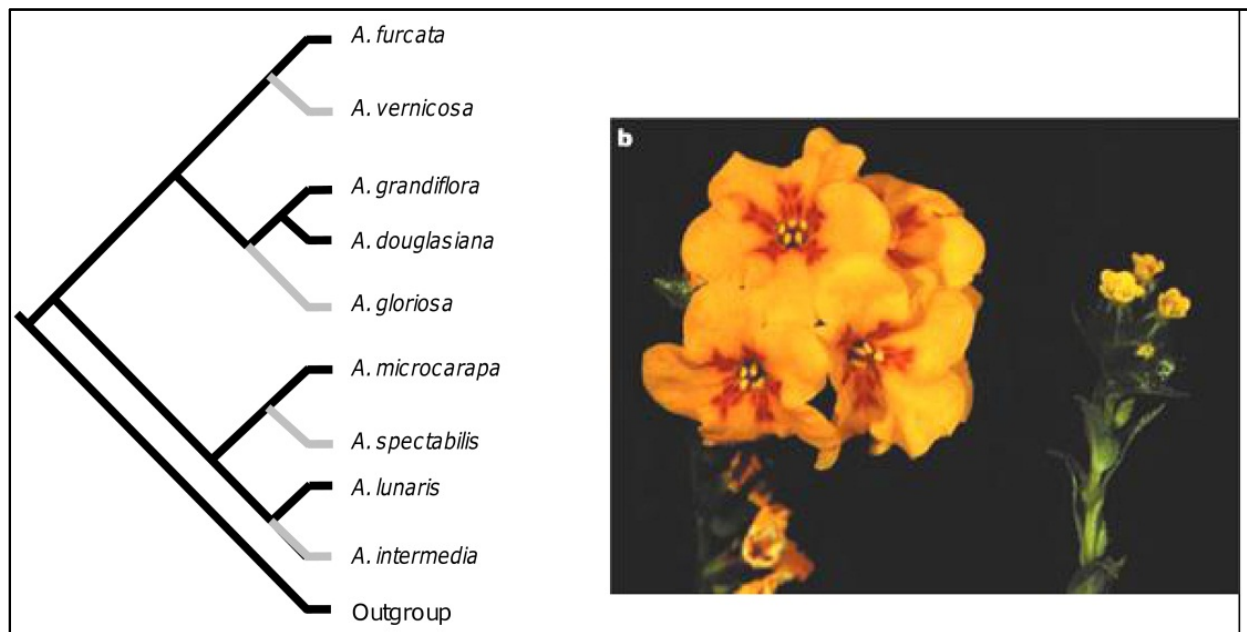

Fig. 1. Evolution of recurrent self-fertilization in the genus *Amsinckia* (Boraginaceae). The phylogenetic reconstruction is based on restriction site variation in the chloroplast genome (Schoen et al. 1997). In gray: branch giving rise to inbred lines, in black branch giving rise to cross-pollinated lines (the ancestor is supposed to cross-pollinated). Photos: left, the cross-pollinator *A. furcata* and right self-pollinating species *A. Vernicosa*. Courtesy of Daniel J. Schoen (McGill University, Canada).

In a recent study, Goldberg et al (2009) have demonstrated in the Solanaceae family that self-compatible species have a higher speciation rates than self-incompatible ones. However, extinction rate is much larger in self-compatible taxa resulting in a higher diversification rates for self-incompatible taxa. The apparent short-term advantages of self-compatible species are counterbalanced by strong species selection, thus favoring obligate outcrossing on the long-term. This study is unique and shows individual selection (or darwinian selection) may be insufficient to cature mating systems evolution in the phylogeny and that higher levels of selection may be at work.

2.4 The enigma of mixed selfing rates

Thanks to suitable techniques to measure plant mating systems, mating system biologists have created an important corpus of data. Two components have contributed to this development. The intensive use of neutral genetic markers (allozymes, microsatellites) have provided operational tools for mating system analysis (see Goodwillie et al 2005 for a recent compilation). In 1980's the distribution of selfing rates was considered to be bimodal with full outcrossers and full selfers (Schemske and Lande 1985) and conform to theoretical

predictions. Admittedly, the few mixed selfers were considered to be transient states evolving towards full outcrossing or full selfing. The question of mixed selfing rates stimulated an important debate among mating system biologists to determine whether those selfing rates were transient states or stable states (Aide 1986; Waller, 1986).

An in-depth analysis and more complete data has revealed first that complete selfer are actually very rare. Second, that mixed selfing rates are relatively frequent, even if outcrossing rates exhibit a bimodal distribution (see Fig 2). Also genetic variations in selfing rates among close populations have been found (Bixby and Levin 1996; Cheptou et al. 2002) which suggests that mating systems respond quickly to selection. This implies that transient states could not be observed in natural populations in the case where disruptive selection operates. This intense debate in the 1990's has allowed the rise of new theoretical models discussing classical assumptions and demonstrating that the stability of mixed mating systems was possible.
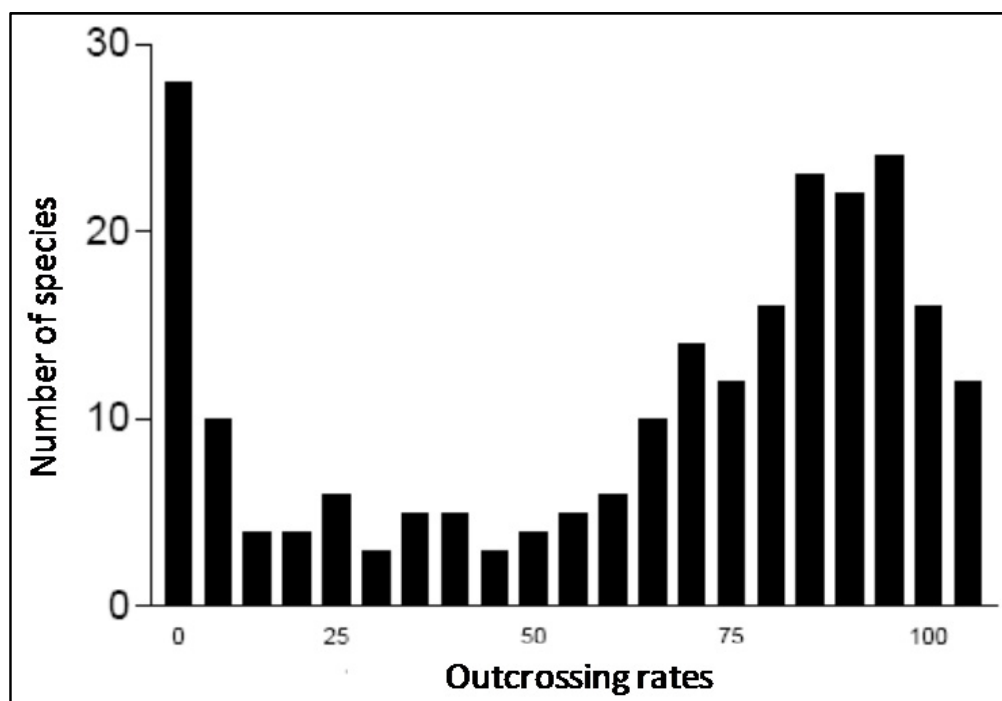

Fig. 2. Distribution of outcrosing rates in flowering plants (data from Vogler and Kalisz, 2001). Data courtesy of Susan Kalisz, University of Pittsburgh, USA.

3. Population genetics of self-fertilisation

3.1 Population genetics consequences of self-fertilization

Because self-fertilization defines gene transmission rules of individuals in a population, it has a predominant influence on major parameters of population genetics such as migration, recombination, selection and drift. As a consequence of mendelian segregation, heterozygotes produce half homozygotes each generation by self-fertilisation. At equilibrium, allelic diversity will be distributed among various classes of homozygotes under complete selfing, thus departing to the classical Hardy-Weinberg equilibrium under random mating. In a quantitative genetics perspective, selfing substantially affect the distribution of additive

variance in a way that increases between-lines genetic variance and decreasing within line genetic variance as a consequence of the purity of the lines (Falconer, 1981). Self-fertilization will also modify the role of genetic drift in populations as consequence of the joint sampling of gametes. In diploid populations, male and female gametes are sampled independently under random mating, which results in an effective population size of twice the number of individuals. Because both female and male gametes are sampled together in individuals of a complete selfing population, the effective populations the population is only half the population size under random mating. The direct consequence is the more pronounced effect of drift in selfing populations resulting in a potential reduction of genetic diversity. Selfing can also affect genetic diversity by cancelling gene flow by pollen, which often disperse farther than seeds (Ghazoul, 2005), and thus increasing genetic drift. Biologists have analyzed the impact of selfing on genetic diversity and its distribution, thanks to the intensive use of neutral genetic markers in plants, or on the maintenance of additive genetic variance in quantitative traits. Using more than 250 plant species, Duminil et al (2009) showed that self-fertilisation increases among-population structure (Fst) and this effect is likely due to both its impact on gene flow (reduced pollen flow under selfing) and the reduced population sizes caused by inbreeding itself. Curiously, pollination modes, which are expected to modulate pollen gene flow, did not impact population structure.

Because selfing impacts the distribution of quantitative genetic variance of traits, one would expect the heritability of traits to be reduced under selfing, which could affect the evolutionary potential of populations. While early results have tended to support this trend (Clay and Levins, 1989), a rigorous analysis found no relationship between the partitioning of genetic variance within and among families and population selfing rates. Thus, empirical data does not support the idea that selfers respond less to selection than outcrossers.

3.2 The genetic basis of inbreeding depression

Inbreeding depression is defined has the reduction of fitness consecutive of one or several generations of inbreeding (*e.g.* selfing). This is a ubiquitous force in living organisms that has been documented in various organisms such as human, insects, birds, fish, crustaceans, ferns and higher plants (Cheptou and Donohue, 2011). Historically, the observations that inbred individuals are less fit than outbred ones have been documented more than 200 years ago by Thomas knight (1799) on vegetables. Darwin (1876) devoted an entire volume documenting the deleterious effects of inbreeding in 57 species. Interestingly, he anticipated a number of evolutionary trends, such as the relationship between inbreeding depression values and mating system of populations, which was to be confirmed by population genetics theory hundred years later. Beyond the empirical results reported in various organisms by empiricists, the rise of population genetics in the second half of the twenty century has allowed to develop a population genetics theory of inbreeding depression and to capture its genetic basis. The question of inbreeding depression can be formulated as follows: what are the genes characteristics required for fitness values to decrease as a consequence of increased homozygosity in a population? The answer can be characterized by considering a single locus encoding for any quantitative trait in a population and analyse the immediate consequence of inbreeding on fitness in this population. In a general way, we can write:

	AA	Aa	aa
Frequencies	D	H	R
Fitness values	*1*	*1-h s*	*1-s*

The mean population fitness can be easily deduced as $\overline{w_1} = 1 - s(h\,H + R)$. $\overline{w_1}$ can be compared to the mean population $\overline{w_2}$, the fitness after inbred mating, say one generation of selfing. After a bit of calculations, it can easily be shown that $\overline{w_2} = 1 - s(\frac{H}{2}(h+1) + R)$. We conclude that inbreeding depression occurs if $\overline{w_1} - \overline{w_2} = \frac{sH}{2}(\frac{1}{2} - h)$ is positive i.e. if $h < 0.5$. Two classical hypotheses satisfying this condition have been defined (Charlesworth and Willis, 2009). The partial dominance hypothesis (0<h<1/2) considers that partially recessive deleterious alleles (s>0) arise by recurrent mutations. The overdominance hypothesis considers that heterozygotes are fitter than both homozygotes (h<0). While overdominant alleles will be maintained at intermediate frequencies in populations as the result of balancing selection, deleterious alleles are typically expected to be at low frequencies as the result of mutation/selection balance. The relative importance of both hypotheses have been subject to intensive debate in the 1970's (Crow, 1993) but it is now admitted that the partial dominance hypothesis is the major source of inbreeding depression (Charlesworth and Willis, 2009). Empirical studies measuring mutation parameters have concluded that the rate of new deleterious mutation lies in the range of 0.1 to 1.0 per zygote per generation, and the reduction of fitness lies between 1 and 10% at homozygous state in metazoans (Schoen, 2005).

Whether natural populations should suffer from inbreeding depression or not depends on whether populations are regular inbreeders or not. While complete outcrossing is often viewed as a way to avoid inbreeding depression, the magnitude of inbreeding depression is in itself (measured as the difference in fitness in selfed and outcrossed offsprings) is not constant and vary with the inbreeding regime as a consequence of mutation selection balance in the populations. Importantly, the way the magnitude of inbreeding depression varies with the selfing regime under the partial dominance hypothesis and under the overdominance hypothesis is the exact opposite. If inbreeding depression is mainly due to overdominant alleles, inbreeding depression increases with selfing as a consequence the higher proportion of homozygote loci in inbred lines. On the contrary, if inbreeding depression is caused by deleterious alleles, inbreeding depression is expected to decrease with inbreeding regime. The reason is that regular inbreeding will expose recessive mutations to selection by producing homozygotes and thus lower the frequencies of deleterious alleles. This process known as the "purging process" has been central in population genetics studies analyzing inbreeding depression. Influential theoretical studies in the 1980-90's have modeled the expected relationship between inbreeding depression and selfing rates as a function of mutations parameters *s, h* (Lande and Shemske, 1985; Charlesworth et al, 1990). This has stimulated a large number of empirical studies attempting to measure inbreeding depression for various organisms with contrasted mating systems. The general trend in the data is mixed (see section 4). In a plant review, Husband and Schemske (1996) found a negative relationship between inbreeding depression and self-fertilisation, though weak, in accordance with expectations. However, a more complete compilation of data did were not able to find a significant decrease of inbreeding depression

with selfing (Winn et al, 2011). Analysing specifically the possibility of purging in populations, Byers and Waller (1999) conclude that purging is an inconsistent forces in natural populations, thus casting doubt about the general applications of theoretical "purging" studies to natural populations.

3.3 Inferring mating system parameters in natural populations

How population genetics parameters vary with inbreeding and more specifically self-fertilization has been central in population genetics theory until its foundation (Malécot, 1948). The intensive use of polymorphic neutral markers (allozymes, microsatellites,…) in the last twenty years has allowed to estimate population selfing rates (and sometimes other parameters related to mating system) in natural populations. Classical methods use information related to homozygosity at one or several loci to infer selfing rates.

3.3.1 Inference from deviation to Hardy Weinberg equilibrium

The most popular method and probably the simplest one is based on the genotypic deviation to hardy-Weinberg equilibrium. Consider a simple locus with two alleles (A, freq. p; a freq. $1-p$). The genotypic frequencies can be written as follows:

	AA	Aa	aa
Hardy-Weinberg:	p^2	$2pq$	q^2
Deviation from H.W.:	$p^2 + pq\,F_{is}$	$2pq\,(1-F_{is})$	$q^2 + pq\,F_{is}$

Under the assumption that heterozygotes deficiency is caused by selfing as the unique source of inbreeding (*e.g.* a large population of partial selfers), the equilibrium value F_{is} is related to selfing rate as $F_{is} = \frac{s}{2-s}$, where s is the population selfing rate. Thus, selfing rates can be easily inferred from genotyping a sample of individuals in a population. While this method is simple, F_{is} can be potentially inflated by other sources of inbreeding (biparental inbreeding) thus biasing upward the estimated selfing rates.

3.3.2 Inference from progeny array analysis

Another classical method to estimate selfing rates is based on the genotypic analysis of progenies. In plants, this can be easily achieved by sampling seeds on a mother plant. The genotypic composition of progeny results from medelian segregation under selfing and the random encounter of maternal alleles with alleles from the pollen pool under outcrossing. Thus, genotyping both the mother and the progeny allows to estimate selfing rates. Interestingly, this method allows inferring not only population estimates but also family estimates providing that sample sizes are adequate. Also, this method allows estimating additional parameters such the number of paternal parents in the outcrossed fraction *i.e.* if outcrossed progeny are full sibs or half sibs.

The MLTR program (Ritland, 1990, Ritland, 2002) is based on this method to infer selfing rates and additional parameters using maximum likelihood estimates. The procedures allows to distinguish the various sources of inbreeding: self-fertilisation and mating among related individuals (biparental inbreeding), through the comparison of multi-locus

segregation and single-locus estimates. While this method provides relevant mating system parameters, its main drawback is that sample size must be large for good statistical inferences.

3.3.3 Inference from identity disequilibria

The two previous methods are based on the link between selfing and heterozygosity. While it is undoubtedly the most intuitive effect of selfing, it is important to recall that partial selfing not only creates heterozygote deficiencies but also creates correlations in heterozygosity among different loci, a process known as identity disequilibria (Weir & Cockerham 1973). Identity disequilibrium is the relative excess in doubly heterozygous genotypes (Weir & Cockerham 1973) for pairs of loci. The identity disequilibrium provides an additional source of information related to selfing available from neutral markers independent from heterozygotes deficiency. The main interest of this method is that, contrary to the previous method, identity disequilibria is relatively insensitive to the non-detection of heterozygotes (null alleles), which is a quite common scoring artifact in the use of molecular markers (e.g. microstaellites). David et al (2007) developed the Rmes software using identity disequilibria to estimate selfing rates. Interestingly, using several dataset, they showed that Fis tends to overestimate selfing rates as a consequence of putative scoring artifacts.

4. Plant mating system evolutionary theory: A long story

Darwin was the first of a long series of evolutionary botanists interested in mating system evolution (Darwin, 1876, 1877). At the heart of this approach was the central role of floral biology and pollination processes. As a consequence, the "pollination biology" tradition emphasizes on the role of ecological contexts. Population genetics, specifically the seminal work of Ronald Fisher, has changed the perspective by considering self-fertilisation as a gene transmission rule *i.e.* by emphasizing on intrinsic components of mating system biology, at the expense of ecological context in which mating system takes place. At the same time, population genetics has laid the foundation for a proper measure of fitness, which has paved the way for modeling evolutionary processes and capturing the role of various factors affecting the evolution of selfing.

4.1 Darwin' tradition versus Fisher's tradition

The first evolutionary principle for the selective advantage of selfing was proposed by Darwin (1876) who considered self-pollination as the mean of ensuring seed set either when outcrossing partners are absent or when pollinators are scarce. This has been referred to as the ''reproductive assurance hypothesis'' (Jain 1976). In the 1950's, Darwin's ideas have been largely popularized by the famous botanist Herbert Baker, who refined the arguments by proposing that such pollen limitation is likely to occur in species subject to recurrent colonization such as island colonizers, weeds or species on their limit range (Cheptou, 2011). Specifically, Baker (1955) proposed that: ''With a self-compatible individual a single propagule is sufficient to start a sexually reproducing colony (after long distance dispersal), making its establishment much more likely than if the chance of the two self-incompatible yet cross-compatible individuals sufficiently close together spatially and temporally is

required''. Thus, reproductive assurance arguments focus on seed production under various ecological contexts *i.e.* on demographical properties of selfing.

While reproductive assurance is quite intuitive, Ronald Fisher highlighted another selective advantage of selfing based on gene transmission mechanisms (Fisher 1941) that defines the automatic avantage of selfing or the cost of outcrossing (Jain, 1976). He argued that genes favoring selfing (mating system modifiers) are automatically selected because they benefit from a 50% transmission advantage compared to ''outcrossing'' genes. This can be formally demonstrated using single locus model (see Annex 1). This can also be intuitively understood by considering that a selfer will transmit 2 copies of its genes in each of its selfed seeds and 1 copy by siring ovules by outcrossing in the population while an outcrosser will transmit only 1 copy in each of its seeds plus 1 copy by siring ovules by outcrossing in the population. It results in a 3:2 advantage for the selfer over the outcrosser (Figure 3). The cost of outcrossing is analogous to the cost of sex in gonochoric species (Maynard-Smith, 1978).
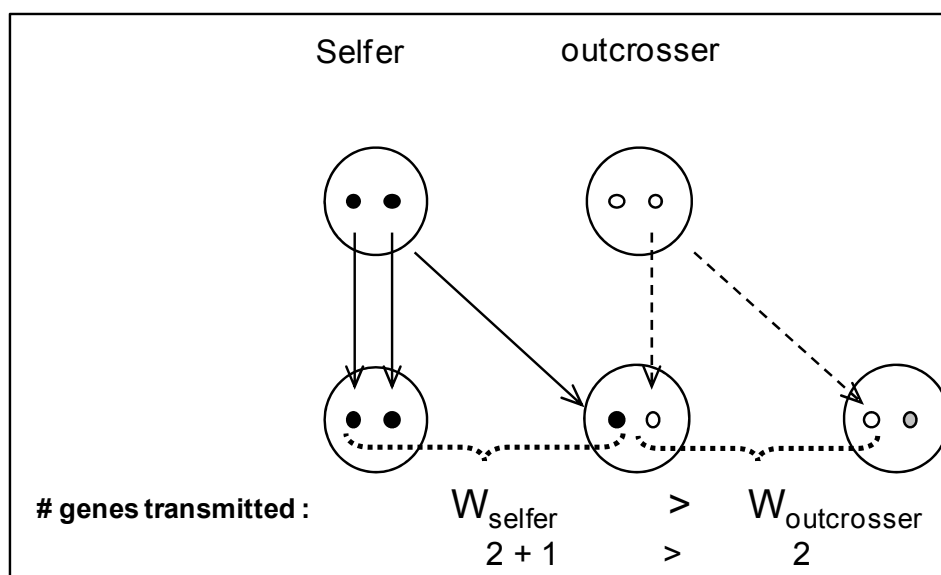

Fig. 3. Transmission pathways from parent to offspring are shown as arrows; solid arrows represent gene transmission to progeny by the parent capable of self-fertilization, while dashed arrows represent transmission pathways for the outcrossing parent. Fitness is expressed as the number of genes transmitted to the progeny via pollen and ovules. Assuming that the number of pollen grains produced is assumed to be large relative to the number of ovules (Bateman's principle), it results that a selfing genotype enjoy a 50% advantage in gene transmission relative to a outcrossing genotype.

While the two selective advantages of selfing described here are often presented without much details in the literature, it is important to note that they are not completely consistent with regards their underlying concept of fitness. The reproductive assurance argument is founded on the demographic advantage of selfing (seed production). Conversely, in the population genetic framework, the advantage of selfing is based on the number of genes transmitted. While the fitness metric defined by Fisher is relevant for evolutionary purpose, seed production is just a component of fitness but does not equate to the number of gene transmitted. In other words, reproductive assurance only considers the female component of fitness. Behind this discrepancy, pollination biologists have sometimes considered selfing

advantage as the advantage of producing more seed (i.e. maternal contribution only) whereas fitness in the population genetics framework results from male and female contribution. In many studies (see for instance Klips and Snow, 1997), selfing advantages in Baker's arguments is based on a wrong fitness metric that does not match with the classical fitness metrics in mating system theory, which casts doubt about evolutionary inferences in such studies.

The major contribution of early population geneticists has been to define an unbiased metrics to measure the selective advantage of selfing, which has paved the way to build general evolutionary model for self-fertilisation.

4.2 Modeling the evolution of self-fertilization

Basically, the three general components: pollen limitation, the cost of outcrossing and inbreeding depression are the cornerstones of most theories for the evolution of self-fertilization. Lloyd (1979, 1992) was the first to model the evolution of self-fertilisation by including these three factors. Here, I present the general framework inspired from Lloyd work that allows deriving general results concerning factors affecting the evolution of selfing. For simplicity, I do not consider a diploid determinism for selfing but a phenotypic formalism, which, for our purpose, does not entail any changes in biological conclusions. Consider a large population of annual plants in which two phenotypes P_1 and P_2 differing for their mating strategies occur. Let be f_1 and f_2 be their respective frequencies. The fitness of each type can be derived as the sum of three components: selfed seeds, outcrossed seeds and pollen exported to outcross ovules in the population. The variables and the parameters of the model are described in Table 2.

Variables	# selfed ovules	# outcrossed ovules	# pollen grains (export)
Phenotype 1	y_1	x_1	p_1
Phénotype 2	y_2	x_2	p_2

Table 2. Variables used in model for the evolution of self-fertilisation (from Lloyd, 1979, Lloyd, 1992).

The deleterious effect of self-fertilisation is captured by the inbreeding depression parameter $\delta = 1 - \frac{w_{self}}{w_{out}}$ where w_{self} is the fitness of inbred progeny and w_{out} is the fitness of outbred progeny. The fitness component *via* pollen export requires to measure the relative succes of a pollen grain in the population. According to the notations, the pollen pool is $(f1p1 + f2p2)$ and the total number of ovules available for outcrossing is $(f1x1 + f2x2)$. Thus, the probablity for a pollen grain to fertilize an ovule is:

$$P = \frac{1}{(f1p1 + f2p2)} \cdot (f1x1 + f2x2) = \frac{\bar{x}}{\bar{p}}$$

Where $\bar{x}$ and $\bar{p}$ are the mean number of ovules per individuals devoted to outcrossing and the mean number of pollen grain exported repectively. Considering that inbreeding depression lowers the survival of selfed offrpsrings by a factor (1-δ), the fitness of the two phenotypes can be derived as:

$$W_1 = 2(1-\delta)y_1 + x_1 + p_1\left(\frac{\bar{x}}{\bar{\bar{p}}}\right)$$

$$W_2 = 2(1-\delta)y_2 + x_2 + p_2\left(\frac{\bar{x}}{\bar{\bar{p}}}\right)$$

At this stage, it is important to note that both fitness depend on each other *via* pollen export, which means that the selective advantage of selfing is frequency dependant. In a general way, phenotype 2 is favored over phenotype 1 if $w_2-w_1>0$, i.e :

$$2(1-\delta) > \left(\frac{x_1-x_2}{y_2-y_1}\right) + \left(\frac{p_1-p_2}{y_2-y_1}\right)\frac{\bar{x}}{\bar{\bar{p}}}$$

$$D_\female \qquad D_\male$$

Decomposing the inequality in such a way allows to analyse the different components of selection on selfing, namely: inbreeding depression (at the left-hand side), the functional relationship between the outcrossing x and selfing y ($D_\female$) and the functional relationship between pollen export p and selfing y ($D_\male$) at the right-hand side. According to Lloyd (1992), the two right-hand side components have a significant biological interpretation. First, the way the outcrossing fraction, x, varies with the increase of selfing ($D_\female$) defines the seed disounting and measures to what extent the outcrossing fraction and the selfing fraction compensate each other. In the hypothetical case where very few ovules are fertilised as the result of low pollination, increasing selfing may have no effect on reducing the outcrossing component ($D_\female =0$). On the opposite, if all the ovules are fertilised, the selfing fraction and outcrossing fraction counterbalance exactly each other ($D_\female=1$). The seed discounting parameter allows to estimate to what extent selfing increases seed production and thus provides a measure of reproductive assurance. Analogously, the pollen discounting parameter ($D_\male$) defines how increasing selfing affects pollen export. Fisher's automatic advantage (see figure 3) implicitly assumes that selfing strategy has no effect on pollen export *i.e.* there is no pollen discounting. As soon as pollen devoted to selfing decreases the amount of pollen export, the pollen discounting is positive thus reducing the 50% advantage of selfing described by Fisher (1941).

The model presented here allows to explore the role of parameters under various scenarios. The simplest case considers that every seed is either outcrossed or selfed, which leads to functional relationship: $x=1-y$. Also, if the number of pollen grains is large compared to the number of ovules (Bateman's principle) and thus pollen export is independant from selfing (*i.e.* $p_1=p_2=\bar{p}$), an inscrease in selfing rate is favored if:

$$\delta < \frac{1}{2}$$

In this context, inbreeding depression values lower than one half select for selfing whereas complete outcrossing is expected if inbreeding depression is higher than one half. I now use the same basic assumptions but I consider that only a fraction e of ovules devoted to outcrossing are actually fertilised because of reduced pollination activity. In this case, an

inscrease in selfing rate is favored if $\delta < 1 - e / 2$ *(e<1),* which means that increase of selfing is easier under pollen limitation. This model has been very influential in mating system evolution and its conclusions are twofold. First, inbreeding depression values is sufficient to predict the direction of selection on selfing and second, it predicts that only complete selfing and complete outcrossing are evolutionary stable. As a consequence, mixed mating system cannot be considered as evolutionary stable in this framework.

4.3 The central role of inbreeding depression

The model exposed in 4.2 has stimulated much theoretical and empirical works on inbreeding depression. On theoretical perspective, much work has been devoted to the joint evolution of self-fertilisation and inbreeding depression. Given the genetic basis of inbreeding depression discussed in 3.2, population genetics models in the 1990's have analysed the evolution of selfing when inbreeding depression is free to evolve as a consequence of mutation/selection balance. These models have however shown that the conclusions with regards to the evolution of selfing were unchanged and the threshold of 0.5 still holds (Lande and Schemske, 1985). Interestingly, these models have allowed to predict the shape of inbreeding depression and genetic load as a function of the population selfing rates (see section 3). While the first population genetics models assumed a complete independence between fitness loci and selfing rate modifier loci, a few models have examined the joint evolution of loci affecting fitness and those affecting mating system. Holsinger (1988) was the first reveal that a more complex evolutionary dynamics evolves in this context. An important conclusion is that the precise 0.5 inbreeding depression threshold no longer holds. There are two reasons for this complex dynamics (Holsinger, 1991). First, there is a tendency for heterozygotes genotypes at one locus to be associated with heterozygotes at the other loci. Second, there is tendency for mating system modifier increasing diversity of fitness offspring to be associated with high fitness genotypes. This implies that an average inbreeding depression value over the whole population is not sufficient to predict the evolutionary outcome and that family inbreeding depression needs to be considered.

In line with the intense theoretical work on inbreeding depression, empiricists have produced a major contribution to inbreeding depression by providing an important corpus of data, using hermaphroditic plants but with contrasted selfing rates. These experiments are typically performed by crossing experimentally plants through outcrossing and selfing (hand pollination) and measure fitness traits on inbred and outbred progenies in order to estimate inbreeding depression. The motivation for such studies was twofold. First, in an evolutionary perspective, inbreeding depression values give information about its consistence with mating system in the populations in the context of the classical model presented in 4.2. Second, the relationship between inbreeding depression values and selfing rates among populations or among species allow inferring the genetic basis of inbreeding depression (overdominance hypothesis *versus* partial dominance hypothesis). In particular the possibility of purging has been at the heart of many studies.

Figure 4 represents the compilation of nearly all inbreeding depression values in plants reported in the literature. This figure shows that the relationship with selfing is not clear-cut and the high variation of inbreeding depression values for a given selfing rate suggests that other factors affect inbreeding depression values.
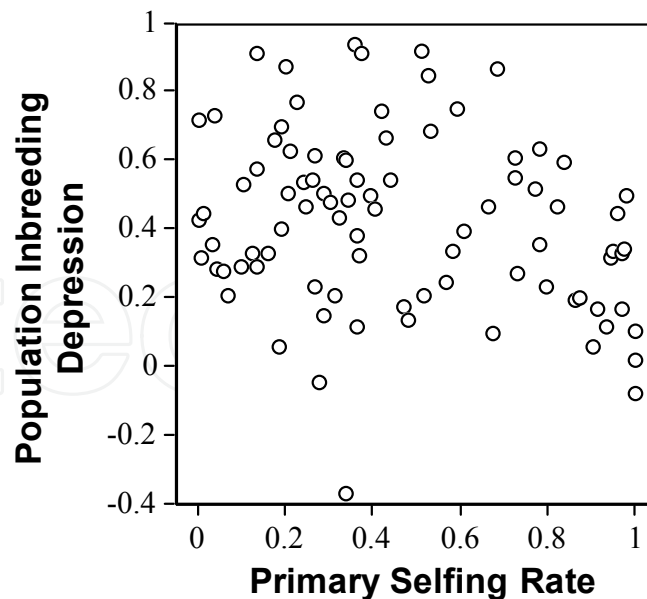
Fig. 4. Relationships between experimental inbreeding depression and primary selfng rates (estimated from microsatellites markers) in 87 plant populations (data taken from Winn et al, 2011).

5. Towards a synthesis between ecology and population genetics

Population genetics theory in the 1980's and 90's has provided a general framework for analyzing the evolution of selfing rates. While the ecological tradition of mating system is ancient and influential, the approach has been rather empirical with little mathematical formalism. Thanks to fruitful confrontation between theory and data, the last twenty years have given rise to a more integrated view, taking into account genetic and ecological factors affecting mating system. Below, I give three directions where the synthesis has been particularly fruitful.

5.1 Pollination biology and gene transmission rules

Pollination biologists have for a long time described with many details the patterns of pollen transfer among plants. Pollen transfer involves various such as wind, water of animals. Insect pollination has been by far the most studied pollination processes. Specific plant adaptations in animal-pollinated plants have been well-studied. A well studied example is heterostyly where two (or three) floral designs differing in the spatial arrangement of female (pistil) and male (stamen) organs. This is typically viewed as an adaptation to the morphogy of insects implying that one type can only mate with the other in the population (Barrett, 2002). In such a system, the pollen removed on plant type 1 sticks in a specific place on insect body and is deposited on the pistil of plant type 2 (and vice versa). In light of Fisher's argument described in fig 3, pollination biology of species may imply that pollen export is dependent on mating strategies which may affect the automatic advantage of selfing. The example of cleistogamous plants widespread in flowering plant (Lord, 1981) provides a comprehensive view of the problem. In such a plant producing both open (chasmogamous) and close (cleistogamous) flowers, selfing rates is mediated by cleistogamy. Because cleistogamy prevents any possibility of pollen export, increasing selfing rates implies a

direct reduction of pollen export *i.e.* complete pollen discounting (see 4.2). It results that the automatic advantage of selfing no longer works in cleistogamous plants. This example highlights that patterns of pollen export are fundamental to capture Fisher's advantage of selfing. This pollination consideration has led to a new class of evolutionary models analyzing the role of pollen discounting in the selection of selfing. In particular, Holsinger (1991) proposed a very elegant and intuitive evolutionary model, the "mass-action model" based on simple pollination mechanism. In his model, selfing rates simply results from the relative portion of self-pollen and outcross pollen deposited on the stigma *i.e.*

$$s = \frac{\# \ self \ pollen}{\# \ self \ pollen \ + \ \# \ outcross \ pollen}$$

Thus, changing the selfing strategy for a plant consists in modifying the exportation of pollen. A fully outcrossing population is a population where all the genotypes export their pollen whereas a full selfing population is a population where all the genotypes do not export their pollen. Because the model assumes compensation between pollen exported and pollen devoted to selfing, pollen discounting is at the heart of the model. The evolutionary dynamics is interesting and allows the evolution of stable mixed selfing on a large range of parameters, which the classical model did not predict. The reasons for such dynamics are quite intuitive. In a full outcrossing population, it is easy to demonstrate that keeping a small portion of its pollen on its own stigmas may be advantageous, if pollen export is costly (pollen lost during travel). In full selfing population (no pollen export), it is advantageous to export a small fraction of its pollen to avoid self-pollen competition on the stigma. These two lines of arguments indicate that evolutionary stable mixed selfing is possible under mass action assumption. More generally, the discussion around the notion of pollen discounting has allowed to reinterpret the automatic advantage of selfing in the context of pollination biology. It allowed to aknowledge that the 50% advantage, often taken for granted in early studies is not a fixed parameter but a consequence floral biology such as the pollen/ovule ratio (Cruden, 1977), itself subject to natural selection.

5.2 The ecology of inbreeding depression

If inbreeding depression experiments have been motivated by theory, an unexpected experimental issue has provided a new direction for the role of inbreeding depression in mating system evolution. Though measuring inbreeding depression may seem simple at first sight, it has revealed that environmental conditions in which plants grow were determinant. While the theory did not reject this idea a priori, the fact that empiricists had no conceptual framework to interpret their results lead some authors to consider it a nuisance or a side effect that should avoided (Barrett and Harder, 1996). Yet, this phenomenon has been identifed by early biologists. In 1876, Darwin wrote:

> *The result was in several cases (but not so invariably as might have been expected) that the crossed plants did not exceed in height the self-fertilized in nearly so great a degree as when grown in pairs in the pots. Thus with the plants Digitalis, which competed together in pots, the crossed were to the self-fertilized in height as 100 to 70; whilst those which were grown separately were only as 100 to 85. Nearly the same result was observed with Brassica. With Nicotiana the crossed were to the self-fertilized in height, when grown extremely crowded*

together in pots, as 100 to 54; when grown much less crowded in pots as 100 to 66, and when grown in the open ground, so as to be subjected to but little competition, as 100 to 72.

Darwin's observation of the environmental dependence of inbreeding depression has since been reported in diverse organisms in experimental studies (Keller & Waller, 2002; Armbruster & Reed, 2005). Interestingly, direct estimates in natural populations based on the change in inbreeding coefficient during plant life cycle have also revealed that inbreeding depression may vary until four times from one year to the other (Dole and Ritland, 1993). These results ask the question of whether environment-dependant change the evolutionary dynamics of self-fertilisation or if it can be considered as a side-effect. Cheptou and Donohue (2011) have discussed this problem and conclude that environment-dependant inbreeding depression is worth to be considered in an ecological and evolutionary perspective. In this context, the relevant question is to identify the pattern of environment-inbreeding depression. Beyond the simple stress dependence of inbreeding depression (Armbruster and Reed, 2005) it is important to capture what causes the environment-dependence. For instance Cheptou and Schoen (2003) have shown experimentally in the genus *Amsinckia* that the identity of competitors was fundamental to predict inbreeding depression in density-regulated populations. By manipulating the proportion inbred and outbred individuals in competing stands (at constant density), Cheptou and Schoen (2003) reported that the magnitude of inbreeding depression is highly sensitive to the inbred/outbred proportions (frequency-dependence). Since this proportion is the direct consequences of population selfing rates in natural populations, the authors conclude that taking into account the environmental feedback caused selfing rates is crucial to capture the selective effect of inbreeding depression on selfing (see also Cheptou and Dieckmann, 2002). Interestingly, taking into account this effect gives a consistent picture for the evolution of selfing in *Amsinckia douglasiana* (Cheptou and Schoen, 2003).

In a theoretical model, Cheptou and Mathias (2001) consider a simple ecological scenario where inbreeding depression vary from year to year because of random environmental variation ($Pr(\delta=\delta_1)=p$, $Pr(\delta=\delta_2)=1-p$). In the context of inbreeding depression/automatic advantage of selfing (see 4.2), the authors demonstrated the evolutionary stability of mixed selfing rates, and found that the evolutionary stable selfing rate is:

$$s^* = \frac{1 + 2\delta_2(p-1) - 2\delta_1 p}{(1-p)\delta_1 - 2\delta_1\delta_2 + \delta_2 p}$$

So far, the evolutionary models including environment-dependant inbreeding depression have been phenomenological models (see however Porcher et al, 2009), with little interest to the genetic basis of environment dependant inbreeding depression. Ronce et al (2009) analyzed a quantitive genetics model where local adaptation occurs. Assuming several environments where optimal phenotypes differ, they showed that inbreeding depression can vary as a function of the distance between the population mean breeding value for a trait under stabilizing selection and the optimal phenotype. In Ronce et al (2009) model, inbreeding depression is a function of the genetic variance for a trait under selection and the strength of stabilizing selection. An important result is that inbreeding depression is always lower when the population is less adapted to its environment compared with well-adapted populations.

More generally, the rise of environment-dependant inbreeding depression has changed the perspective regarding the evolution of selfing. Experimental studies analyzing inbreeding depression in 2010's now take into account environment in their designs. This phenomenon challenges the applicability of mutation–selection balance models where the deleterious effects is fixed. To what extent is inbreeding depression caused by unconditionally deleterious alleles or by loci under balancing selection? This problematic revitalizes the question of the genetic basis of inbreeding depression and the maintenance of diversity for alleles contributing to inbreeding depression in natural populations.

5.3 Mating system and metapopulation dynamics

In Baker's view, the importance of space and spatio-temporal heterogeneity is at the heart of the evolution of selfing. Indeed, by considering colonization processes as determinants in pollination services, Baker points out that not only population processes are relevant in mating system evolution but also among population processes *i.e.* metapopulation processes. Curiously, most of mating system models have assumed evolutionary processes in a single population in a stable environment until recently. There are two reasons for this fact. First, population genetic theory has implicitly adhered to the classical assumption of a unique population. Second, the fitness metric considered in Baker's arguments does not match with classical mating system theory (see 4.1), which does facilitate the mix between the two traditions.

Two recent models (Pannell and Barrett, 1998; Dornier et al., 2008) have however provided a mathematical formalization for Baker's law where pollination is related to the number of mates. Hence, their assumption is close to Baker's first argument: 'with a self-compatible individual a single propagule is sufficient to start a sexually reproducing colony, making its establishment much more likely than if the chance growth of two self-incompatible yet cross compatible individuals sufficiently close together spatially and temporally is required'. While Pannell and Barrett (1998) analysed the advantage of colonization by a single individual allowed by selfing, Dornier et al. (2008) considered a metapopulation model with an explicit Allee effect function and random extinction of patches. Interestingly, Dornier et al. (2008) derived analytically a metapopulation viability criterion that is dependent on the selfing rate. Whereas full out-crossers can form a viable metapopulation, only partial selfers and full selfers are able to recover from very low density at the regional scale. Both models demonstrate the intuitive conclusion that when the number of colonizers is low, selfing is favored. Dornier et al (2008) revealed an interesting feature of the model. Because inbreeding depression affect demography, two colonizers for an out-crosser may have the same probability of arriving in a colonizing area than one colonizer for a selfer. For the same set of parameters, the number of colonizers can increase with outcrossing rate and favor outcrossing, so that mating strategy tends to self-reinforce itself. By disentangling forces at work in Baker's law, these models have demonstrated than selfing is not necessarily selected in colonizing organism, which echoes with empirical data (Cheptou, 2011). Another class of models analyzing the joint evolution of selfing and dispersal traits under stochastic pollination has revealed that the classical colonizer syndrome which assumes that disperser are also selfers is far from being the rule and that the opposite syndrome emerges from metapopulation dynamics (Cheptou and Massol, 2009).

6. Conclusion

In this review, I attempted to present a general overview of the field by focusing on the major trends of the discipline. Mating system biologists have studied plant and its evolution for more than two hundred years. As such, plant mating system has fed one of the most important fields of research in evolutionary biology and it is still very active. Interestingly, this field has many connections with major theme of research in population genetics (role of mutations), pollination biology and even genetic breeding program in agronomy. The important corpus of data coupled with intensive theory allowed us to analyse processes with a large perspective. Plant mating system studies provide an integrative analysis of the processes articulating genetical components in ecological context. To a certain extent, one could say that the domain has reached maturity. Also, the long story of mating system biology has revealed that mating system is a complex trait that cannot so easily summarize by a simple metric such as selfing rate. In this respect, mating system may be consider as a syndrome of traits and considering the joint evolution of integrated traits is an interesting perspective to follow. Finally, enlarging mating system concepts to spatially heterogeneous landscapes is undoubtedly a fruitful approach. Incidentally, it could help to understand how plants will react to changes in pollination environment in the context of pollinator decline.

7. Appendix 1

The automatic advantage of selfing (Fisher, 1941).

Let us consider a biallelic locus coding for selfing rates. For simplicity, consider the allele A encoding for self-fertilisation and the allele a encoding for outcrossing. Assuming that A is dominant over a, this leads to three genotypes (two phenotypes):

	AA	Aa	aa
Selfing rates	100%	100%	0%

(f_1, f_2, f_3 are the genotypes frequencies of AA, Aa, aa respecively and $p = f_1 + \frac{f_2}{2}$ and $q = f_3 + \frac{f_2}{2}$ are the allelic frequencies of A and a respectively).

Let us now consider the genotypic frequencies at the next generations (denoted by f_i'):

$$f_1' = f_1 + \frac{f_2}{4}$$

$$f_2' = \frac{f_2}{4} + f_3.p$$

$$f_3' = \frac{f_2}{4} + f_3.q$$

And thus allelic frequencies at the next generation:

$$p' = f_1' + \frac{f_2'}{2} \quad = \quad f_1 + \frac{f_2}{4} + \frac{f_2}{4} + \frac{f_3}{2} p$$

Variation in the frequency of allele a is :

$$p' - p = f_1 + \frac{f_2}{2} + \frac{f_3}{2} \, p - \left(f_1 + \frac{f_2}{2} \right)$$

$$p' - p = \frac{f_3}{2} \, p$$

Because allelic and genotypic frequencies are by definition positive (or null), this shows allele A encoding for self-fertilisation increases in frequency until fixation, thus demonstrating the automatic advantage of selfing.

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