Autopolyploid establishment under gametophytic self-incompatibility: the impact of self-fertilization and pollen limitation

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Data availability: The simulation models are available at https://github.com/DianeDouet/GSI_autotetraploids

Abstract

Polyploidy is widespread in plants, yet the establishment of neo-polyploids is limited by minority cytotype exclusion (MCE). As polyploidy has been associated with higher selfing rates in empirical studies, a shift from self-incompatibility (SI) to self-compatibility (SC) may help overcome MCE, particularly under gametophytic SI (GSI) with non-self-recognition where an automatic shift to SC is associated with polyploidy. We investigated theoretically the joint evolution of polyploidy and self-compatibility and its impact on tetraploid establishment in initially diploid populations with GSI under different pollen limitation scenarios, and with fixed or variable selfing rates for polyploids. It is shown that, for high pollen limitation scenarios, autotetraploids can invade an initially diploid population only when the selfing rates are high. Under low pollen limitation, the conditions for tetraploid invasion are less restrictive (selfing rates above 0.3). These results apply to scenarios with either fixed or variable selfing rates in polyploids, but in the latter, high mutation rates of the selfing rate are needed for polyploidy to invade. These results suggest that tetraploid establishment is possible through the evolution of selfing, without introducing a non-functional S-allele. However, the conditions strongly depend on the degree of pollen limitation.

Keywords— tetraploids, self-compatibility, unreduced gamete, selfing rate, mating systems

1 Introduction

Polyploidy, characterized by having more than two sets of homologous chromosomes, plays a significant role in speciation and adaptation (Otto and Whitton, 2000; Van de Peer et al., 2021). It is a widespread phenomenon in plants, as about 35% of extant Angiosperms are recent polyploids (Wood et al., 2009) and many Angiosperm families show genomic signatures of ancient polyploidy events (Jiao et al., 2011; Van de Peer et al., 2017). Yet, the establishment of neo-polyploids within diploid populations remains challenging for several reasons. First, polyploidization arises with several costs in neo-polyploid lineages, including genomic instability, mitotic and meiotic abnormalities, and a reduction in fitness (Comai, 2005; Otto, 2007; Doyle and Coate, 2019; Porturas et al., 2019; Clo and Kolář, 2021). In addition to these intrinsic costs of polyploidization, neo-polyploids are also facing a frequency-dependent disadvantage in mating. According to the "minority cytotype exclusion" process, reproductive opportunities for neo-tetraploids are limited due to their scarcity and the fact that fertilization between a diploid and a tetraploid results in triploid offspring that are often non-viable, sterile, or suffer from lower fertility (Levin, 1975; Ramsey and Schemske, 1998; Salony et al., 2025).

These short-term challenges raise the question of the establishment of newly formed polyploids in initially diploid populations. Many theoretical models have been proposed to address this question, offering hypotheses on how neo-polyploids could overcome minority cytotype exclusion (MCE). A first mechanism would be that new polyploid lineages are fitter than their diploid counterparts. This scenario seems unlikely under stable conditions (Porturas et al., 2019; Clo and Kolář, 2021; Salony et al., 2024), but could be reasonable during periods of environmental turmoil (Bomblies, 2020; Van de Peer et al., 2021). Other theoretical models have focused on spatial segregation (by colonizing new habitats or by establishing at the edge of a species range for instance), as it would decrease reproductive interactions among ploidy levels, reducing the disadvantage of the minority cytotype (Baack, 2005; Griswold, 2021; Kauai et al., 2023), and favor rapid local adaptation of polyploids (Zwaenepoel, 2025). Other models have also explored the impact of different factors, such as the rate of unreduced gametes that lead to the formation of polyploids (Felber, 1991; Clo et al., 2022; Gerstner et al., 2024). Finally, another class of models has investigated the evolution of dif-

ferent mating strategies that favors within-cytotype interactions, such as assortative mating (Husband, 2004; Oswald and Nuismer, 2011), asexuality (Van Drunen and Friedman, 2022), or self-fertilization (Gaynor et al., 2025; Griswold, 2021; Rausch and Morgan, 2005). The current article focuses on the last-mentioned mating strategy.

Models investigating the effect of self-fertilization found that an increased selfing rate may facilitate polyploid establishment, as it provides reproductive assurance (Jain, 1976), as well as a mean to reduce incoming gene flow from neighboring diploids (Antonovics, 1968). Therefore, it allows polyploid to escape MCE (Rausch and Morgan, 2005), even though this statement only holds when polyploids are at least as fit as their diploid counterparts (see, for example, Clo et al. (2022)). Indeed, a relationship between self-fertilization and polyploidy is often established (Stebbins, 1950; Barringer, 2007). However, this relationship is still debated (Mable, 2004; Duan et al., 2024). In addition, distinctions between autopolyploids (sets of chromosomes from the same species) and allopolyploids (from different species) should be considered when interpreting these trends, as it leads to different patterns, with allopolyploid species showing higher selfing rates on average than their diploid counterparts, while autopolyploids were found to have significantly higher outcrossing rates than allopolyploids (Husband et al., 2008). Moreover, some studies report that polyploids experience less inbreeding depression than their diploid counterparts, at least in the early stages of establishment, potentially facilitating the evolution of selfing (Lande and Schemske, 1985; Otto and Whitton, 2000; Clo and Kolář, 2022). However, other models predict increased inbreeding depression in polyploids under certain genetic assumptions, such as the dominance of deleterious alleles (Ronfort, 1999). These conflicting predictions highlight the complexity of the relationship between polyploidy and the evolution of mating systems.

A correlation between ploidy level and increased selfing rates could potentially involve a shift from self-incompatibility (SI) to self-compatibility (SC) in association with genome duplication (Mable, 2004). Indeed, about 45% of Angiosperm species possess a functional self-incompatibility system preventing self-fertilization in hermaphrodites (Ferrer et al., 2025). Depending on the type of SI system, the S-phenotype of the pollen is either determined by its haploid S-genotype (gametophytic SI (GSI)) or by the diploid S-genotype of its parent plant (sporophytic SI (SSI)) (Bateman, 1952). SI systems can also be based either on self-

recognition (key-lock system) or on collaborative non-self-recognition (toxin-antitoxin system) (Vekemans and Castric, 2021). Among all SI systems, one is of particular interest when considering the joint evolution of polyploidy and self-compatibility, which is the gametophytic self-incompatibility (GSI) system with collaborative non-self-recognition (Fujii et al., 2016). First, this system is the most common multiallelic SI system, already identified in 7 angiosperm families within the Eudicots (Ramanauskas et al., 2025). Second, a transition from SI to SC can be easily explained in such systems, because genome duplication mechanistically disrupts the SI reaction in heterozygous pollen through a mechanism known as competitive interaction (Lewis, 1947; Charlesworth et al., 2005; Tsukamoto et al., 2005). Indeed, tetraploid individuals mainly produce diploid pollen which, when carrying two different S-alleles, contains all the necessary anti-toxins to enable self-fertilization (Fujii et al., 2016). However, selfing is also associated with increased homozygosity, which could potentially restore functional SI in tetraploids after some generations of self-fertilization, by producing homozygous pollen at the S-locus. The mechanisms underlying GSI are well established (Newbigin et al., 1993; Franklin-Tong and Franklin, 2003; Fujii et al., 2016), and numerous studies have focused on GSI in diploid populations, particularly regarding the conditions that maintain SI (Harkness et al., 2021; Brom et al., 2020) and the diversification of S-haplotypes (Uyenoyama et al., 2001; Gervais et al., 2014; Stetsenko et al., 2023). However, less is known about how SI systems respond to polyploidization. In particular, theoretical models are still needed to better understand how selection can disrupt SI during the formation and establishment of polyploids within diploid populations.

Other factors, such as pollen limitation and inbreeding depression, are considered to influence the shift from SI to SC . Indeed, studies suggest that SC is often favored under pollen-limited conditions (Charlesworth and Charlesworth, 1979; Goodwillie, 1999; Porcher and Lande, 2005). SI can become disadvantageous in such environments, as incomplete reproductive compensation increases its evolutionary costs, a phenomenon known as the "S-Allee effect" (Wagenius et al., 2007; Leducq et al., 2010), though this does not necessarily result in a complete transition to SC (Vallejo-Marín and Uyenoyama, 2004). The joint evolution of self-fertilization and inbreeding depression has also been explored through theoretical models. These studies show that mutations causing significant increases in selfing rates are favored

by selection and can spread through populations despite high levels of inbreeding depression, thanks to the purging of deleterious or lethal mutations (Charlesworth et al., 1990; Lande et al., 1994). However, while high selfing rates provide reproductive assurance under pollen limitation, complete selfing is often not evolutionarily stable (Porcher and Lande, 2005). It can become a disadvantage due to pollen discounting, which in turn promotes the maintenance of intermediate selfing rates in populations (Holsinger, 1991; Johnston, 1998).

This work aims to better understand the consequences of the mechanistic breakdown of GSI with non-self-recognition associated with polyploidy, on the establishment of tetraploid individuals in a diploid population, under different pollen limitation scenarios. Different theoretical approaches are conducted, where the initial population is diploid and tetraploids can appear afterward through the production of unreduced gametes. The first approach is a neutral model consisting of an analytical and a simulation model. In this approach, all tetraploids are considered to be self-compatible, while diploids are strictly self-incompatible, and individuals do not have an assigned fitness, nor an S-genotype (alleles at the S-locus determining self-incompatibility). The second approach is a more complex simulation model with a GSI system with non-self-recognition, and selection according to a quantitative genetic model, in which we investigated how the mechanistic disruption of the GSI system in autotetraploid individuals, associated with changes in the selfing rate (either fixed or able to evolve through time), affects the likelihood of autopolyploid establishment.

2 Models and Methods

The notations and values used in the models and simulations are detailed in Table 1.

2.1 Neutral model

The goal is to determine the selfing rates at which tetraploids invade an initially diploid population, considering a few assumptions. In the following models, tetraploids can appear in an initially diploid population through the production of unreduced gametes only. All diploids are considered to be self-incompatible, while all tetraploids are considered to be self-compatible. Individuals are not identified by their S-genotype, or fitness, but only by their

Symbol	Meaning	Default values
N_{pop}	Population size	1000
p_u	Probability of producing unreduced gametes	0.05
s	Selfing rate (for SC individuals)	
d_n	Frequency of diploids in the population at generation n	
q_n	Frequency of tetraploids in the population at generation n	
L	Number of loci	50
U	Mutation rate per haplotype	0.005
d	Dosage effect	0.67
V_e	Variance of environmental effects	1
ω^2	Strength of selection	1
a^2	Variance of mutational effects on the genome	0.05
U_{SI}	Mutation rate at the S-locus	10^{-5}
U_{SR}	Mutation rate on the selfing rate	$10^{-5}, 10^{-3}, 10^{-1}$
σ^2	Variance of mutational effects on the selfing rate	$0.05, 0.1, 0.25$

Table 1: Summary of notations and values

ploidy level. In short, for fertilization to occur, the only requirement is that both gametes have the same number of chromosomes and are at most diploid.

2.1.1 Analytical model

The frequency of diploids $\tilde{d}_{n+1}$ (resp. tetraploids $\tilde{q}_{n+1}$) in the next generation is determined by calculating the probability of drawing two haploid (resp. diploid) gametes of the population and of them meeting. The following expressions for these frequencies derive from Schematic 1:

$$\tilde{d}_{n+1} = (1-p_u)^2 d_n^2 \tag{1}$$

$$\tilde{q}_{n+1} = p_u^2 d_n^2 + p_u(1-p_u)(2-s)d_n q_n + (1-s)(1-p_u)^2 q_n^2 + (1-p_u)^2 s q_n. \tag{2}$$

As not all gamete encounters result in a new individual for the next generation, these frequencies must be normalized by their sum to ensure that $d_{n+1} + q_{n+1} = 1$.

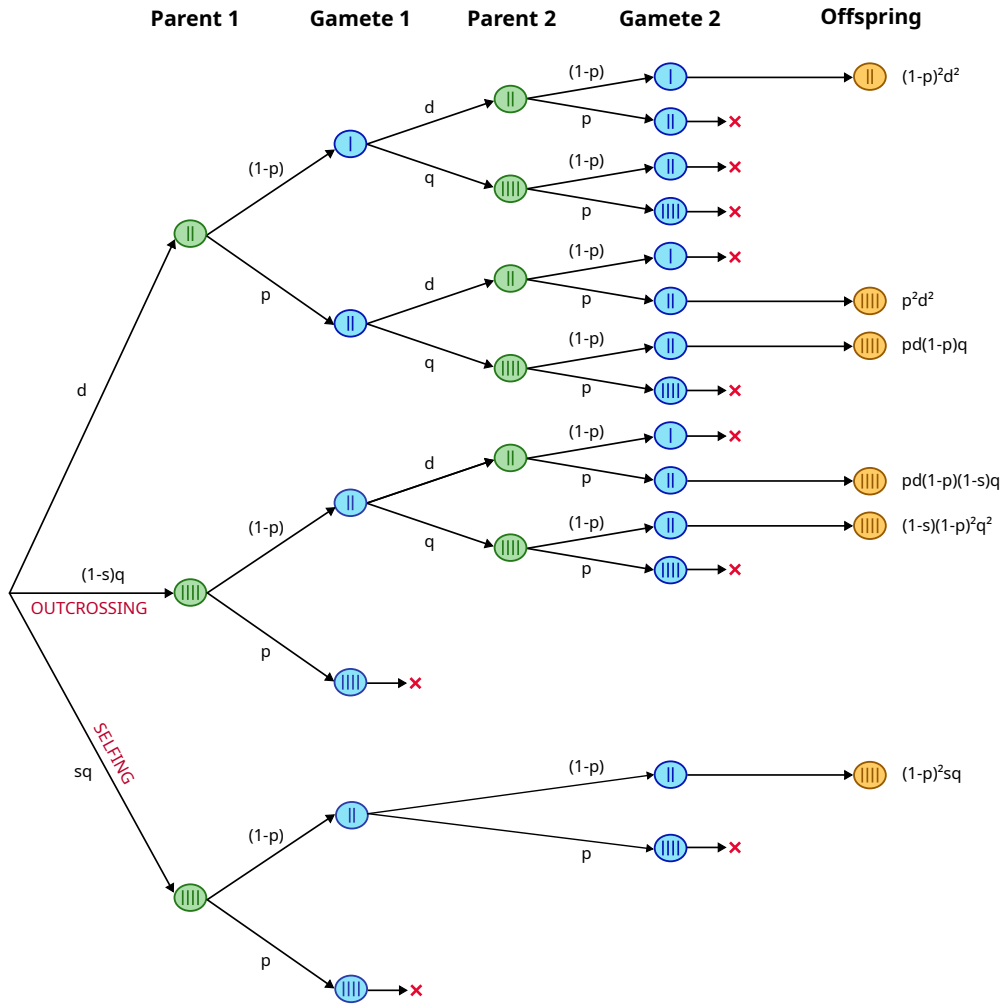

Figure 1: Probability tree to determine the frequencies of diploid and tetraploid individuals in the population at the next generation. A maternal parent is randomly drawn from the population and can be a diploid (obligated outcrosser), an outcrosser, or a selfing polyploid. This parent has a probability p of producing an unreduced gamete, and a probability $(1-p)$ of producing a reduced one. If reproduction occurs through outcrossing, a pollen donor is selected from the population, either diploid or polyploid, with the same probabilities of producing reduced or unreduced gametes. In the case of selfing, the pollen comes from the maternal parent and can be either reduced or unreduced. Reproduction occurs only if both gametes are of the same size and at most diploid. Otherwise, no offspring are produced. This analytical model represents a scenario with high pollen limitation.

2.1.2 Simulation model

A simulation model is developed to observe the frequency of tetraploids at equilibrium within an initially diploid population of constant size N_{pop}.

At the beginning of the simulation, N_{pop} diploid individuals are generated, each characterized only by their ploidy level. The selfing rate is fixed and is the same for each individual throughout the simulation. In each generation, the first parent is randomly selected from the population and has a probability p_u of producing unreduced gametes. At this stage, the first parent can either engage in outcrossing or selfing. If the first parent is diploid, or if it is a tetraploid and the selfing rate is not high enough, a second distinct parent is randomly chosen. This second parent also has a probability p_u of producing unreduced gametes. If the first parent is a tetraploid, selfing is possible as all tetraploids are considered self-compatible here. In that case, selfing occurs with a probability equal to the selfing rate s. A new individual is added to the next generation only if both gametes are at most diploid and have the same number of chromosomes. Otherwise, no offspring are produced, and a new first parent is selected until the desired number of offspring N_{pop} is reached.

2.2 Gametophytic self-incompatibility (GSI) model

2.2.1 General assumptions

A simulation model is built to observe the effects of self-fertilization on the maintenance of tetraploid individuals in a population of constant size N_{pop}. This population is considered to have a gametophytic self-incompatibility system with collaborative non-self recognition. The population is initially diploid, and tetraploid individuals can appear in the population through the production of unreduced gametes. Higher levels of ploidy (such as hexaploids) are not considered here. Each individual has several S-alleles and several chromosomes equal to its ploidy level. Each chromosome contains L loci. The selfing rate is either fixed and the same for all individuals, or it can evolve during the simulation, where each individual inherits the mean selfing rate of its parents.

The fitness of an individual is computed using a quantitative genetic model similar to the

one in Clo (2022). The phenotypic trait value z of an individual is defined as:

$$z = g + e \tag{3}$$

where e is a random environmental effect drawn from a normal distribution with mean 0 and variance V_e, and g denotes the genotype of an individual, calculated as follows:

$$g_{px} = d \sum_{i=0}^{L-1} \sum_{j=0}^{p-1} (g_i^{M_j} + g_i^{P_j}) \tag{4}$$

where $g_i^{M_j}$ (resp. $g_i^{P_j}$) is the value stored in the locus i of the maternal (resp. paternal) chromosome j, p is the ploidy level, and d is the dosage factor accounting for the effect of ploidy on genotypic values (set to 1 for diploids). In other words, the genotype of an individual is the sum of all values stored in its genome, scaled by the dosage factor for polyploid populations.

The fitness W_Z of an individual with phenotype z is given by:

$$W_Z = e^{-\frac{\delta^2}{2\omega^2}} \tag{5}$$

where δ is the deviation of the phenotypic trait value z from the optimal trait value (set to 0), and ω^2 denotes the width of the fitness function, i.e. the strength of selection.

2.2.2 Simulation model

At the beginning of the simulation, N_{pop} identical diploid genomes are created with 2 chromosomes per individual. The value initially stored in each locus is the optimum value 0. S-genotypes are also created, with 2 S-alleles per individual randomly chosen among all possible 100 initial S-alleles. A "potential" selfing rate is also attributed to each individual (in the form of an extra locus), which is the same for all in the case of a fixed selfing rate s, and 0 in the case where the selfing rate can evolve. This selfing rate is only realized for self-compatible (SC) individuals, whereas self-incompatible (SI) individuals are obligate outcrossers independently of the value of the parameter.

The next generation is obtained as follows: a first maternal parent is selected with a probability relative to its fitness W, and produces unreduced gametes with probability p_u, as

all individuals in the population. If this parent is SC, it engages in self-fertilization with a probability equal to its selfing rate. If self-fertilization occurs, a new individual is added to the next generation as long as the gametes have the same number of chromosomes and are at most diploid. If the first parent is SI, it necessarily engages in outcrossing and a distinct paternal parent is selected, as well as its pollen grain. In that case, fertilization occurs only if the fitness of the paternal parent is large enough, and if both parents have equal-sized compatible gametes (in terms of the SI system) that are at most diploid. Otherwise, no new individual is added to the population, and the process is repeated with a new paternal parent until fertilization is achieved or until the set number of attempts with the same maternal plant is exceeded (1, 5, or 20 attempts). The number of attempts mimics pollen limitation scenarios (Vekemans et al., 1998), 1 attempt being the maximal limitation (i.e. one ovule receives a single pollen grain), and 20 attempts modeling low pollen limitation (i.e. one ovule receives up to 20 pollen grains before being rejected). If the number of attempts is exceeded, a new maternal parent is selected, and the process continues until the desired population size N_{pop} is reached. Each parent passes on a gamete to the next generation, and one or two of their S-alleles, depending on the size of the gamete. Crossovers are modeled here as a random permutation between alleles present at the same locus on homologous chromosomes, i.e. free recombination among adjacent loci. The selfing rate of the new individual is the average of the selfing rates of its parents. Next, mutations are introduced within the genome of the new individual formed.

A simulation run consists of three phases in which different types of mutation occur. In the first phase (2 000 generations), all individuals remain diploids and are subject to mutations in their S-genotypes. To be more precise, each S-allele can mutate to one the $k-1$ ($k = 100$) other possible S-alleles with probability U_{SI}. The number of mutations is drawn from a binomial distribution with parameters $(N_{\text{pop}} \times \text{ploidy}, U_{SI})$, and their positions are chosen at random. In the case where the selfing rate can evolve, mutations on an individual's selfing rate are also introduced in the first phase. The number of mutations is drawn from a binomial distribution with parameters (N_{pop}, U_{SR}), and the individuals subject to the mutation are randomly chosen among the population. The additive value of the mutation is drawn from a normal distribution with parameters 0 and σ^2, controlling the speed of evolution toward higher

selfing rates, and selfing rates are restricted to remain between 0 and 1. In the second phase (2 000 generations), mutations to the L fitness loci coding for the quantitative traits under selection can also occur. The number of mutations per haplotype is drawn from a Poisson distribution with parameter U, and their positions in the genome are randomly sampled from the L possible loci. The additive value of this mutation is then drawn from a normal distribution with parameters 0 and a^2. In the last phase (200 000 generations), unreduced gametes are introduced during the reproduction phase with probability p_u, and tetraploid individuals can appear in the population.

At the end of the simulation, the frequency of tetraploids in the population is computed, as well as three other frequencies: the frequency of SC individuals, the frequency of SC pollen (i.e. heterozygous pollen) produced by these individuals, and the frequency of individuals engaging in selfing averaged over the last 10 000 generations. Inbreeding depression is also computed using the following formula:

$$\mathrm{ID} = 1 - \frac{W_{\mathrm{s}}}{W_{\mathrm{oc}}} \tag{6}$$

where W_{s} is the fitness of selfed individuals, and W_{oc} the fitness of randomly outcrossed individuals in the population. Each fitness is computed by sampling 100 individuals in the population. The fitness values of diploids (after reaching an equilibrium, before introducing unreduced gametes in the population) and of tetraploids (at the end of the simulation) are also outputs of the simulation model. In the case where the selfing rate can evolve, the value stored in the locus controlling the selfing rate is observed as well, for diploids and tetraploids.

3 Results

3.1 Neutral model

3.1.1 Analytical results

Equilibria

Using the fact that $d_{n+1} = d_n$ at equilibrium and $q_n = 1 - d_n$ for all n, we find two equilibria

$\{d_{\text{eq1}}, q_{\text{eq1}}\} = \{0, 1\}$ and $\{d_{\text{eq2}}, q_{\text{eq2}}\} = \{d^*, q^*\}$ with:

$$d^* = \frac{3 - 8p_u + 5p_u^2 - s + 3p_u s - 2p_u^2 s + (1 - p_u)\sqrt{\Delta}}{2(2 - 6p_u + 5p_u^2 - s + 3p_u s - 2p_u^2 s)} \tag{7}$$

where $\Delta = 1 - 6p_u + 5p_u^2 - 2s + 10p_u s - 12p_u^2 s + s^2 - 4p_u s^2 + 4p_u^2 s^2$, and $q^* = 1 - d^*$.

The second equilibrium $\{d^*, q^*\}$ is valid as long as $\Delta \geq 0$. If $\Delta < 0$, the only possible equilibrium is $\{0, 1\}$, which implies that tetraploids have invaded the population. Therefore, the threshold selfing rate at which tetraploids invade the initially diploid population is the solution to the equation $\Delta = 0$, which is the following:

$$s_t = \frac{-1 + 5p_u}{-1 + 2p_u} \tag{8}$$

Using the equations above, we obtain the frequency of tetraploids in the population at equilibrium as a function of the selfing rate:

$$q_{\text{eq}}(s) = \begin{cases} 1 - d^* & \text{if} \quad s < \frac{-1+5p_u}{-1+2p_u} \\ 1 & \text{else} \end{cases} \tag{9}$$

To validate the analytical expressions for the threshold selfing rate and the number of tetraploids at equilibrium, we conducted both numerical and analytical analyses for comparison. Figure S1 confirms the accuracy of these expressions.

Stability

In order to determine the stability of these equilibria, we use a standard stability analysis (see e.g. (Otto and Day, 2011, Chapter 5)) and *Wolfram Mathematica*. First, we differentiate the function $f(d_n) = d_{n+1}$. Since we consider discrete generations here, an equilibrium d_{eq} is stable if $|f'(d_{\text{eq}})| < 1$.

Because $f'(0) = 0$ for all values of p_u and s, the first equilibrium $\{d_{\text{eq1}}, q_{\text{eq1}}\} = \{0, 1\}$ is always stable, regardless of the parameter values.

For the second equilibrium, we found that $|f'(d^*)| < 1$ holds when

$$s < \frac{-1 + 5p_u}{-1 + 2p_u} \tag{10}$$

and when the rate of unreduced gamete production p_u remains below 0.2, a range considered realistic for this type of biological system. Note here, that the equilibrium $\{d_{\text{eq2}}, q_{\text{eq2}}\} = \{d^*, q^*\}$ is stable when $s < s_t$, which is precisely its range of validity. In other words, when $p_u < 0.2$, the equilibrium $\{d^*, q^*\}$ is always stable when it exists.

The equilibrium reached by the system depends on the value s encoded at the selfing rate locus and on the initial conditions. Specifically, the equilibrium (d^*, q^*) does not hold when $s \geq s_t$, whereas the equilibrium $(0, 1)$ (corresponding to tetraploid invasion) is always stable. However, since we consider initially diploid populations here, i.e. $d_0 = 1$ and $q_0 = 0$, the system converges toward the equilibrium (d^*, q^*) for selfing rates below the threshold s_t. This suggests that the probability of tetraploid invasion is zero when selfing rates are below this threshold.

3.1.2 Simulation results

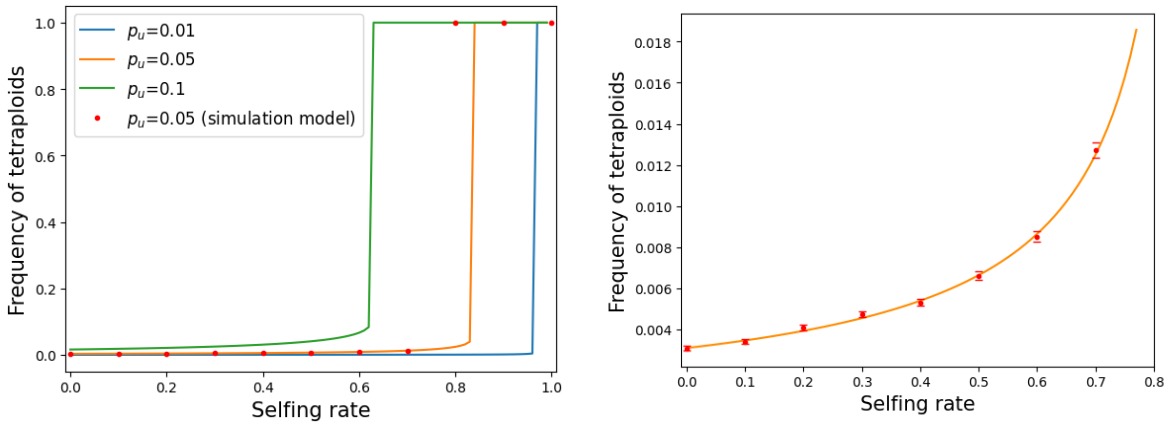

Figure 2: Frequency of tetraploids at equilibrium as a function of the selfing rate for different values of p_u obtained using the neutral model (left), and a zoomed version for $p_u = 0.05$ (right). The full lines represent the results obtained with the analytical model, while the red dots are obtained using the simulation model (50 runs), and the red dashes represent the 95% confidence intervals.

Figure 2 presents the frequency of tetraploids in the population at equilibrium using the neutral model. First, the results obtained with the analytical model match those obtained using the individual-based simulations for selfing rates lower than 0.8 (Figure 2). Therefore, the frequency of tetraploids at equilibrium depends exclusively on the probability of producing unreduced gametes p_u according to Section 2.1.1. However, the threshold selfing rate for which

tetraploids invade the population obtained with the simulation model is slightly lower than the one obtained analytically (Figure 2).

Moreover, it can be observed that the higher the probability of producing unreduced gametes, the lower the selfing rate threshold allowing tetraploids to invade, which is expected. More importantly, Figure 2 shows that tetraploids are able to establish in the initially diploid population, only when the selfing rate is quite high. Focusing on $p_u = 0.05$, the selfing rate needs to be higher than 0.8 for the tetraploids to invade the population. Tetraploids will invade the population when the selfing rate is high enough for them to overcome minority cytotype exclusion, a threshold selfing rate that depends only on the rate of unreduced gametes.

3.2 GSI model

3.2.1 Fixed selfing rates

We explored different scenarios of pollen limitation, where the first maternal parent is rejected after 1, 5 or 20 unsuccessful reproduction attempts. Under high pollen limitation, tetraploid invasion occurs only when selfing rates exceed 0.8 (Figures 3a and S2a), which is consistent with the results from the neutral model (Figure 2). In contrast, under low pollen limitation, tetraploid invasion occurs at much lower selfing rates (Figure 4a). Specifically, when selfing rates exceed 0.3, tetraploids always invade the population in our simulations. Even at a selfing rate of 0.1, tetraploid invasion was observed in a few simulations, and in 30% of the simulations at a selfing rate of 0.2. The most striking difference between the high pollen limitation scenarios (Figures 3 and S2) and the low pollen limitation scenario (Figure 4) lies in the value of the threshold selfing rate required for tetraploids to invade an initially diploid population. This difference between pollen limitation scenarios can be explained as follows: the higher the number of attempts before rejecting the maternal parent, the higher the likelihood of finding a compatible mate under challenging conditions, e.g. finding a diploid pollen grain (either an unreduced gamete from a diploid or a reduced gamete from a tetraploid individual) to fertilize a diploid ovule produced by a tetraploid individual.

Nonetheless, the different pollen limitation scenarios exhibit similar patterns. Even though all tetraploids are SC, the frequency of SC pollen produced by SC individuals decreases with increasing selfing rate (Figures 3c, S2c, and 4c), revealing a drop in heterozygosity at the

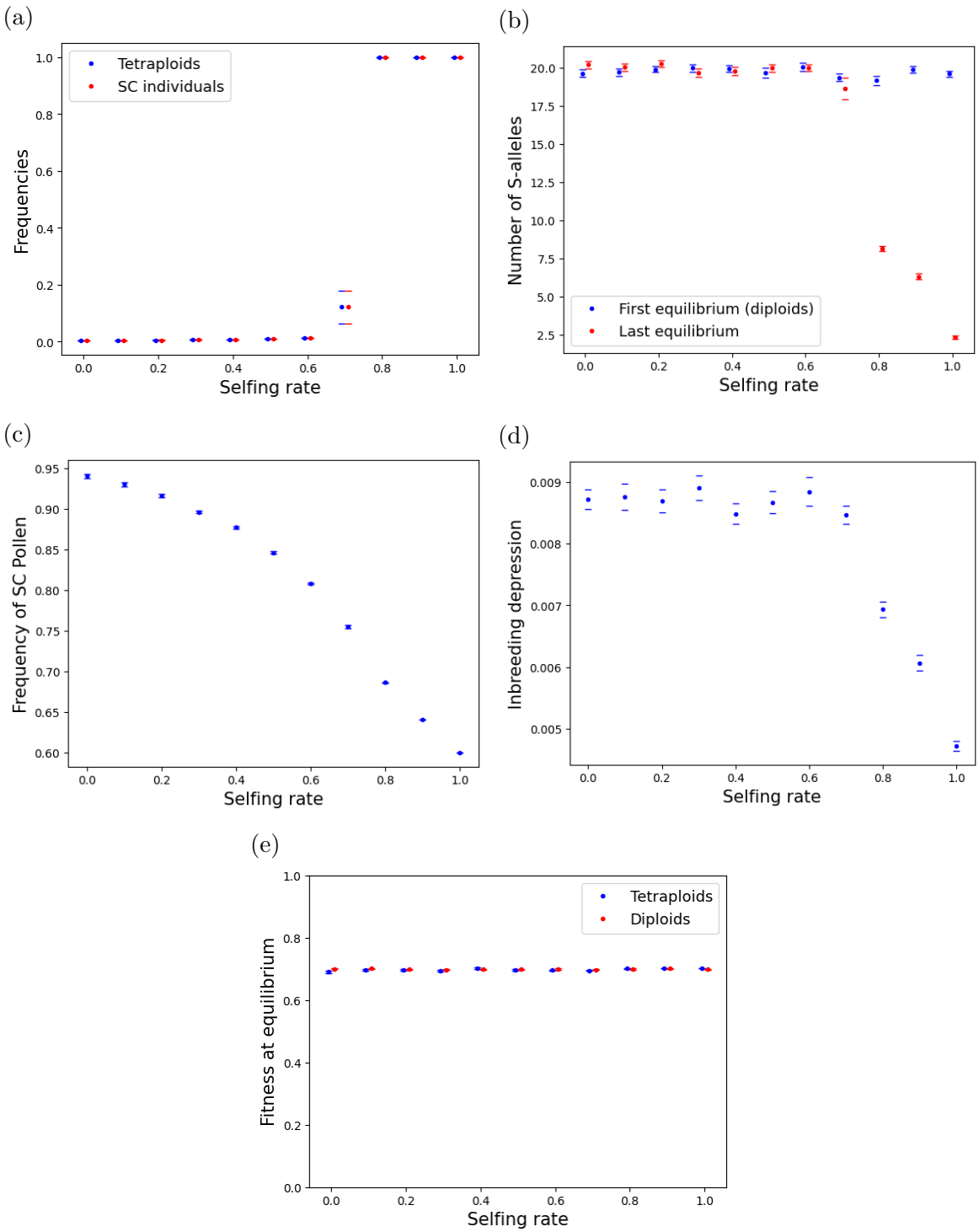

Figure 3: (a) Frequencies of tetraploids and SC individuals, (b) number of S-alleles at equilibrium for diploids and at the end of the simulation, (c) frequency of SC pollen produced by SC individuals, (d) inbreeding depression over the last 10000 generations, and (e) fitness of diploids and tetraploids at equilibrium when the selfing rate is fixed. Error bars stand for 95% confidence intervals. Results of 30 simulation runs under high pollen limitation (1 attempt) for each selfing rate using the parameters detailed in Table 1, specifically $N_{\text{pop}} = 1000$ and $p_u = 0.05$.

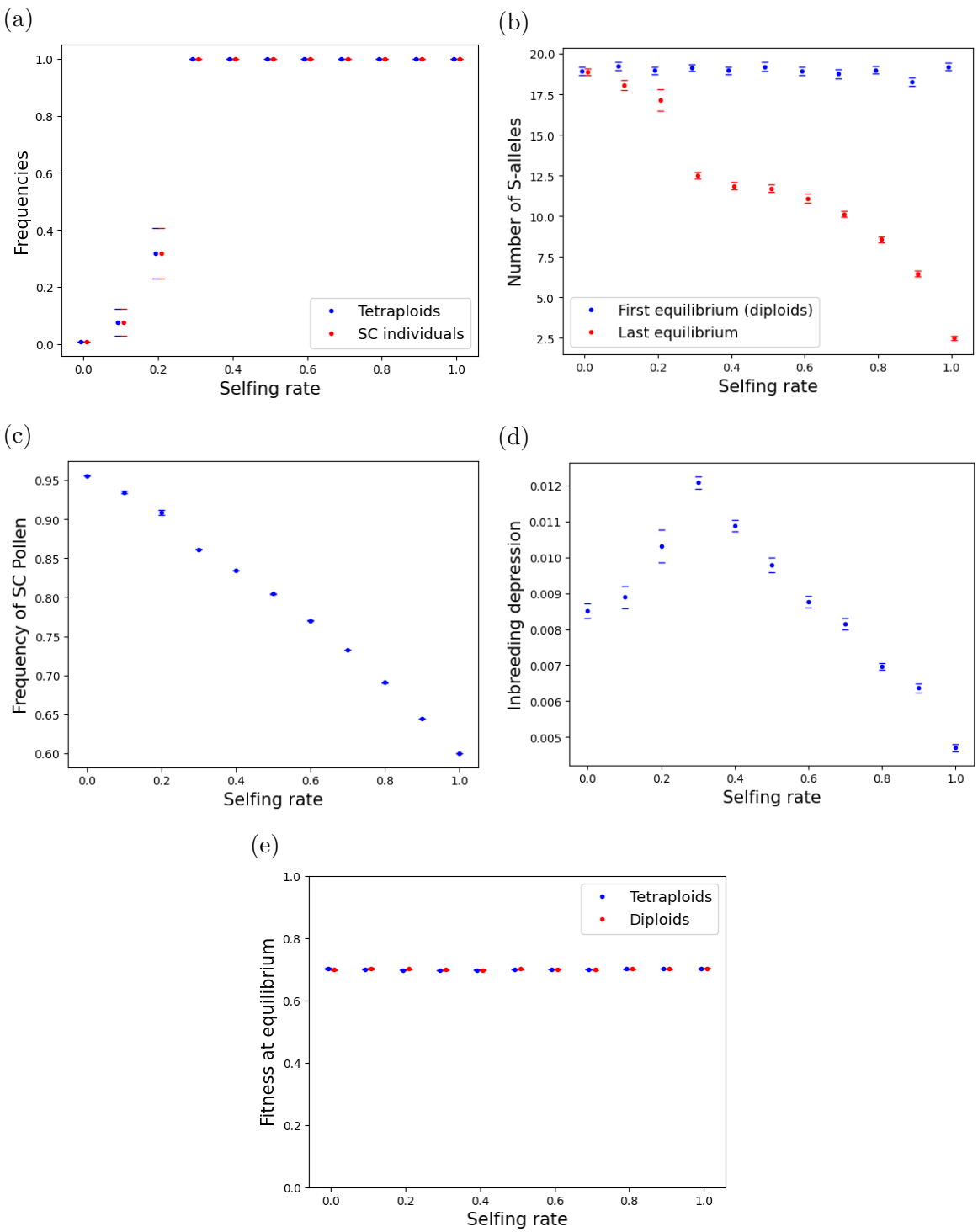

Figure 4: (a) Frequencies of tetraploids and SC individuals, (b) number of S-alleles at equilibrium for diploids and at the end of the simulation, (c) frequency of SC pollen produced by SC individuals, (d) inbreeding depression over the last 10000 generations, and (e) fitness of diploids and tetraploids at equilibrium when the selfing rate is fixed. Error bars stand for 95% confidence intervals. Results of 30 simulation runs under low pollen limitation (20 attempts) for each selfing rate using the parameters detailed in Table 1, specifically $N_{\text{pop}} = 1000$ and $p_u = 0.05$.

S-locus. Furthermore, in cases where tetraploids invade the population, an increase in the selfing rate is also associated with a decrease in both the number of S-alleles maintained within the population (Figures 3b, S2b, and 4b) and the level of inbreeding depression at the end of the simulation (Figures 3d, S2d, and 4d). These last observations, i.e. a decrease in heterozygosity, a loss of diversity, and a lower inbreeding depression, remain unchanged under different pollen limitation conditions and are consistent with what is expected for highly selfing populations. In addition, Figures 3e, S2e, and 4e show no difference between the fitness of diploids and tetraploids at equilibrium, which explains the consistency of the results under high pollen limitation with those from the neutral model.

3.2.2 Evolving selfing rates

When the selfing rate (or self-pollen rate for diploids) of each individual is allowed to evolve, Figures 5, S3, and 6 show that tetraploid invasion depends mainly on the mutation rate U_{SR} and on the extent of pollen limitation. For a realistic mutation rate of $U_{\mathrm{SR}} = 10^{-5}$, tetraploids never invade the population, regardless of the pollen limitation scenario and of the variance of mutational effects on the selfing rate σ^2 (Figures 5a, S3a, and 6a). Although some individuals with high selfing rates (above 0.8) appear in the population, their frequency remains too low to enable tetraploid invasion. At higher mutation rates ($U_{\mathrm{SR}} = 10^{-3}$ and $U_{\mathrm{SR}} = 10^{-1}$), individuals reach a wide range of selfing (or self-pollen) rates between 0 and 1. However, under high pollen limitation, tetraploids never invade the population, regardless of the other parameters (Figures 5b, 5c, S3b, and S3c). In contrast, Figures 6b and 6c indicate that tetraploid invasion always occurs under low pollen limitation when the mutation rate U_{SR} is not too low, regardless of the variance σ^2, suggesting once again that the absence of pollen limitation plays a key role in tetraploid establishment.

4 Discussion

In this paper, we investigated the impact of self-fertilization on the establishment of tetraploids within initially diploid populations under a GSI system with non-self-recognition. A key functional property of such SI systems is that whole-genome duplication results in an automatic

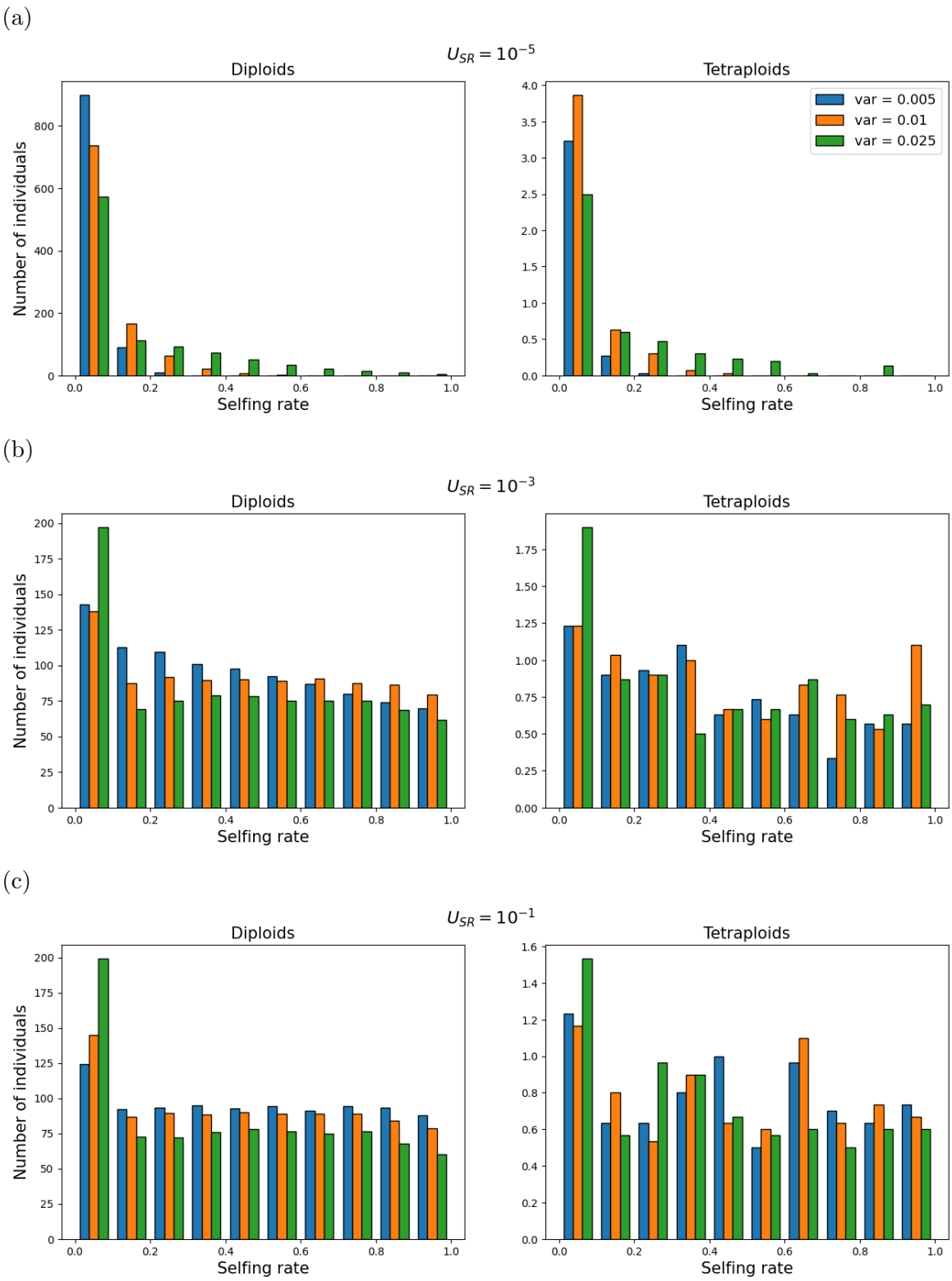

Figure 5: Distribution of the selfing rates of diploids (left) and tetraploids (right) at the end of the simulation for three different values of the variance $\sigma^2 = 0.05, 0.1$ and 0.25 and for different values of the mutation rate: (a) $U_{\mathrm{SR}} = 10^{-5}$, (b) $U_{\mathrm{SR}} = 10^{-3}$ and (c) $U_{\mathrm{SR}} = 10^{-1}$. Results averaged over 30 simulation runs under high pollen limitation (1 attempt) when the selfing rate can evolve using the parameters detailed in Table 1, specifically $N_{\mathrm{pop}} = 1000$ and $p_u = 0.05$.

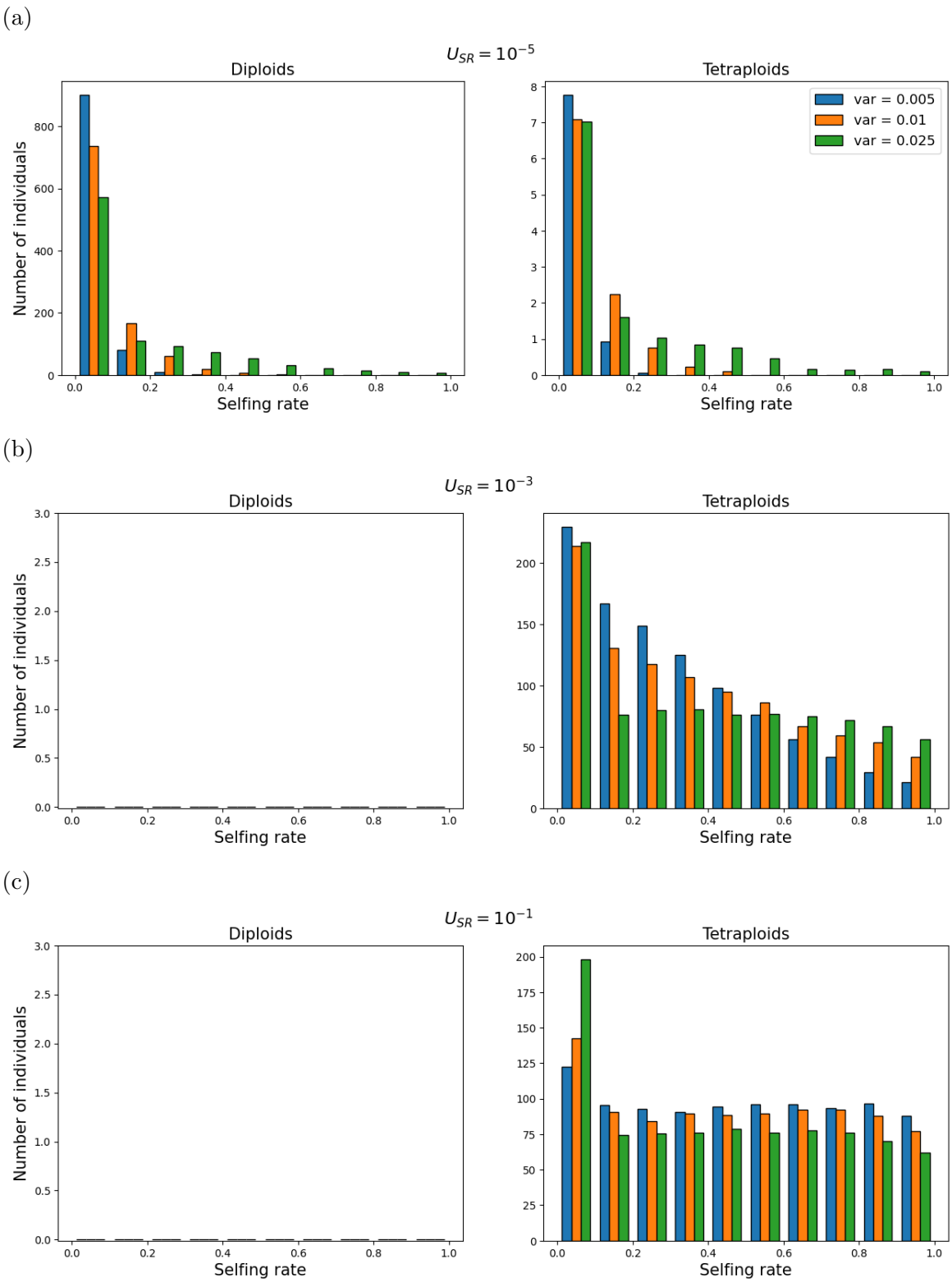

Figure 6: Distribution of the selfing rates of diploids (left) and tetraploids (right) at the end of the simulation for three different values of the variance $\sigma^2 = 0.05, 0.1$ and 0.25 and for different values of the mutation rate: (a) $U_{\mathrm{SR}} = 10^{-5}$, (b) $U_{\mathrm{SR}} = 10^{-3}$ and (c) $U_{\mathrm{SR}} = 10^{-1}$. Results averaged over 30 simulation runs under low pollen limitation (20 attempts) when the selfing rate can evolve using the parameters detailed in Table 1, specifically $N_{\mathrm{pop}} = 1000$ and $p_u = 0.05$.

shift from SI to SC, without the need to introduce a non-functional S-allele (Fujii et al., 2016). Our results indicate that tetraploid establishment is possible through the evolution of self-fertilization alone, i.e. without introducing an extrinsic fitness advantage of polyploidy, although the conditions for invasion vary depending on the degree of pollen limitation.

Evolution of selfing and tetraploid establishment

Under high pollen limitation, we found that tetraploid invasion is restricted to cases where the selfing rate of the entire population is high (above 0.8), and does not occur through the evolution of selfing, regardless of parameter values. Although the selfing rate threshold required for tetraploid invasion is high, it is comparable to values observed in some polyploid species. For instance, Barringer (2007) reported that polyploid annuals have a mean level of self-fertilization close to 0.8, while herbaceous and woody perennials exhibit lower rates on average (around 0.5 and 0.3, respectively). Our threshold selfing rate is also in line with the average outcrossing rate of 0.2 found in allopolyploids by Husband et al. (2008), while autopolyploids show significantly higher outcrossing rates on average ($t = 0.64$) though exceptions exist - for example, *T.hookeri* autopolyploids have an outcrossing rate as low as 0.03. Under low pollen limitation, our results indicate that tetraploid invasion occurs from much lower selfing rates (above 0.3, and even for selfing rates as low as 0.1 and 0.2 in some simulation runs). When selfing rates are allowed to evolve, tetraploids successfully invade the population under low pollen limitation as long as the mutation rate U_{SR} is sufficiently high ($\geq 10^{-3}$). Since selfing provides reproductive assurance, one might expect SC tetraploids to be more favored in pollen-limited environments. However, our results suggest the opposite: a realistic evolution of the selfing rate following whole-genome duplication (i.e. selfing rates going from 0 to $0.3 - 0.5$) would be more likely in stable conditions with reasonably large populations (low pollen limitation scenario) than in colonization conditions with strong bottlenecks and fewer potential mates (high pollen limitation scenario). This seems to contradict previous studies predicting that pollen-limited environments favor the evolution of self-fertilization toward high selfing rates (Porcher and Lande, 2005; Vallejo-Marín and Uyenoyama, 2004). However, these studies focus exclusively on diploid populations, while those that address tetraploid establishment typically examine other factors, such as environmental constraints or pollen dispersal (Griswold, 2021), rather than scenarios where pollen is limited. Our results can

be explained as follows: under low pollen limitation, tetraploids can also rely on outcrossing to overcome MCE as they are more likely to receive compatible diploid pollen, either from diploid donors producing unreduced gametes or from other tetraploid individuals. In contrast, under strong pollen limitation, they need to rely almost exclusively on self-pollen to receive diploid pollen, which requires higher values of the selfing rate. Overall, these findings align with theoretical models suggesting that higher selfing rates increase the likelihood of polyploid persistence (Baack, 2005; Rausch and Morgan, 2005). However, Clo et al. (2022) showed that self-fertilization can negatively impact tetraploid establishment when polyploidy is associated with a fitness cost. Note that diploids and tetraploids exhibit no differences in fitness in our simulations.

S-allele diversity, homozygosity and inbreeding depression

We also found that the diversity of S-alleles in the population is impacted by tetraploid establishment. In diploids, the number of S-alleles is maintained by strong negative frequency-dependent selection, as a pollen with a rare S-allele is more likely to find a compatible mate compared to a pollen with a frequent S-allele (Wright, 1939). Our results for the number of S-alleles maintained at equilibrium in the diploid population are consistent with the estimate given by the formula in Yokoyama and Nei (1979), which predicts approximately 20 alleles for a population of our size under GSI. When tetraploid SC individuals invade the population, the number of S-alleles present in the population decreases with increased selfing rates, reflecting a loss of diversity at the S-locus. This pattern is consistent with the fact that selfing is associated with a reduction in genetic diversity in general, especially in highly selfing populations (Charlesworth and Charlesworth, 1995; Lande and Porcher, 2015; Abu Awad and Roze, 2018), and with the fact that the negative frequency-dependent selection acting on the S-locus is relaxed due to functional disruption of the SI reaction under polyploidy.

However, a minimal number of S-alleles still needs to be maintained to ensure SC (two S-alleles in that case), since fully homozygous tetraploids at the S-locus would revert to SI and could not self-fertilize anymore. In our simulations, selfing reaches very high levels when considering functional S-alleles only, i.e. without introducing a non-functional S-allele into the population. That is specific to GSI with non-self-recognition, as polyploidization automatically renders the SI system leaky. This contrasts with sporophytic SI systems, such as those in

the Brassicaceae, where the breakdown of SI requires the presence of a non-functional S-allele (Vekemans et al., 2014; Novikova et al., 2023). From an empirical point of view, the recent sequencing of a pistil transcriptome of a polyploid *Rebutia pygmaea* (Cactaceae) revealed the presence of at least four S-RNase alleles (B. Igic, personal communication). In addition, more than two S-alleles have also been reported in some tetraploid individuals of *Lycium parishii* (Solanaceae) (Savage and Miller, 2006). However, the self-incompatibility status of polyploid individuals and the functionality of their S-alleles have not been established in these two cases. Hence, due to limited empirical evidence from polyploid species with a collaborative non-self recognition GSI system, it remains unclear whether such species can maintain functional S-alleles following polyploidization, or if they eventually fix a non-functional S-allele after an intermediate phase. Further research is needed on the subject to fill this knowledge gap, for instance through large-scale sequencing of S-RNases from recent polyploids and by studying selfing rates in Solanaceae.

On a different note, higher selfing rates are also associated with greater homozygosity (Burgarella and Glémin, 2017), which is consistent with our observation of reduced heterozygosity at the S-locus among SC individuals as selfing increases. Our simulations also show that inbreeding depression declines with rising selfing rates, which is expected as increased homozygosity facilitates purging of deleterious alleles (Ronfort, 1999; Charlesworth and Willis, 2009).

Perspectives

Our study focuses on selfing as a strategy to overcome MCE, but other factors can also promote the establishment and persistence of polyploids. For example, we did not model reproductive isolation in outcrossing, such as assortative mating, which could enhance the chances of tetraploid establishment (Oswald and Nuismer, 2011). Polyploidy is often associated with differences in floral traits and flowering time, which can lead to reproductive isolation, either by attracting different pollinators or by reducing overlap in reproductive periods (Segraves and Thompson, 1999; Vamosi et al., 2007). More generally, strong assortative mating hinders the exclusion of tetraploids in populations where unreduced gametes are introduced, therefore facilitating their ability to overcome MCE (Husband and Sabara, 2004). We also assumed that triploid individuals are sterile or non-viable, a common assumption in

theoretical models (Levin, 1975; Ramsey and Schemske, 1998; Felber, 1991), and supported by empirical studies reporting reduced fitness in triploid individuals (Husband and Sabara, 2004; Burton and Husband, 2000). However, both theoretical and empirical work suggest that the presence of a triploid bridge can facilitate tetraploid establishment, depending on the fitness of triploid individuals (Husband, 2004; Köhler et al., 2010; Schinkel et al., 2017; Felber and Bever, 1997). Apart from potential extensions, the model could also be adapted to other types of self-incompatibility systems, such as GSI with self-recognition or sporophytic self-incompatibility (SSI), which do not lead to automatic functional breakdown under polyploidy (Hauck et al., 2006; Duan et al., 2024). In those systems, the breakdown of SI necessarily occurs through the spread of a mutated non-functional SC allele. In addition, under SSI, the results may vary depending on the dominance relationships between S-alleles (Novikova et al., 2023; Duan et al., 2024) and the level of inbreeding depression. As a result, additional factors and parameters would need to be examined compared to the current model.

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