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# A general stochastic model for sporophytic self-incompatibility

Sylvain Billiard\* and Viet Chi Tran<sup>† ‡</sup>

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## Abstract

Disentangling the processes leading populations to extinction is a major topic in ecology and conservation biology. The difficulty to find a mate in many species is one of these processes. Here, we investigate the impact, on the extinction probability, of self-incompatibility in flowering plants, where several inter-compatible classes of individuals exist but individuals of the same class cannot mate. We model pollen limitation through different relationships between mate availability and fertilization success. After deriving a general stochastic model, we focus on the simple case of distylous plant species where only two classes of individuals exist. We first investigate the dynamics of such a species in a large population limit and then, we look for an approximation of the extinction probability in small populations. This leads us to consider inhomogeneous random walks on the positive quadrant. We compare the dynamics of distylous species to self-fertile species with and without inbreeding depression, to investigate the conditions under which self-incompatible species could be less sensitive to extinction while they can suffer more pollen limitation.

**Keywords:** birth and death process, ODE approximations, inhomogeneous random walk on the positive quadrant, inbreeding depression, extinction probability, mating system, distyly.

**AMS Codes:** 92D40, 92D25, 60J80.

## 1 Introduction

In this work, we are interested in a plant population and in particular, in modelling its specific sexual mating system and especially highlighting several phenomena which can affect its dynamics: stochasticity in the demography, pollen limitation, boundary effects. First, the fate of small populations depends on stochastic processes such as demographic stochasticity (Lande [25]), which refers to a variance due to randomness in the death and reproduction events. Second, when populations are small or at low density, there can happen Allee effects (Allee *et al.* [1]), *i.e.* when a positive relationship between the size of the population and the per capita growth rate appears. In sexual species, the birth rate may depend on the availability in mating partner, what is called the "mate finding Allee effect" (Gascoigne *et al.* [17]). For example, in species with separate sexes, the mean reproductive rate of a population may be low because one of the mating partner (for instance the opposite sex) is rare (Engen *et al.* [13], Saether *et al.* [37], Bessa-Gomes *et al.* [7]). In gonochoric and dioecious species, disequilibria between sexes can limit reproduction, and these biases can be expected to be higher in small populations because of stochasticity. Finally, at the extreme, the mate finding Allee effect can result in boundary conditions where compatible mates disappear, leading inevitably the population

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to extinction.

Many hermaphroditic species of Angiosperms (flowering plants) have mating systems which allow fertilization only among specific classes of individuals, between long-styled and short-styled plants in distylous species (Barrett and Shore [5]), or among different mating types in self-incompatible species (more than 50 percent of Angiosperms, Iqbal *et al.* [20]). Self-incompatibility systems (SI) avoid selfing and mating between close individuals: SI prevents reproduction between mates sharing identical S-locus alleles (the allele which determines whether individuals are compatible, by coding for some proteins carried as identifiers by the pollen and ovules), and especially self-fertilization. It was hypothesized that this mating system evolved to avoid inbreeding depression, *i.e.* the decrease in fitness when mating occurs between kin individuals [33, 32, 34]. In this system, individuals carrying rare S-locus alleles have access to more possible mates than individuals carrying common S-alleles, which generates negative frequency-dependent selection on the S-locus (Wright [45]).

In Angiosperms, mate finding is moreover mainly passive since it depends on pollen vectors such as insects or wind. This can result in "pollen limitation", when a given plant does not receive enough pollen to fertilize all the ovules it produces. Pollen limitation has been found in many species and can have many evolutionary and ecological consequences, from the evolution of mating system to the increase of extinction probability in small populations (Ashman *et al.* [2]). If a class of individuals goes extinct, other classes have less mating opportunities leading to a lower mean reproduction rate, or even can not mate anymore, leading to extinction. Pollen limitation and mating systems are interacting phenomena which can have a strong impact on the fate of populations (see Leducq *et al.* [27] and references therein). Pollen limitation can be increased in strict allogamous species and the probability of disappearance of a class of individuals can be increased by pollen limitation. It has been shown indeed that pollen limitation is higher in outcrossing species than in selfing species (Larson and Barrett [26]).

However, few theoretical investigations have been done so far to measure the impact of pollen limitation, mating systems and their interactions on the extinction and establishment of populations. It is yet a central question since many Angiosperms families are strictly allogamous because of SI. Three models of the demography have been investigated specifically for a given species (Kirchner *et al.* [22], Wagenius *et al.* [44], Hoebee *et al.* [19]), which thus lack generalities. Levin *et al.* [28] performed spatially explicit, individual centered simulations for plant populations similar to what is considered here. Most importantly, in all models but in Wagenius *et al.* [44]), the supposed SI systems were either gametophytic (only the content of the gametes is expressed) or a caricatural sporophytic system with only codominance between S-alleles. In species with sporophytic SI system (SSI), the mating phenotypes of pollen and pistils are determined by the diploid parental genotypes at the S-locus and hence dominance interactions are possible among S-alleles (Bateman [6]), which can be very complex (Castric and Vekemans [10]). The results from the previous studies can therefore not be generalized to SSI systems species, and especially not to distylous species, which is a particular case of SSI with only two alleles and consequently only two classes of individuals. Finally, the different processes affecting the extinction probability of SI populations (pollen limitation, demographic stochasticity and boundary effect) can not be disentangled in these previous investigations, which is our purpose here.

Our goals here are, first to develop a general model to describe the dynamics of a plant population with SSI, with and without pollen limitation and second to use this model to investigate the relative impact of pollen limitation and demographic stochasticity on the fate of populations in the particular case of a distylous species. We begin with a general stochastic individual centered model, in continuous time, for sporophytic self-incompatibility (Section 2). We explicitly model the genetic determinism of the self-incompatibility phenotype and compute the reproduction rate of each possible genotype. We assume different relationships between the compatible mate availability and the reproductive success, which reflects different models of pollen limitation. Second, we focus on the simple case of distylous species. We analyze the dynamics of distylous species assuming a large population and

using approximations by ordinary differential equations. We exhibit different behaviors depending on the relationships between the birth and death parameters. We also compare these behaviors with self-fertile species, with or without inbreeding depression and pollen limitation (Section 3). Third, we consider extinction in small distylous populations (Section 4). This leads us to study inhomogeneous random walks on the positive quadrant. We use coupling arguments to show that the behaviors of the random walks, namely whether they are subcritical, critical or supercritical, depend on the same criteria as for large populations. Finally, individual based simulations are performed (Section 5).

## 2 Microscopic modelling

In this section, we first describe the individual dynamics. Then, we precise the different models of reproduction rates. Following Champagnat *et al.* [11], Stochastic Differential Equations (SDEs) that describe mathematically the random evolution in time of the population and their large population approximation using Ordinary Differential Equations (ODEs) are proposed.

### 2.1 Description of the dynamics at the individual level

**Self-incompatibility genotype** We assume that SSI is controlled by a gene at a single locus, called the S-locus, where  $n$  alleles segregate. These alleles are numbered from 1 to  $n$ . We assume that individuals are diploid and hermaphroditic. Each individual genotype is characterized by two alleles  $\{S^1, S^2\}$ , with  $S^1, S^2 \in \llbracket 1, n \rrbracket = \{1, \dots, n\}$ . Since the order of the alleles is not important, for  $u, v \in \llbracket 1, n \rrbracket$ ,  $\{u, v\}$  and  $\{v, u\}$  are equivalent.

We denote by  $E = \{(u, v) \in \llbracket 1, n \rrbracket^2, u \leq v\}$  the space of the different possible genotypes. The set  $E$  is finite, with  $\text{Card}(E) = n(n-1)/2$ .

**Individual-centered description** The population at time  $t$  is described by a point measure on  $E$

$$Z_t(du, dv) = \sum_{i=1}^{N_t} \delta_{(S^1(i), S^2(i))}(du, dv) = \sum_{1 \leq u' \leq v' \leq n} N_t^{u'v'} \delta_{u', v'}(du, dv) \quad (2.1)$$

where  $N_t$  is the number of individuals alive at time  $t$ ,  $N_t^{u'v'}$  is the number of individuals with genotype  $(u', v') \in E$ , and each individual  $i$  is represented by a Dirac mass weighting its genotype  $(S^1(i), S^2(i))$ . Point measures that are considered have finite mass. In the sequel, we denote by  $\mathcal{M}_F(E)$  the set of finite measures on  $E$ . Since  $E$  is a finite space, the weak, vague convergence topologies and the topology associated with the total variation norm on  $\mathcal{M}_F(E)$  all coincide.

Integrating the measure (2.1) with respect to chosen real functions  $f$  on  $E$  provides summaries of the population. Let us denote  $\langle Z_t, f \rangle = \int_E f(u, v) Z_t(du, dv) = \sum_{i=1}^{N_t} f(S^1(i), S^2(i))$ .

If we choose for instance  $f = 1$  then,  $\langle Z_t, 1 \rangle = N_t$ . If we choose  $f = \mathbb{1}_{(u', v')}$  for  $(u', v') \in E$ , then  $\langle Z_t, \mathbb{1}_{(u', v')} \rangle = N_t^{u'v'}$ .

**Self-incompatibility phenotype** SSI phenotype is the production of recognition proteins at the surface of pollen and stigmas (stigmas contain ovules and are the plant's structure on which pollen is deposited). These proteins can be of  $n$  different types (or specificities) depending on the plant's genotype and on the dominance relationships between the  $n$  alleles. For  $u \in \llbracket 1, n \rrbracket$ , let us denote by  $e_u$  the vector with all components equal to zero except the component  $u$  which is equal to 1. For an individual of genotype  $\{u, v\}$ , the stigmas and pollen it produces have respectively the phenotype  $\Phi_S(e_u + e_v) \in \{0, e_u, e_v, e_u + e_v\}$  and  $\Phi_P(e_u + e_v) \in \{0, e_u, e_v, e_u + e_v\}$ . The maps  $\Phi_P$  and  $\Phi_S$  encode the expression of the genotype into the phenotype. For instance, if  $\Phi_P(e_u + e_v) = e_u$ , then  $u$  is strictly dominant over  $v$  in pollen (proteins produced at the surface of pollen are of the single type  $u$ ). If

$\Phi_P(e_u + e_v) = e_u + e_v$ , then  $u$  and  $v$  are codominant in pollen (proteins produced at the surface of pollen are of both types  $u$  and  $v$ ). If  $\Phi_P(e_u + e_v) = 0$  then the pollen can mate with every possible ovule. A cross is incompatible if pollen and stigmas share proteins of the same type. In other words, a stigma  $\{u, v\}$  and a pollen  $\{u', v'\}$  can cross if and only if

$$\Phi_S(e_u + e_v) \cdot \Phi_P(e_{u'} + e_{v'}) = 0, \quad (2.2)$$

where  $x \cdot y$  is the scalar product of  $x, y \in \mathbb{R}^n$ . Notice that an individual can self-fertilize if  $\Phi_S(e_u + e_v) \cdot \Phi_P(e_u + e_v) = 0$ . Let:

$$\Theta_S^{uv} = \{(u', v') \in E, 1 \leq u' \leq v' \leq n \text{ and } \Phi_S(e_u + e_v) \cdot \Phi_P(e_{u'} + e_{v'}) = 0\} \quad (2.3)$$

denote the set of genotypes compatible with stigmas  $\{u, v\}$ . The size of the population producing pollen compatible with stigmas  $\{u, v\}$  is hence:

$$\bar{N}_t^{uv} = \sum_{(u', v') \in E \in \Theta_S^{uv}} N_t^{u'v'} = \int_E \mathbb{1}_{\Phi_S(e_u + e_v) \cdot \Phi_P(e_{u'} + e_{v'}) = 0} Z_t(du', dv'). \quad (2.4)$$

Notice that the set  $\Theta_P^{uv}$  of genotypes compatible with pollen  $\{u, v\}$  is not necessarily  $\Theta_S^{uv}$  since we may have  $\Phi_S(e_u + e_v) \cdot \Phi_P(e_{u'} + e_{v'}) \neq \Phi_P(e_u + e_v) \cdot \Phi_S(e_{u'} + e_{v'})$ .

**Mating probabilities** Each plant receives pollen from the other individuals of the population. We assume that the quantity of pollen of type  $(u, v) \in E$  received by a plant is equal to the proportion of plants of type  $(u, v)$  in the population. The probability that the ovule of an individual with genotype  $(u', v')$  is fertilized by a pollen from an individual with genotype  $(u, v)$  is denoted by  $p^{u'v'}(u, v)$ . This probability takes into account the quantity of pollen received by the pistil and the compatibility conditions (2.2). This is detailed in Section 2.2.

**Segregation** When the ovule is of type  $\{u, v\}$  and the pollen of type  $\{u', v'\}$ , then the new individual is of type  $\{u, u'\}$ ,  $\{u, v'\}$ ,  $\{v, u'\}$  or  $\{v, v'\}$  with probability 1/4.

**Reproduction rate** Plants  $(u, v)$  produce ovules in continuous time with an individual rate  $r(\bar{N}_t^{uv})$  that can possibly depend on the size of the compatible population or be a constant. In the sequel, we assume that this rate is bounded by a positive constant  $\bar{r} > 0$ . Once produced, the ovules may be fertilized or not depending on the pollen arriving on the stigmas.

The functional forms of  $r(\cdot)$  and the choice of the mating probabilities  $p^{u'v'}(u, v)$  are further discussed in Section 2.2.

**Death** The plants die with the constant death rate  $d > 0$ . This death rate is kept simple and the complexity of the model is put on the reproduction system.

## 2.2 Mating probabilities and reproduction rates

In this section, we describe five types of reproduction considered in this paper. Three of them describe SI systems: Wright's model [45], the fecundity selection model (Vekemans *et al.* [41]) and the dependence model, which we introduce. The relationships between reproduction rate and mate availability for these three models are represented in Fig. 1. Two other models are also introduced for comparison: the self-compatible cases with and without inbreeding depression.

Boundary conditions, *i.e.* discontinuities of the reproduction rate that occur when a genotype in the population has no more mate, are observed in the Wright's and dependence models. In the case of fecundity selection model, even if there is SI, the reproduction rate is proportional to the size of the

compatible population and vanishes continuously at the boundary. In self-compatible cases, there is no boundary effect because an individual can mate with any other individuals, even itself.

In Wright's model and in the ideal case of self-compatibility without inbreeding depression, there is no pollen limitation. In the fecundity selection model, the latter is taken into account through the probability of fertilization. In the dependence model and in the case of inbreeding depression, it is the functional form of the rate of production of "efficient" ovules that describes this phenomenon.

### 2.2.1 Model 1: Wright's model

First, following Wright's model [45], an ovule  $(u, v)$  is produced at rate  $r(\bar{N}_t^{uv}) = \bar{r}$ . It is fertilized by a pollen produced by an individual of genotype  $(u', v')$  with a probability that depends on the frequencies in the compatible population:

$$\bar{p}_t^{uv}(u', v') = \frac{N_t^{u', v'}}{\bar{N}_t^{uv}} \mathbb{1}_{\{(u', v') \in \Theta_S^{uv}\}}. \quad (2.5)$$

Notice that  $\bar{p}_t^{uv}(u', v') = 0$  when  $\bar{N}_t^{uv} = 0$ . The individual reproduction can hence take only two values:  $\bar{r}$  if there is at least one compatible individual in the population, 0 otherwise. Reproduction does not depend on the quantity of compatible pollen a plant receives.

### 2.2.2 Model 2: Dependence model

Another way to model the pollen limitation and the self-incompatibility is to consider the probability  $\bar{p}_t^{uv}(u', v')$  of (2.5) together with a rate  $r(\cdot)$  that depends on the total number of compatible individuals in the population with the following form:

$$r(N) = \bar{r} \frac{e^{\alpha N}}{\beta + e^{\alpha N}}. \quad (2.6)$$

where  $\bar{r}$ ,  $\alpha$  and  $\beta$  are positive constants. This model will be termed "dependence model" in the sequel. It is a generalization of Wright's model where instead of  $\bar{r}$ , we have a reproduction rate that depends on the size of the compatible population  $\bar{N}_t^{uv}$  when reproduction is allowed. This is again pollen limitation: among the  $\bar{r}$  ovules produced in a time unit, only  $r(\bar{N}_t^{uv})$  end up in producing a new individual. For a large compatible population is large, the rate tends to its supremum value:

$$\lim_{N \rightarrow +\infty} \bar{r} \frac{e^{\alpha N}}{\beta + e^{\alpha N}} \mathbb{1}_{N>0} = \bar{r}.$$

The Wright's model can be viewed as the limiting case of (2.6) when the parameter  $\alpha \rightarrow +\infty$ , that is when there is no pollen limitation.

Notice also that this model exhibits boundary effects since

$$\lim_{N \rightarrow 0} \frac{e^{\alpha N}}{\beta + e^{\alpha N}} \mathbb{1}_{N>0} = \frac{\bar{r}}{1 + \beta} > 0.$$

Because we assume that a single plant produces a lot of pollen, even in cases where we consider pollen limitation, there is a discontinuity at the set  $\{\bar{N}_t^{uv} = 0\}$  when  $r(0) > 0$ . As soon as there exists a small number of compatible plants, all individuals  $\{u, v\}$  start producing new individuals at a positive rate.

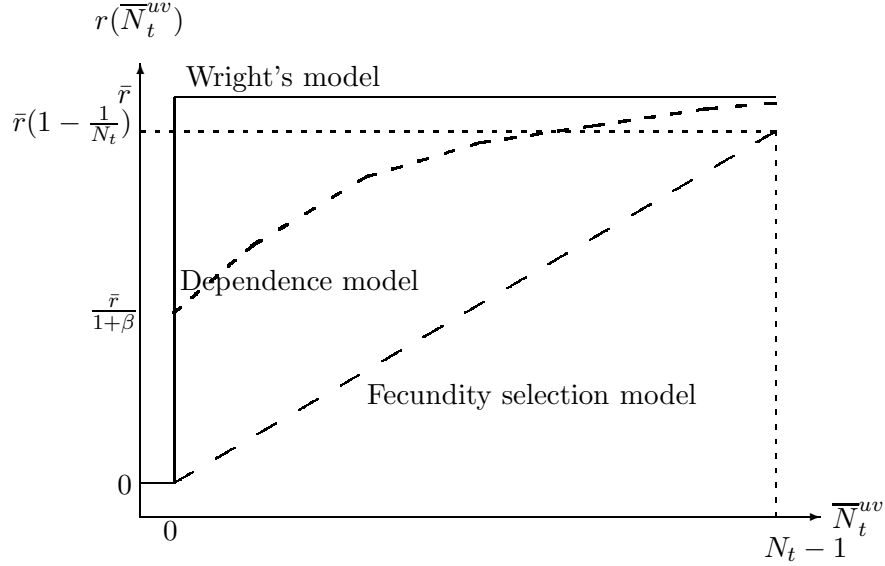


Figure 1: Relationships between the individual reproductive rates of genotype  $\{u, v\}$  and the number of compatible individuals  $\bar{N}^{u,v}$  for the three models of mating we assumed: Thin line: The Wright's model; Dashed line: The fecundity selection model; Thick dashed line: The dependence model.

### 2.2.3 Model 3: Fecundity selection model

In the fecundity selection model (Vekemans *et al.* [41]), ovules are produced with a rate  $r(\bar{N}_t^{uv}, N_t) = \bar{r}$ . Probability of fertilization by a pollen  $(u', v')$  is

$$\tilde{p}_t^{uv}(u', v') = \frac{N_t^{u', v'}}{N_t} \mathbb{1}_{(u', v') \in \Theta_S^{uv}}. \quad (2.7)$$

If the ovule chooses an incompatible pollen, then the ovule is not fertilized and lost.

Under the fecundity selection model, the reproduction rate of an individual  $(u, v)$  is hence  $\bar{r}\bar{N}_t^{uv}/N_t$ . The individual reproduction rate is directly proportional to the frequency of compatible individuals in the total population, which consequently promotes pollen limitation.

### 2.2.4 Rates of reproduction and gamete production

In the models of Sections 2.2.1, 2.2.2 and 2.2.3 the rate at which pollen produced by individuals of type  $\{u, v\}$  fertilizes ovules in the population  $Z_t$  is:

$$\sum_{(u', v') \in E} r(\bar{N}_t^{u'v'}) N_t^{u'v'} p^{u'v'}(u, v) \quad (2.8)$$

where we recall that  $p^{u'v'}(u, v)$  is the mating probability of an ovule produced by an individual  $(u', v')$  by a pollen produced by an individual  $(u, v)$ . Under the Wright's model or the dependence model,  $p^{u'v'}(u, v) = \bar{p}^{u'v'}(u, v)$ , while under the fecundity selection model,  $p^{u'v'}(u, v) = \tilde{p}^{u'v'}(u, v)$ .

Hence, offspring with genotype  $\{u, v\}$  are produced in the population represented by  $Z_t$  with the rate:

$$\begin{aligned}
r^{uv}(Z_t) = & \mathbb{1}_{u \neq v} \left[ \frac{1}{4} \left( \sum_{u' \neq u} \sum_{v' \neq v} r(\bar{N}_t^{uu'}) N_t^{uu'} p^{uu'}(v, v') + r(\bar{N}_t^{vv'}) N_t^{vv'} p^{vv'}(u, u') \right) \right. \\
& + \frac{1}{2} \left( \sum_{v' \neq v} r(\bar{N}_t^{uu}) N_t^{uu} p^{uu}(v, v') + \sum_{u' \neq u} r(\bar{N}_t^{uu'}) N_t^{uu'} p^{uu'}(v, v) \right) \\
& + \frac{1}{2} \left( \sum_{u' \neq u} r(\bar{N}_t^{vv}) N_t^{vv} p^{vv}(u, u') + \sum_{v' \neq v} r(\bar{N}_t^{vv'}) N_t^{vv'} p^{vv'}(u, u) \right) \\
& + \left. \left( r(\bar{N}_t^{uu}) N_t^{uu} p^{uu}(v, v) + r(\bar{N}_t^{vv}) N_t^{vv} p^{vv}(u, u) \right) \right] \\
& + \mathbb{1}_{u=v} \left[ \frac{1}{4} \sum_{u', v' \in [1, n] \setminus \{u\}} r(\bar{N}_t^{uu'}) N_t^{uu'} p^{uu'}(u, v') + r(\bar{N}_t^{uu}) N_t^{uu} p^{uu}(u, u) \right. \\
& \left. + \frac{1}{2} \left( \sum_{u' \neq u} r(\bar{N}_t^{uu'}) N_t^{uu'} p^{uu'}(u, u) + \sum_{v' \neq u} r(\bar{N}_t^{uu}) N_t^{uu} p^{uu}(u, v') \right) \right]. \quad (2.9)
\end{aligned}$$

The formula (2.9) does not simplify in general because of the possible asymmetry of dominance relationships between alleles in pollen and stigmas. We distinguish whether the allele  $u$  comes from the pollen or the pistil, and similarly for  $v$ . In (2.9), we separated the different terms according to the homozygosity or heterozygosity of the parents.

The rate (2.9) gives access to the number of seeds of each type  $\{u, v\}$  that is produced at time  $t$ . There is a *mass dependence* with respect to the parent who brings the ovules and a *frequency dependence* with respect to the one who brings the pollen. The case of infinite populations is considered in [8].

To end this section, we present two alternative models, without SI, which will allow comparisons with the three models introduced in Sections 2.2.1, 2.2.2 and 2.2.3. Model 4 describes a self-compatible case without any penalization of self-fertilization, whereas Model 5 introduces inbreeding depression.

### 2.2.5 Model 4: Self-compatible case without pollen limitation nor inbreeding depression

To carry comparisons, it is natural to investigate the case where there is no self-incompatibility, no pollen limitation and no inbreeding depression. Without self-incompatibility and when the reproduction  $\bar{r}$  is constant, the rate of production of an individual of type  $\{u, v\}$  becomes:

$$\begin{aligned}
\tilde{r}^{uv}(Z_t) &= \frac{2\bar{r}}{N_t} \left( \frac{1}{2} \sum_{u' \neq u} N_t^{uu'} + N_t^{uu} \right) \left( \frac{1}{2} \sum_{v' \neq v} N_t^{vv'} + N_t^{vv} \right) \quad \text{if } u \neq v \\
\tilde{r}^{uu}(Z_t) &= \frac{\bar{r}}{N_t} \left( \frac{1}{2} \sum_{u' \neq u} N_t^{uu'} + N_t^{uu} \right)^2 \quad \text{if } u = v. \quad (2.10)
\end{aligned}$$

In this rate, we recognize the number of couples that can be constituted with one parent of trait  $u$  and one parent of trait  $v$ ,  $\sum_{u'=1}^n N_t^{uu'} \sum_{v'=1}^n N_t^{vv'}$ , divided by the total size of the population because of the frequency dependence, and with a correction for homozygous individuals. Notice that the genotypic frequency appears naturally since in this case,  $p_t^{uv}(u', v') = \bar{p}_t^{uv}(u', v') = \tilde{p}_t^{uv}(u', v') = N_t^{u', v'} / N_t$  is the proportion of individual  $\{u', v'\}$  in the population.

### 2.2.6 Model 5: Self-compatible case with pollen limitation and inbreeding depression

Recall that inbreeding depression is the phenomenon which describes the decrease in fitness when mating occurs between kin individuals [32, 33, 34]. A detailed study of inbreeding depression would be interesting and deserve a paper for itself. Our purpose here is to provide a schematic point of



comparison for SSIs. For the sake of simplicity, we assume here that inbreeding depression is suffered by offspring produced by self-fertilization only.

Among the ovules produced by the plant, a fraction  $s \in [0, 1]$  are self-fertilized, *i.e.* are fertilized by the pollen of the plant that has produced them. Among these, a fraction  $\delta \in [0, 1]$  is not viable. The rate of production of new individuals through other matings is of the form (2.6) except that the maximal rate is now  $(1 - s)\bar{r}$  which corresponds to the ovules that have not been self-fertilized. We hence consider the following rate in the case of pollen limitation:

$$r(N) = (1 - \delta)s\bar{r} + (1 - s)\bar{r}\frac{e^{\alpha(N-1)}}{\beta + e^{\alpha(N-1)}}. \quad (2.11)$$

In the sequel, this model will be termed by Self-Compatibility with Inbreeding Depression model (SCID). In the presence of self-fertilization, the effect of pollen limitation is lower: the reproduction rate of individuals is less dependent on the quantity of pollen received from the other individuals.

In the case of the rate (2.11), the rate of production of an individual of type  $\{u, v\}$ , at time  $t$  is:

$$\begin{aligned} \hat{r}^{uv}(Z_t) &= 2(1 - s)\frac{\bar{r}}{N_t}\frac{e^{\alpha N_t}}{\beta + e^{\alpha N_t}}\left(\frac{1}{2}\sum_{u' \neq u} N_t^{uu'} + N_t^{uu}\right)\left(\frac{1}{2}\sum_{v' \neq v} N_t^{vv'} + N_t^{vv}\right) \\ &\quad + \frac{(1 - \delta)s\bar{r}}{2}N_t^{uv} \quad \text{if } u \neq v \\ \hat{r}^{uu}(Z_t) &= (1 - s)\frac{\bar{r}}{N_t}\frac{e^{\alpha N_t}}{\beta + e^{\alpha N_t}}\left(\frac{1}{2}\sum_{u' \neq u} N_t^{uu'} + N_t^{uu}\right)^2 + (1 - \delta)s\bar{r}N_t^{uu} \quad \text{if } u = v. \end{aligned} \quad (2.12)$$

### 2.3 SDE description and their ODE approximations

Following Fournier and Méléard [16], we can express the evolution of the population  $(Z_t)_{t \in \mathbb{R}_+}$  by mean of a SDE driven by a Poisson point measure. This equation is given in Appendix A.2 and corresponds to the mathematical formulation of the individual-based algorithm of Section 5.1. From this, the evolution of  $N_t^{uv}$  can be derived:

$$N_t^{uv} = N_0^{uv} - \int_0^t (r^{uv}(Z_s) - d.N_s^{uv})ds + M_s^{uv} \quad (2.13)$$

where  $M^{uv}$  is a square integrable martingale starting at 0 that can be written explicitly in term of the Poisson point measure and with bracket:

$$\langle M^{uv} \rangle_t = \int_0^t (r^{uv}(Z_s) - d.N_s^{uv})ds. \quad (2.14)$$

These SDEs are linked in large population with classical ordinary differential equations (ODEs) of population dynamics, which are more usual in the biological literature (see (2.19) in the sequel). In similar cases with such nonlinear dynamics, we know that these ODEs arise as deterministic approximations of the stochastic equation under a certain large population limit (see [11, 14, 16, 40]). Apart from providing the mathematical frame under which the SDEs can be approximated by ODEs, these limit theorems may be interesting for statistical estimation, in particular for linking individual-based statistics with parameter estimates for the ODE (*e.g.* [9, 12]).

**Definition 2.1.** *I) We consider the following sequence of processes  $(Z^K)_{K \in \mathbb{N}^*}$ , where  $\mathbb{N}^* = \mathbb{N} \setminus \{0\}$ .*

*(i) Let  $(Z_0^K)_{K \in \mathbb{N}^*}$  be initial conditions such that there exists a deterministic finite measure on  $E$ ,  $\xi_0 \in \mathcal{M}_F(E)$  such that:*

$$\lim_{K \rightarrow +\infty} K^{-1}Z_0^K(du, dv) = \xi_0(du, dv) \quad \text{and} \quad \exists \varepsilon > 0, \sup_{K \in \mathbb{N}^*} \mathbb{E}((N_0^K/K)^{2+\varepsilon}) < +\infty, \quad (2.15)$$

where  $N_t^K = \langle Z_t^K, 1 \rangle$  is the size of the population described by  $Z_t^K$ .

(ii) The reproduction rate  $r(x)$  is replaced by  $r^K(x) = r(x/K)$ . The death rate  $d$  is unchanged.

II) We also introduce the following sequence of renormalized processes  $(Z^{(K)})_{K \in \mathbb{N}^*}$  defined by:

$$\forall K \in \mathbb{N}^*, \forall t \in \mathbb{R}_+, Z_t^{(K)}(du, dv) = \frac{1}{K} Z_t^K(du, dv). \quad (2.16)$$

We define by  $N_t^{(K)} = N_t^K/K$  the mass of  $Z_t^{(K)}$ , that is the renormalized size of the population.

We use exponents  $(K)$  with brackets for the renormalized quantities and exponents  $K$  without brackets for the non-renormalized ones. Let us give some comments on Definition 2.1. Point  $(I - i)$  means that the initial population is of order  $K$ . To counterbalance this effect, we renormalize the size of the individuals in  $1/K$  (Point II) so that the population mass remains of the order of a constant. The renormalization of the reproduction rate in  $(I - ii)$  is a kind of localization factor: if the size of the population is larger, only the neighborhood of a give individual will affect its reproduction rate. The moment condition in (2.15) is technical and ensures that (see [16] for a proof):

$$\forall T \in \mathbb{R}_+, \sup_{K \in \mathbb{N}^*} \mathbb{E} \left( \sup_{t \in [0, T]} (N_t^{(K)})^2 \right) < +\infty. \quad (2.17)$$

The ODEs are obtained when  $K \rightarrow +\infty$ . The corresponding limit theorem is stated in the next proposition and proved in appendix.

**Proposition 2.2.** *The sequence of renormalized processes  $(Z^{(K)})_{K \in \mathbb{N}^*}$  converges uniformly, when  $K \rightarrow +\infty$  to the process of  $\mathcal{C}(\mathbb{R}_+, \mathcal{M}_F(E))$  such that:*

$$\xi_t(du, dv) = \sum_{1 \leq u' \leq v' \leq n} n_t^{u'v'} \delta_{u', v'}(du, dv), \quad (2.18)$$

where for every  $(u', v') \in E$ ,  $n_t^{u'v'}$  is the continuous number of plants of type  $\{u', v'\}$  at time  $t$  and satisfies the following ODE:

$$\frac{dn_t^{u'v'}}{dt} = r^{u'v'}(\xi_t) - d \cdot n_t^{u'v'} \quad (2.19)$$

where  $r^{u'v'}(\xi_t)$  is obtained from (2.9) by replacing all the  $N^{uv}$ 's by  $n^{uv}$ 's.

## 2.4 Particular case of distylous flowers

The most simple case of SSI is distylous species where  $n = 2$  and  $\Phi_P = \Phi_S \equiv \Phi$ . We detail this case, which will be considered carefully in all the rest of the paper.

In this case, the possible genotypes are  $\{1, 1\}$ ,  $\{1, 2\}$  and  $\{2, 2\}$ . The population can be described by  $N^{11}$ ,  $N^{12}$  and  $N^{22}$ . Two alleles 1 and 2 are codominant if:

$$\Phi(2e_1) = e_1, \quad \Phi(2e_2) = e_2, \quad \Phi(e_1 + e_2) = e_1 + e_2. \quad (2.20)$$

The allele 2 is dominant and 1 is recessive if:

$$\Phi(2e_1) = e_1, \quad \Phi(2e_2) = e_2, \quad \Phi(e_1 + e_2) = e_2. \quad (2.21)$$

**Proposition 2.3.** *In the case of codominance (2.20), there is almost sure extinction of the population.*

*Proof.* Since  $\Phi(e_1 + e_2) \cdot \Phi(e_1) = \Phi(e_1 + e_2) \cdot \Phi(e_2) = 1$  and  $\Phi(e_1 + e_2) \cdot \Phi(e_1 + e_2) = 2$ , heterozygous individuals  $\{1, 2\}$  are unable to mate with any individual. The only possible match is between individuals  $\{1, 1\}$  and  $\{2, 2\}$ , but this produces individuals  $\{1, 2\}$  which have no compatible mate. Hence, there is at most two generations of individuals. Since the death rate is a positive constant  $d > 0$ , extinction happens in finite time almost surely. ■

In the sequel, we will therefore consider the case where allele 1 and 2 are not codominant, which corresponds to what happens in natural populations. Let us consider the case where 2 is dominant and 1 recessive (2.21), the symmetric case being treated in the same manner. In this case,  $\{1, 1\}$  can mate with  $\{1, 2\}$  and  $\{2, 2\}$  whereas the latter can only mate with  $\{1, 1\}$ . The sizes of the respective compatible populations (2.4) are:

$$\bar{N}_t^{11} = N_t^{12} + N_t^{22}, \quad \bar{N}_t^{12} = N_t^{11}, \quad \bar{N}_t^{22} = N_t^{11}. \quad (2.22)$$

First, since none of these matings produces offsprings of type  $\{2, 2\}$ , this type is only present in the first generation and hence disappears in finite time almost surely. For the sake of simplicity, we assume that the initial condition is only made of individuals of genotypes  $\{1, 1\}$  and  $\{1, 2\}$ . In this case, the type  $\{2, 2\}$  never appears and  $N_t^{12} = N_t - N_t^{11}$ . Individuals of type  $\{1, 1\}$  can only reproduce with  $\{1, 2\}$  and reciprocally. As soon as one of the type  $\{1, 1\}$  or  $\{1, 2\}$  disappears, the whole population is bounded to extinction since the remaining type can not reproduce any more. We are lead to study random walks on the positive quadrant, absorbed on the axis  $\{x = 0\}$  and  $\{y = 0\}$ .

Let us consider Wright's model (Model 1 of Section 2.2.1 as an illustration. In the absence of  $\{2, 2\}$ , we have the simplification  $\bar{p}^{11}(1, 2) = \bar{p}^{12}(1, 1) = 1$ . Our random walk is given by the equations (2.13).

$$\begin{aligned} N_t^{11} &= N_0^{11} + \int_0^t \left( \frac{1}{2} (r(N_s^{12})N_s^{11} + r(N_s^{11})N_s^{12}) \mathbb{1}_{N_s^{11} > 0} \mathbb{1}_{N_s^{12} > 0} - d.N_s^{11} \right) ds + M_s^{11} \\ N_t^{12} &= N_0^{12} + \int_0^t \left( \frac{1}{2} (r(N_s^{12})N_s^{11} + r(N_s^{11})N_s^{12}) \mathbb{1}_{N_s^{11} > 0} \mathbb{1}_{N_s^{12} > 0} - d.N_s^{12} \right) ds + M_s^{12}. \end{aligned} \quad (2.23)$$

A particular significance is given to the escape time from the first quadrant:

$$\tau = \inf\{t \in \mathbb{R}_+, N_t^{11} = 0 \text{ or } N_t^{12} = 0\}. \quad (2.24)$$

On the set  $\{\tau < +\infty\}$ , the population gets extinct in finite time almost surely, whereas on the set  $\{\tau = +\infty\}$  the population survives forever.

### 3 Large populations of distylous flowers

We consider the three models introduced in Sections 2.2.1-2.2.3 for the distylous populations of Section 2.4 and address the questions of determining when SSI are advantageous with respect to self-fertilization and inbreeding depression. The study is carried in the case where the population is large and the ODEs studied in Section 2.3 are used. The case of small population is tackled in Section 4. In Sections 3.1 to 3.3, we study the stationary solutions and their stabilities in the case of Models 1 to 3 (Sections 2.2.1 to 2.2.3). Threshold phenomena and asymmetries are highlighted. In Section 3.4, comparisons between a SSI and a system with self-fertility and inbreeding depression are studied.

For Wright (Model 1) and dependence (Model 2) models, the ODEs approximations become:

$$\begin{pmatrix} n_t^{11} \\ n_t^{12} \end{pmatrix} = \begin{pmatrix} n_0^{11} \\ n_0^{12} \end{pmatrix} + \int_0^t \begin{pmatrix} \frac{1}{2} (r(n_s^{12})n_s^{11} + r(n_s^{11})n_s^{12}) \mathbb{1}_{n_s^{11} > 0} \mathbb{1}_{n_s^{12} > 0} - dn_s^{11} \\ \frac{1}{2} (r(n_s^{12})n_s^{11} + r(n_s^{11})n_s^{12}) \mathbb{1}_{n_s^{11} > 0} \mathbb{1}_{n_s^{12} > 0} - dn_s^{12} \end{pmatrix} ds, \quad (3.1)$$

which gives with classical arguments on the regularity of solutions:

$$\begin{aligned}\frac{dn_t^{11}}{dt} &= \frac{1}{2}(r(n_t^{12})n_t^{11} + r(n_t^{11})n_t^{12})\mathbb{1}_{n_t^{11}>0}\mathbb{1}_{n_t^{12}>0} - dn_t^{11} \\ \frac{dn_t^{12}}{dt} &= \frac{1}{2}(r(n_t^{12})n_t^{11} + r(n_t^{11})n_t^{12})\mathbb{1}_{n_t^{11}>0}\mathbb{1}_{n_t^{12}>0} - dn_t^{12},\end{aligned}\quad (3.2)$$

with the initial conditions  $(n_0^{11}, n_0^{12})$ . The roles of  $n^{11}$  and  $n^{12}$  are symmetric. It is easy to see that when  $n^{11}$  vanishes, the solutions remain on the boundary  $\{n^{11} = 0\}$ . There is existence and uniqueness of the solutions on  $(\mathbb{R}_+^*)^2$ ,  $\{0\} \times \mathbb{R}_+$  and  $\mathbb{R}_+ \times \{0\}$ , from which we deduce the existence of a unique solution for every initial condition  $(n_0^{11}, n_0^{12})$ .

### 3.1 Wright's model (Model 1) in a large population

Let us consider Wright's model *i.e.* (3.2) with a constant individual reproduction rate  $\bar{r}$ . The system (3.2) without the indicator in the right hand sides becomes:

$$\frac{d}{dt} \begin{pmatrix} n_t^{11} \\ n_t^{12} \end{pmatrix} = A \begin{pmatrix} n_t^{11} \\ n_t^{12} \end{pmatrix} \quad \text{where} \quad A = \begin{pmatrix} \frac{\bar{r}}{2} - d & \frac{\bar{r}}{2} \\ \frac{\bar{r}}{2} & \frac{\bar{r}}{2} - d \end{pmatrix} = \frac{\bar{r}}{2}J - dI, \quad (3.3)$$

where  $J$  is the square  $2 \times 2$ -matrix filled with ones and  $I$  is the identity  $2 \times 2$  matrix.

**Proposition 3.1.** *In the case of a constant individual reproduction rate  $\bar{r}$ , there exists a unique solution for (3.2), which coincides with the solution of (3.3) on  $\mathbb{R}_+$ :*

$$\begin{aligned}n_t^{11} &= \frac{1}{2} \left( n_0^{11} (e^{(r-d)t} + e^{-dt}) + n_0^{12} (e^{(r-d)t} - e^{-dt}) \right) \\ n_t^{12} &= \frac{1}{2} \left( n_0^{11} (e^{(r-d)t} - e^{-dt}) + n_0^{12} (e^{(r-d)t} + e^{-dt}) \right).\end{aligned}\quad (3.4)$$

and:

$$\lim_{t \rightarrow +\infty} e^{-(r-d)t} n_t^{11} = \lim_{t \rightarrow +\infty} e^{-(r-d)t} n_t^{12} = (n_0^{11} + n_0^{12})/2.$$

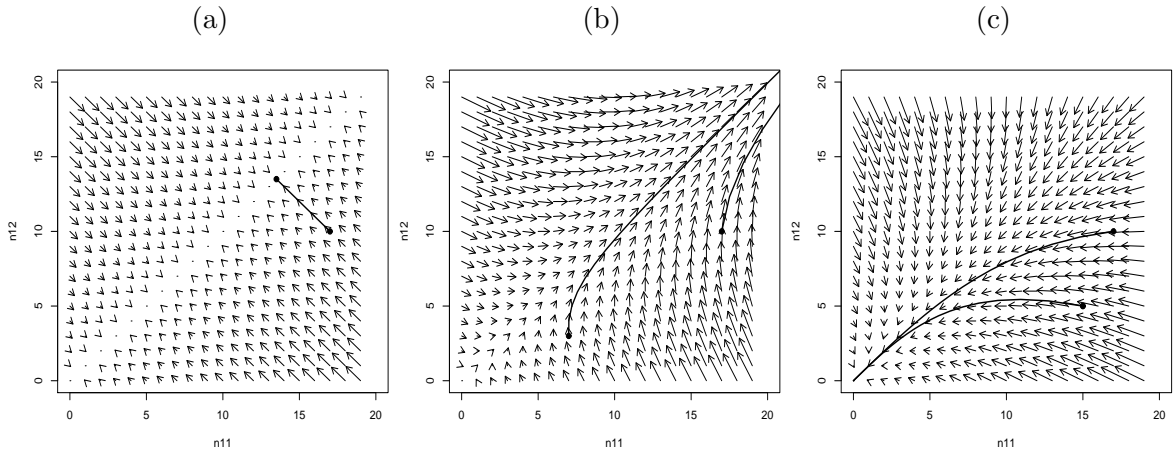


Figure 2: Solutions  $(n_t^{11}, n_t^{12})_{t \geq 0}$  of (3.2) in the (a): critical ( $r = 2, d = 2$ ), (b): supercritical ( $r = 4, d = 3$ ) and (c): subcritical ( $r = 2, d = 3$ ) cases.

**Corollary 3.2.** *We recover a natural disjonction between  $r > d$ ,  $r < d$  and  $r = d$ . The first case is the supercritical case where there is survival of the population, which size grows to infinity. In the second case, there is asymptotic extinction of the population and we will denote it by subcritical case. In the third case, the critical case, the solution converges to an equilibrium.*

**Remark 3.3.** *It is remarkable that in the large population approximation, for constant reproduction rates, the behavior is the same as for the case of compatible reproduction, in which the ODE for the population size is:*

$$\frac{dn}{dt} = (r - d)n.$$

*Proof of Prop. 3.1.* Existence and uniqueness of the solutions of (3.3) in  $C^\infty(\mathbb{R}_+, \mathbb{R}^2)$  hold by Cauchy-Lipschitz theorem. In every cases, the solutions of (3.2) coincide with the solution of (3.3) until one of the component equals zero. Let us denote by  $t^0$  the time at which this happens and which may be infinite in case the trajectory of the solution of (3.3) does not intersect the abscissa or ordinate axes. This implies existence and uniqueness until the time  $t^0$  of the solution of (3.2).

Let us solve (3.3). The matrix  $A$  admits  $r - d$  and  $-d$  as eigenvalues respectively associated with the eigenvectors  $(1/\sqrt{2}, 1/\sqrt{2})$  and  $(1/\sqrt{2}, -1/\sqrt{2})$ . For the system (3.3), there is a unique solution for every initial condition  $(n_0^{11}, n_0^{12}) \in (0, +\infty)^2$  such that  $t \mapsto (n_t^{11}, n_t^{12})$  is of class  $C^\infty$ .

$$\begin{pmatrix} n_t^{11} \\ n_t^{12} \end{pmatrix} = \frac{1}{\sqrt{2}} \begin{pmatrix} 1 & 1 \\ 1 & -1 \end{pmatrix} \begin{pmatrix} C_0 e^{(r-d)t} \\ C_1 e^{-d.t} \end{pmatrix}. \quad (3.5)$$

The constants  $C_0$  and  $C_1$  are obtained from the initial condition. Solving (3.5) in  $(C_0, C_1)$  for  $t = 0$ :

$$C_0 = \frac{\sqrt{2}}{2}(n_0^{11} + n_0^{12}), \quad C_1 = \frac{\sqrt{2}}{2}(n_0^{11} - n_0^{12}). \quad (3.6)$$

Hence this provides (3.4).

The question is whether the trajectories of (3.4) remain in the positive quadrant.

$$n_t^{11} = 0 \quad \Leftrightarrow \quad n_0^{11}(e^{rt} + 1) + n_0^{12}(e^{rt} - 1) = 0 \quad \Leftrightarrow \quad e^{rt} = \frac{n_0^{12} - n_0^{11}}{n_0^{11} + n_0^{12}}. \quad (3.7)$$

This equation has no positive solution in  $t$  since the right hand side is smaller than 1 (and possibly non positive). Similar computation holds if one solves  $n_t^{12} = 0$ . Hence, the solutions of (3.2) and (3.3) coincide on  $\mathbb{R}_+$  and  $t_0 = +\infty$ .

The long time behavior is obtained by noticing that whatever the case, the dominant factor in (3.4) is  $\exp((r - d)t)$ . ■

### 3.2 Dependence model (Model 2) in a large population

We now turn to the study in the case of a variable individual reproduction rate  $r(\cdot)$ . First, we consider the general case of a bounded continuous nonnegative function  $r(\cdot)$ , and then we focus on the functional form given in the Dependence model ((2.6) of Section 2.2.2). The ODEs limits are given in (3.2). Conclusions are summed up at the end of the subsection.

Let us start with a bounded continuous nonnegative function  $r(\cdot)$ . The trivial solution  $(0, 0)$  provides the first stationary solution. Let us look for a non trivial stationary solution. Because of the symmetry in  $n^{11}$  and  $n^{12}$ , if a nontrivial stationary solution exists, it satisfies  $n^{11,*} = n^{12,*} := n^*$ . The latter value solves:

$$r(n^*)n^* = dn^* \quad \Leftrightarrow \quad r(n^*) = d. \quad (3.8)$$

The number of non trivial stationary solutions depends on the number of roots of (3.8).

**Remark 3.4.** *Notice that the total population size at equilibrium is then  $2n^*$ , which is twice the size at equilibrium in absence of self-incompatibility. Indeed, in the latter case, the size of the population at equilibrium satisfies (3.8) and is thus  $n^*$ .*

We now examine the stability of the stationary solutions and recall the definitions in Verhulst [43].

**Definition 3.5.** An equilibrium  $x^*$  is a positive attractor if there exists a neighborhood of  $x^*$  such that the solutions associated with any initial condition in this neighborhood converge to  $x^*$  when  $t \rightarrow +\infty$ . In the case where this property holds for  $t \rightarrow -\infty$ , we say that  $x^*$  is a negative attractor.

**Proposition 3.6.** The trivial equilibrium  $(0, 0)$  is:

- (i) a positive attractor if  $r(0) < d$ ,
- (ii) a saddle point if  $r(0) > d$ .

*Proof of Prop 3.6.* Because of the indicators in (3.2), we know that once one component has reached zero, it can not escape. We consider the stability of the trivial solution  $(0, 0)$  for the ODE (3.2) without the indicators as we know that before one of component reaches zero, these systems have the same solutions. We use the classical linearization methods (e.g. Verhulst [42], Chap. 3). The linearization of the ODE without indicators around an equilibrium  $(n^{11}, n^{12})$  leads us to consider the Jacobian matrix of the system at this point:

$$\mathfrak{J}(n^{11}, n^{12}) = \begin{pmatrix} \frac{r(n^{12})}{2} + \frac{r'(n^{11})n^{12}}{2} - d & \frac{r'(n^{12})n^{11}}{2} + \frac{r(n^{11})}{2} \\ \frac{r(n^{12})}{2} + \frac{r'(n^{11})n^{12}}{2} & \frac{r'(n^{12})n^{11}}{2} + \frac{r(n^{11})}{2} - d \end{pmatrix} \quad (3.9)$$

For the equilibrium  $(0, 0)$ , we obtain:

$$\mathfrak{J}(0, 0) = \begin{pmatrix} \frac{r(0)}{2} - d & \frac{r(0)}{2} \\ \frac{r(0)}{2} & \frac{r(0)}{2} - d \end{pmatrix} = \frac{r(0)}{2} J - dI. \quad (3.10)$$

This matrix is the same as the matrix  $A$  in (3.3) and its eigenvalues are  $r(0) - d$  and  $-d$  respectively associated with the eigenvectors  $(1/\sqrt{2}, 1/\sqrt{2})$  and  $(1/\sqrt{2}, -1/\sqrt{2})$ . If  $r(0) < d$ , then both eigenvalues are non positive and  $(0, 0)$  is a positive attractor for the system without indicators, and hence also for (3.2). If  $r(0) > d$  then there is a positive and a negative eigenvalue. In this case,  $(0, 0)$  is a saddle point for the system without indicators. This entails as in the proof of Prop 3.1 that  $n_t^{11} + n_t^{12}$  converges to  $+\infty$  while  $n_t^{11} - n_t^{12}$  converges to zero. Thus, in the neighborhood from zero, for (3.2) and because of the indicators, if the trajectories remain in the positive quadrant, then the solutions are the same as for the system without indicator: there is no extinction. ■

**Proposition 3.7.** For an equilibrium  $(n^*, n^*)$  with  $n^* > 0$ :

- (i) If  $r'(n^*) < 0$ , then the equilibrium is a positive attractor,
- (ii) if  $r'(n^*) > 0$ , then the equilibrium is a saddle point.

*Proof.* For the point  $(n^*, n^*)$  the Jacobian matrix of (3.9) becomes:

$$\mathfrak{J}(n^*, n^*) = \begin{pmatrix} \frac{r(n^*)}{2} + \frac{r'(n^*)n^*}{2} - d & \frac{r(n^*)}{2} + \frac{r'(n^*)n^*}{2} \\ \frac{r(n^*)}{2} + \frac{r'(n^*)n^*}{2} & \frac{r(n^*)}{2} + \frac{r'(n^*)n^*}{2} - d \end{pmatrix} = \left( \frac{r(n^*)}{2} + \frac{r'(n^*)n^*}{2} \right) J - dI. \quad (3.11)$$

This matrix is again of the same form as  $A$  introduced in (3.3). The eigenvalues of  $\mathfrak{J}(n^*, n^*)$  are hence  $r(n^*) + r'(n^*)n^* - d$  and  $-d$ , respectively associated with the eigenvectors  $(1/\sqrt{2}, 1/\sqrt{2})$  and  $(1/\sqrt{2}, -1/\sqrt{2})$ . Recalling that  $r(n^*) = d$ , we can simplify the expression of the first eigenvalue:  $r(n^*) + r'(n^*)n^* - d = r'(n^*)n^*$ , which is of the sign of  $r'(n^*)$ . As before, the behavior at the neighborhood of the equilibrium depends on the sign of the eigenvalues. ■

Let us now focus on the particular form (2.6) for the reproduction rate. We compute the stationary solutions  $(n^{11,*}, n^{12,*})$  of (3.2) by starting from (3.8):

$$r(n^*)n^* = dn^* \quad \Leftrightarrow \quad r(n^*) = d \quad \Leftrightarrow \quad \bar{r} \frac{e^{\alpha n^*}}{e^{\alpha n^*} + \beta} = d \Leftrightarrow \quad n^* = \frac{1}{\alpha} \log \left( \frac{\beta d}{\bar{r} - d} \right). \quad (3.12)$$

Of course, we see that the log is well defined iff  $\beta > 0$  and  $\bar{r} > d$ . Moreover, the equilibrium  $(n^*, n^*)$  belongs to the positive quadrant iff

$$\frac{\beta d}{\bar{r} - d} > 1 \quad \Leftrightarrow \quad \bar{r} < d(1 + \beta). \quad (3.13)$$

Since  $r(0) = \frac{\bar{r}}{1+\beta}$ , we notice that the stability condition for the trivial equilibrium,  $r(0) < d$ , is equivalent to the condition (3.13) for the existence of a non-trivial stationary solution. Hence, if  $r(0) < d$ ,  $(0, 0)$  is a positive attractor and there is no other equilibrium, and if  $r(0) > d$ ,  $(0, 0)$  is a repulsive attractor. Indeed,  $(0, 0)$  is a saddle point for the system (3.2) without the indicators. Since the stable variety is the vectorial line of direction  $(1, -1)$  which intersects the positive quadrant only at  $(0, 0)$ , then for the system (3.2), the equilibrium  $(0, 0)$  is a negative attractor.

Moreover, the equilibrium  $(n^*, n^*)$  is always a saddle point as:

$$r'(n) = \bar{r} \frac{\alpha e^{\alpha n} (\beta + e^{\alpha n}) - \alpha e^{2\alpha n}}{(\beta + e^{\alpha n})^2} = \frac{\bar{r} \alpha \beta e^{\alpha n}}{(\beta + e^{\alpha n})^2}, \quad (3.14)$$

is always positive. The stable (resp. unstable) variety is locally the affine line of direction  $(1, -1)$  (resp. the affine line of direction  $(1, 1)$ ). If we draw the affine line of direction  $(1, -1)$  going through  $(n^*, n^*)$  on Fig. 3 (c), it can be seen for a given initial condition  $n_0 = n_0^{11} + n_0^{12}$  close to  $2n^*$  that the trajectories either lead to  $+\infty$  or 0 when  $t \rightarrow +\infty$ , depending on the asymmetry of the initial condition in  $n_0^{11}$  and  $n_0^{12}$ .

In conclusion:

- If  $\bar{r} < d$ , every trajectory converges to  $(0, 0)$ .
- If  $d < \bar{r} < d(1 + \beta)$ , there exists a non-trivial equilibrium that is a saddle point. Trajectories either converge to  $(0, 0)$  or  $\lim_{t \rightarrow +\infty} n_t^{11} = \lim_{t \rightarrow +\infty} n_t^{12} = +\infty$ .
- If  $\bar{r} > d(1 + \beta)$ , there is no non-trivial equilibrium in the positive quadrant as the growth rate is too strong.  $(0, 0)$  is a negative attractor and  $\lim_{t \rightarrow +\infty} n_t^{11} = \lim_{t \rightarrow +\infty} n_t^{12} = +\infty$ .

Let us give two numerical applications illustrated by simulations. For  $\alpha = 1$ ,  $\beta = 1$ ,  $d = 3$  and  $\bar{r} = 3.1$ , we obtain  $n^* = 3.4$ . Since  $r(0) = 1.55$  is smaller than  $d = 3$ ,  $(0, 0)$  is a positive attractor in this case. The solutions hence either converge to zero or to infinity, given the initial condition. For  $\bar{r} = 7$ ,  $n^* = -0.3$  and this equilibrium is not in the positive quadrant. Moreover  $r(0) = 3.5 > d$  and  $(0, 0)$  is a negative attractor and every solution tends to infinity.

**Remark 3.8.** *Let us give some remarks based on the consideration of (3.12). Threshold phenomena appear: when  $d < \bar{r} < d(1 + \beta)$ , we see that contrarily to the case of absence of pollen limitation (Wright's model), there may be either survival or extinction. If the size of the population is too small (if the initial condition belongs to the attracting domain of  $(0, 0)$ ) then there is extinction. There is a threshold implying that survival is possible only for sufficiently large population.*

*On Fig. 3, we see that the minimum size to ensure survival also depends on the composition of the population. It is smaller for population with 1/2 individuals of type  $\{1, 1\}$  and 1/2 individuals of type  $\{1, 2\}$ . Thus, the symmetry in mating partners matters for survival or extinction (Fig. 3 (c)).*

*To ensure survival whatever the initial condition, one needs a reproduction rate sufficiently large ( $\bar{r} = d(1 + \beta)$ ) to totally compensate the pollen limitation.*

### 3.3 Fecundity selection model (Model 3) in a large population

We finally study the case of Model 3 (Section 2.2.3). The rate of production of genotypes  $\{1, 1\}$  is:

$$\bar{r} \frac{N_t^{11} N_t^{12}}{N_t}, \quad (3.15)$$

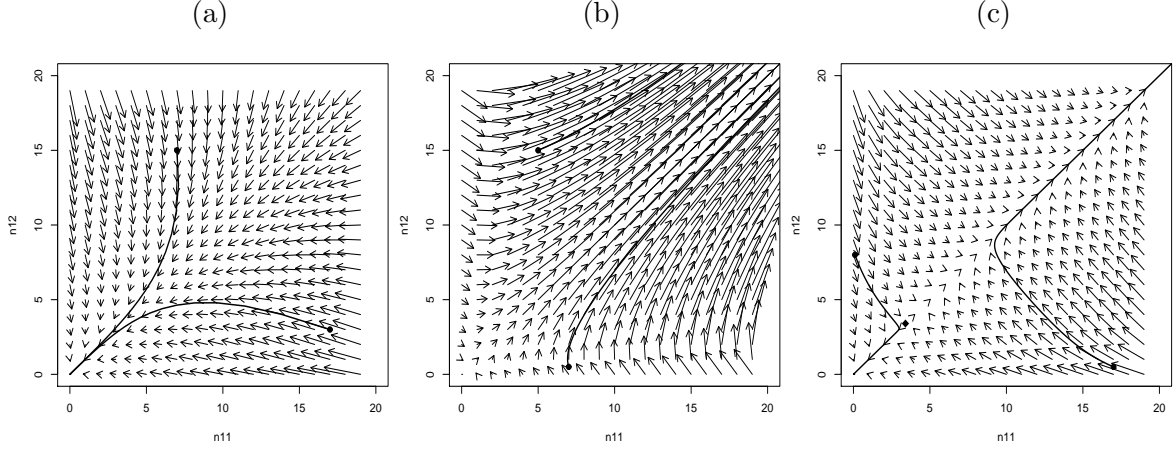


Figure 3: Solutions  $(n_t^{11}, n_t^{12})_{t \geq 0}$  of (3.2) for a reproduction rate of the form (2.6). (a):  $r(0) = 2$ ,  $d = 3$ , (b):  $r(0) = 7$ ,  $d = 3$ , (c):  $r(0) = 3.1$ ,  $d = 3$ . In the example (c), it is seen that at the neighborhood of  $2n^*$ , for similar initial population sizes, populations with higher symmetry are more likely to survive than very disymmetric populations.

which now does not present any discontinuity on the boundaries  $\{N_t^{11} = 0\}$  and  $\{N_t^{12} = 0\}$  any more. The ODE approximation is now:

$$\frac{dn_t^{11}}{dt} = \bar{r} \frac{n_t^{11} n_t^{12}}{n_t^{11} + n_t^{12}} - dn_t^{11}, \quad \frac{dn_t^{12}}{dt} = \bar{r} \frac{n_t^{11} n_t^{12}}{n_t^{11} + n_t^{12}} - dn_t^{12}, \quad (3.16)$$

which admits a unique solution on  $(\mathbb{R}_+^*)^2$ .

**Proposition 3.9.** *Similarly to Wright's model, we have a disjunction into three cases:*

- (i) *If  $r < 2d$  we are in the subcritical case and  $\lim_{t \rightarrow +\infty} n_t^{11} = \lim_{t \rightarrow +\infty} n_t^{12} = 0$ .*
- (ii) *If  $r = 2d$  we are in the critical case and  $(n_t^{11}, n_t^{12})_{t \in \mathbb{R}_+}$  converges to an equilibrium  $(n^*, n^*)$ .*
- (iii) *If  $r > 2d$  we are in the supercritical case and  $\lim_{t \rightarrow +\infty} n_t^{11} = \lim_{t \rightarrow +\infty} n_t^{12} = +\infty$ .*

*The additional coefficient 2 in the criteria comes from the fact that at equilibrium, the probability of mating success of an ovule is 1/2 contrarily to the case of (3.8) where it is 1.*

*Proof.* By symmetry, a non-trivial equilibrium exists iff:

$$\bar{r}n^* = 2dn^* \quad \Leftrightarrow \quad \bar{r} = 2d. \quad (3.17)$$

To obtain the stability of the non-trivial equilibria, we compute the Jacobian matrix of the system (3.16) at  $(n^{11}, n^{12})$ :

$$\mathfrak{J}(n^{11}, n^{12}) = \begin{pmatrix} \bar{r} \left( \frac{n^{12}}{n^{11} + n^{12}} \right)^2 - d & \bar{r} \left( \frac{n^{11}}{n^{11} + n^{12}} \right)^2 \\ \bar{r} \left( \frac{n^{12}}{n^{11} + n^{12}} \right)^2 & \bar{r} \left( \frac{n^{11}}{n^{11} + n^{12}} \right)^2 - d \end{pmatrix} \quad (3.18)$$

For an equilibrium  $(n^*, n^*)$ ,  $\mathfrak{J}(n^*, n^*) = \frac{\bar{r}}{4}J - dI$ , and we are lead to a discussion similar to (3.11). A difficulty arises at the trivial equilibrium  $(0, 0)$  since  $\mathfrak{J}(0, 0)$  is not defined:

$$\lim_{n^{11}, n^{12} \rightarrow 0} \bar{r} \left( \frac{n^{12}}{n^{11} + n^{12}} \right)^2 = \bar{r} \lim_{n^{11}, n^{12} \rightarrow 0} \left( \frac{n^{12}}{n^{11} + n^{12}} \right)^2, \quad (3.19)$$

which is not defined. Thus, the stability of the equilibrium  $(0, 0)$  has to be studied more carefully.

We consider the ODE satisfied by the total size  $n_t = n_t^{11} + n_t^{12}$  of the population and by  $z_t = n_t^{11} \times n_t^{12}$ :

$$\frac{dn_t}{dt} = 2\bar{r} \frac{n_t^{11} n_t^{12}}{n_t^{11} + n_t^{12}} - dn_t, \quad \frac{dz_t}{dt} = \frac{dn_t^{11}}{dt} n_t^{12} + n_t^{11} \frac{dn_t^{12}}{dt} = (\bar{r} - 2d) z_t. \quad (3.20)$$



As a consequence, when  $\bar{r} < 2d$ , there is asymptotic extinction of at least one of the type  $\{1, 1\}$  or  $\{1, 2\}$ , let us assume that it is  $n^{11}$ . Since:

$$\frac{dn_t^{12}}{dt} \leq \bar{r}n_t^{11} - dn_t^{12} \leq \varepsilon - dn_t^{12} \quad (3.21)$$

for a sufficiently large time, one deduce that  $n^{12}$  also converges to zero.

If  $\bar{r} > 2d$ ,

$$\lim_{t \rightarrow +\infty} n_t^{11} \times n_t^{12} = +\infty.$$

One at least of the two subpopulation sizes  $\{1, 1\}$  or  $\{1, 2\}$  tends to infinity. Let us assume that it is  $n^{11}$  and that  $n_t^{11} > n_t^{12}$  for sufficiently large  $t$  (implying that  $n_t^{11}/n_t > 1/2$ ). Writing:

$$\frac{dn_t^{12}}{dt} \geq \bar{r}n_t^{12} - dn_t^{12}, \quad (3.22)$$

we see that  $n^{12}$  also necessarily tends to infinity.

We finally turn to the case where  $\bar{r} = 2d$ . If  $n_t^{11} < n_t^{12}$ , then  $n_t^{11}/2 < n_t^{11}n_t^{12}/n_t < n_t^{12}/2$ , and

$$\frac{dn_t^{11}}{dt} > \left(\frac{\bar{r}}{2} - d\right)n_t^{11} = 0 \quad \text{and} \quad \frac{dn_t^{12}}{dt} < \left(\frac{\bar{r}}{2} - d\right)n_t^{12} = 0.$$

Thus,  $n^{11}$  increases and  $n^{12}$  decreases until they converge to the state where  $n^{11} = n^{12}$ . ■

### 3.4 Comparison with the self-compatible case with inbreeding depression (SCID)

Now that our three models of interest have been considered, we wish to carry comparisons with the SCID cases. Under which condition do our models predict that SSI are advantageous (in some sense defined in the sequel) with respect to self-fertilization ?

#### 3.4.1 Self-compatible distylous population with inbreeding depression

We consider here reproduction rates of the form (2.11). In the case of self-compatible populations with inbreeding depression, the size  $n_t$  of the population in a large population limit follows the ODE:

$$\frac{dn_t}{dt} = \left( (1 - \delta)s\bar{r} + (1 - s)\bar{r}\frac{e^{\alpha n_t}}{\beta + e^{\alpha n_t}} - d \right) n_t. \quad (3.23)$$

The trivial solution defines an equilibrium and:

**Proposition 3.10.** *A non-trivial equilibrium to (3.23) exists iff*

$$\beta[d - \bar{r}s(1 - \delta)] > [\bar{r}(1 - \delta s) - d] > 0. \quad (3.24)$$

(i) *If (3.24) is satisfied, the non-trivial equilibrium  $n^*$  is given by:*

$$n^* = \frac{1}{\alpha} \log \left( \frac{\beta(d - (1 - \delta)s\bar{r})}{\bar{r}(1 - \delta s) - d} \right) \quad (3.25)$$

*This equilibrium is repulsive and 0 is a locally positive attractor. If  $n_0 < n^*$  then the solution converges to zero, else, it grows to infinity.*

(ii) *Else, there is no non-trivial equilibrium in the positive quadrant and there are three possibilities:*

- *If  $\bar{r}(1 - \delta s) - d < 0 \iff \bar{r}(1 - \delta s) < d$ , then there is extinction ( $d$  is too large).*
- *If  $\beta[d - \bar{r}s(1 - \delta)] < 0 \iff \bar{r}s(1 - \delta) > d$ , then there is growth to infinity ( $d$  is too small).*

- If  $[\bar{r}(1 - \delta s) - d] > \beta[d - \bar{r}s(1 - \delta)] > 0$ , then there is growth to infinity ( $d$  is not large enough).

*Proof.* A non-trivial equilibrium  $n^*$  of (3.23) satisfies necessarily:

$$(1 - s)\bar{r} \frac{e^{\alpha n^*}}{\beta + e^{\alpha n^*}} = d - (1 - \delta)s\bar{r} \quad \Leftrightarrow \quad n^* = \frac{1}{\alpha} \log \left( \frac{\beta(d - (1 - \delta)s\bar{r})}{(1 - s)\bar{r} - d + (1 - \delta)s\bar{r}} \right)$$

which provides (3.25) if the log is well defined:

$$(1 - \delta)s\bar{r} < d < (1 - \delta s)\bar{r}. \quad (3.26)$$

By comparison arguments, it is easy to prove that for  $d > (1 - \delta s)\bar{r}$ , every solution converges to 0 as the bracket in the r.h.s. of (3.23) is strictly negative. For  $d < (1 - \delta)s\bar{r}$ , this bracket remains strictly positive and the solutions converge to  $+\infty$ . Under the condition (3.26),  $n^*$  is strictly positive iff

$$\begin{aligned} \beta(d - (1 - \delta)s\bar{r}) > (1 - \delta s)\bar{r} - d &\quad \Leftrightarrow \quad (1 + \beta)d > \bar{r}(1 - \delta s + \beta s(1 - \delta)) \\ &\quad \Leftrightarrow \quad \beta[d - \bar{r}s(1 - \delta)] > [\bar{r}(1 - \delta s) - d]. \end{aligned} \quad (3.27)$$

Notice that when (3.26) is satisfied, the brackets in (3.27) are positive. Equation (3.27) says whether the parameter  $d$  in (3.26) is closer to the lower bound of (3.26) (*i.e.*  $0 < \beta(d - \bar{r}s(1 - \delta)) < \bar{r}(1 - \delta s) - d$ , implying growth of the population size to infinity) or of its upper bound (*i.e.* (3.24), under which there exists a non-trivial equilibrium). Hence, we obtain (3.24) as sufficient and necessary condition for the existence of a non-trivial equilibrium in the positive quarter plane.

On (3.24), we see that the situation is similar to (3.12) with  $d - (1 - \delta)s\bar{r}$  instead of  $d$  and  $(1 - s)\bar{r}$  instead of  $\bar{r}$ . Self-fertilization amounts to a reduction of the natural mortality since individuals can at least breed themselves. However, this introduces a limitation of the maximal number of individuals that can be produced by other matings.

To study the stability of the equilibria 0 and  $n^*$ , we linearize the system and repeat the computation of (3.10) and (3.11). The stability of  $n^*$  depends on the sign of  $r(n^*) + r'(n^*)n^* - d = r'(n^*)n^*$  which is here always positive by (3.14) and by the remark of the preceding paragraph. Hence,  $n^*$  is a negative attractor. The trivial equilibrium 0 is a positive attractor iff

$$r(0) < d \quad \Leftrightarrow \quad (1 - \delta)s\bar{r} + \frac{(1 - s)\bar{r}}{1 + \beta} < d \quad \Leftrightarrow \quad (1 - \delta s + \beta s(1 - \delta))\bar{r} < d(1 + \beta). \quad (3.28)$$

We recognize here the condition (3.27) of existence of a non-trivial equilibrium, which leads to the announced result (i). In the case where (3.24) is not fulfilled, the behavior of the solutions is obtained by comparisons with simple ODEs. ■

### 3.4.2 Comparison with the self-incompatible case

It is natural to compare the self-compatible distylous model of Section 3.4.1 with the SI distylous model of Section 3.2, with the same reproduction rate (2.6). To carry the comparison, we introduce the following criteria:

- We compare, when they exist, the population sizes at the non-trivial equilibria. Heuristically, these sizes provide the limit between the two extreme behaviors that are growth to infinity and extinction. When this equilibrium size is high, large populations are needed to avoid extinction and the population is more "fragile". The corresponding model will be said to be less advantageous.

- We can also compare the range of parameters  $r$  and  $d$  (for fixed  $s$  and  $\delta$ ) for which the population gets extinct. We will say that with respect to this second criterion, the more advantageous conditions correspond to the smaller ranges of such parameters.

We sum up the results of Sections 3.2 and 3.4.1 in Table 1:

Case	Case description	Behavior of the population size
Wright's model (Model 1)		
Case (a.1)	$\bar{r} < d$	Convergence to 0
Case (b.1)	$\bar{r} = d$	Convergence to a stationary solution
Case (c.1)	$\bar{r} > d$	Divergence to $+\infty$
Dependence model (Model 2)		
Case (a.2)	$\bar{r} < d$	Convergence to 0
Case (b.2)	$d < \bar{r} < d(1 + \beta)$	Existence of a saddle point
Case (c.2)	$\bar{r} > d(1 + \beta)$	Divergence to $+\infty$
Fecundity selection model (Model 3)		
Case (a.3)	$\bar{r} < 2d$	Convergence to 0
Case (b.3)	$\bar{r} = 2d$	Convergence to a stationary solution
Case (c.3)	$\bar{r} > 2d$	Divergence to $+\infty$
Self-compatible model without inbreeding depression (Model 4)		
Case (a.4)	$\bar{r} < d$	Convergence to 0
Case (b.4)	$\bar{r} = d$	Convergence to a stationary solution
Case (c.4)	$\bar{r} > d$	Divergence to $+\infty$
Self-compatible with inbreeding depression (SCID) model (Model 5)		
Case (a.5)	$(1 - \delta s)\bar{r} < d$	Convergence to 0
Case (a.5)	$\beta(d - \bar{r}s(1 - \delta)) > \bar{r}(1 - \delta s) - d > 0$	Existence of a repulsive equilibrium
Case (a.5)	$\bar{r} > d \min\left(\frac{1}{(1-\delta)s}, \frac{1+\beta}{1+\beta s - s\delta(1+\beta)}\right)$	Divergence to $+\infty$

Table 1: Summary of the behavior of the population size in the Sections 3.2 and 3.4.1 depending on the respective values of  $\bar{r}$ ,  $d$ ,  $s$  and  $\delta$ . The condition for Case (a.5) is obtained by saying that we have divergence to  $+\infty$  in the SCID model if  $(1 - \delta)s\bar{r} > d$  or if  $(1 - \delta)s\bar{r} < d < \bar{r}s(1 - \delta)$  and  $\bar{r}(1 - \delta s) - d > \beta(d - \bar{r}s(1 - \delta)) > 0$ .

Models 1, 3 and 4 are similar. We have convergence to zero or divergence to infinity except in the particular case when  $\bar{r} = d$  or  $\bar{r} = 2d$ . This shows that under fecundity selection, distylous species are more fragile than under Wright's model or self-compatibility without inbreeding depression. This is expected since there is no pollen limitation or self-incompatibility in the two latter models. Notice also that in absence of pollen limitation, the equilibria and critical, sub- and supercritical regions correspond in Models 1 and 4.

In the sequel, we compare Models 2 and 5, for which there exists a range of parameters for which extinction or divergence to infinity coincide, depending on the initial condition. These models have a similar modelization of pollen limitation (see (2.6)). The difference relies on the penalization by SI in the first case and by inbreeding depression in the second case. This comparison allows us to investigate the conditions on the parameters under which distyly is advantageous on self-fertilization.

**Comparison with respect to the range of parameters** The cases (a.2),  $\dots$ , (c.2), (a.5),  $\dots$  (c.5) are defined in Table 1. Let us consider the set of parameters for which the population gets extinct whatever its initial condition (Cases (a.2) and (a.5)). Since  $\delta > 0$  and  $s > 0$ , we see that this region is larger for the SCID model which in this respect appears as less advantageous than the SI model. The parameter  $(1 - \delta s)$  in Case (a.5) can indeed be interpreted as the proportion of seeds which survived,

*i.e.* when excluding the fraction of non-viable seeds produced by self-fertilization. This term thus appears as an extra death parameter that is not present in the SI model. In our large population setting, this penalty is more important than the loss of partners that may face individuals in the SI model.

We now turn to the Cases (c.2) and (c.5) where the population size diverges to infinity. The SI model is advantageous on the SCID model iff:

$$(1 + \beta) \leq \min\left(\frac{1}{(1 - \delta)s}, \frac{1 + \beta}{1 + \beta s - s\delta(1 + \beta)}\right)$$

$$\Leftrightarrow \frac{1}{1 + \beta} \geq \min(s(1 - \delta), 1 - \delta) = s(1 - \delta).$$

This condition shows that when the self-fertilization has a too low efficiency, *i.e.* when inbreeding depression is large, it is less advantageous than SI. The latter efficiency is expressed by comparing the fraction of viable seeds produced by self-fertilization to the initial fraction  $1/1 + \beta = r(0)/\bar{r}$  of seeds produced without self-fertilization when only an infinitesimal quantity of compatible individuals is present.

**Comparison with respect to the size of the population at equilibrium** Let us now consider the case when both (b.2) and (b.5) are satisfied. When there exists a non-trivial equilibrium, we have seen that the behavior of the solution is determined by its initial condition. The size of the equilibrium provides an idea of how many individuals are necessary to allow survival, even if in cases as in (3.12), the symmetry of the initial condition may matter. Let us thus compare the sizes at equilibrium in (3.12) and (3.25). The size of the population at equilibrium in the SCID model is equal to the size of the population in the SI model when:

$$\frac{1}{\alpha} \log\left(\frac{\beta(d - (1 - \delta)s\bar{r})}{(1 - \delta s)\bar{r} - d}\right) = \frac{2}{\alpha} \log\left(\frac{\beta d}{\bar{r} - d}\right) \Leftrightarrow \frac{\beta(d - (1 - \delta)s\bar{r})}{(1 - \delta s)\bar{r} - d} = \left(\frac{\beta d}{\bar{r} - d}\right)^2. \quad (3.29)$$

Let us study:

$$f(s, \delta) = \frac{\beta d - \beta\bar{r}(1 - \delta)s}{(\bar{r} - d) - \bar{r}\delta s}. \quad (3.30)$$

Notice that  $s = 0$  corresponds to the self-compatible case without inbreeding depression:  $f(0, \delta) = \beta d/(\bar{r} - d)$ . The case  $s = 1$  provides a model of compatible population with reproduction rate  $\bar{r}(1 - \delta)$  and we have  $f(1, \delta) = -\beta$ . For any given  $\delta \in [0, 1]$ ,  $f(\cdot, \delta)$  is a homographic function of  $s$ , defined on  $[0, 1] \setminus \{s_0\}$  with  $s_0 := (\bar{r} - d)/\bar{r}\delta$ . The latter value belongs to  $[0, 1]$  iff

$$d < \bar{r} < \frac{d}{1 - \delta}. \quad (3.31)$$

On the domain  $[0, 1] \setminus \{s_0\}$ :

$$\partial_s f(s, \delta) = -\frac{\beta\bar{r}(\bar{r}(1 - \delta) - d)}{((\bar{r} - d) - \bar{r}\delta s)^2}, \quad (3.32)$$

which has the same sign as  $d - \bar{r}(1 - \delta)$ .

In a nutshell,

- If  $d < \bar{r}(1 - \delta)$ , the  $s \mapsto f(s, \delta)$  is a decreasing continuous function on  $[0, 1]$ , upper bounded by  $f(0, \delta) = \beta d/(\bar{r} - d) < (\beta d/(\bar{r} - d))^2$  (which is larger than 1 in Case (b.2)). In this case, there is no solution to (3.29). The size at equilibrium of the model with self-fertilization is always lower than its counterpart with self-incompatible reproduction: the cost of self-incompatibility may not be counterbalanced in this case.

- If  $d > \bar{r}(1 - \delta)$ , then  $f(\cdot, \delta)$  is an increasing function from  $[0, s_0)$  into  $[f(0, \delta), +\infty)$  and from  $(s_0, 1]$  to  $(-\infty, -\beta]$ . Thus,  $s_0$  is the highest fraction of self-fertilization that allows the existence of an equilibrium (3.25) and we will thus only consider  $s < s_0$ . There exists a unique solution  $r_0 \in [0, s_0)$  to (3.29) given by:

$$r_0 = \frac{\left(\frac{\beta d}{\bar{r}-d}\right)^2 (\bar{r} - d) - \beta d}{\bar{r} \left(\delta \left(\frac{\beta d}{\bar{r}-d}\right)^2 - \beta(1 - \delta)\right)}.$$

For any  $s \in (r_0, s_0)$ , the size of the equilibrium in the self-incompatible case is smaller than its counterpart with possible self-inbreeding. This means that if the fraction of descendants produced by self-fertilization is too high, then it is advantageous to switch to self-incompatibility.

## 4 Small distylous populations

We now consider cases in which the deterministic approximation may not be taken. In this section, we focus on the cases with constant rate of ovule production (Wright's model (Model 1), the fecundity selection model (Model 3) and their counterpart with possible self-fertilization (Model 4)), for which computations are tractable. Simulations for the other models are carried in Section 5. We are interested in the study of extinction probabilities.

In the sequel, we will denote by  $(T_k)_{k \in \mathbb{N}}$  the successive jump times of the process  $(N_t^{11}, N_t^{12})_{t \geq 0}$ , with the convention  $T_0 = 0$ . We will be led to consider the continuous time process  $(N_t^{11}, N_t^{12})_{t \geq 0}$  as well as the discrete time process  $(N_{T_k}^{11}, N_{T_k}^{12})_{k \in \mathbb{N}}$ .

The denominations for super and subcritical cases are used for small populations but with some slight differences with the case considered in Section 3: even when the reproduction rate is very high in comparison of the death rate, there may always be a probability of extinction by demographic stochasticity. With the terminology of branching processes (*e.g.* [3]), we say that we are in the supercritical case if there is a positive probability of survival. In the subcritical case, there is almost sure extinction.

### 4.1 Wright's model (Model 1) in a small population

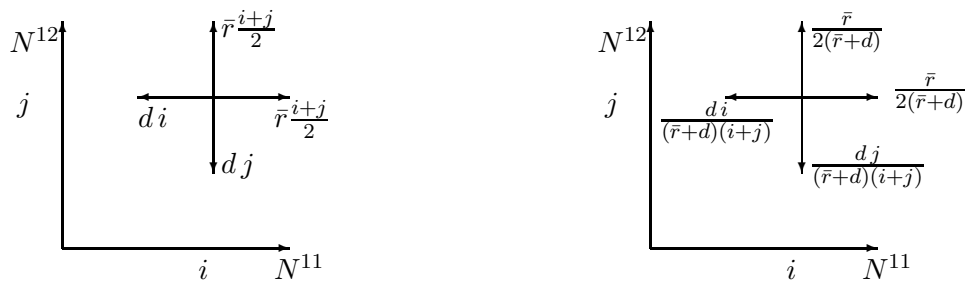


Figure 4: Evolution of the distylous system  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  in Wright's model (Model 1). Rates of events are pictured on the left, while transition probabilities of the embedded Markov chain are represented on the right.

#### 4.1.1 Extinction probabilities: recurrence equation

A technical difficulty comes from the fact that the transition rates of  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  and the transition probabilities of the associated discrete time Markov chain vary with the position (see Fig. 4).

Techniques developed in the literature of random walks on positive quadrants usually focus on homogeneous random walks (*e.g.* Klein Haneveld and Pittenger [18], Fayolle *et al.* [15], Kurkova and Raschel [23]).

For  $i, j \in \mathbb{N}$ , we denote by  $p_{i,j} = \mathbb{P}_{ij}(\exists t \geq 0, N_t^{11} = 0 \text{ or } N_t^{12} = 0)$ , where  $\mathbb{P}_{ij}$  means that we start with the initial condition  $N_0^{11} = i$  and  $N_0^{12} = j$ . By symmetry arguments, we have:

$$\forall i, j \in \mathbb{N}, \quad p_{i,j} = p_{j,i}. \quad (4.1)$$

Moreover,

$$\text{when } i = 0 \text{ or } j = 0, \quad p_{i,j} = 1. \quad (4.2)$$

We first establish a recurrence equation satisfied by their extinction probabilities:

**Proposition 4.1.** (i) *The extinction probabilities  $p_{i,j}$  for  $i, j \in \mathbb{N}^*$  satisfy the following recurrence equations:*

$$p_{i,j} = \frac{di}{(\bar{r} + d)(i + j)} p_{i-1,j} + \frac{dj}{(\bar{r} + d)(i + j)} p_{i,j-1} + \frac{\bar{r}}{2(\bar{r} + d)} p_{i,j+1} + \frac{\bar{r}}{2(\bar{r} + d)} p_{i+1,j}. \quad (4.3)$$

Hence the family  $(p_{i,j})_{i,j \in \mathbb{N}}$  is a solution of the Dirichlet problem (4.3) with boundary condition (4.2). Uniqueness of the solution may not hold, but the extinction probabilities  $(p_{i,j})_{i,j \in \mathbb{N}}$  define the smallest positive solution of this problem.

(ii) *We deduce from (4.3) that:*

$$di(p_{i,j} - p_{i-1,j}) + dj(p_{i,j} - p_{i,j-1}) = \frac{\bar{r}(i + j)}{2} [(p_{i,j+1} - p_{i,j}) + (p_{i+1,j} - p_{i,j})]. \quad (4.4)$$

(iii) *Assume that the probabilities  $p_{i,1}$  for  $i \in \mathbb{N}^*$  are given. Then, the other probabilities  $p_{i,j}$  are completely determined.*

*Proof.* We refer to [24] for the proof, which follows classical arguments found in [4] or [35]. ■

The recurrence equation (4.3) may not admit a unique positive solution. Point (iii) of Prop. 4.1 tells us that to every boundary condition  $(p_{i,1}, i \in \mathbb{N})$  corresponds a solution. Point (i) tells us that the smallest positive solution gives the extinction probabilities  $p_{i,j}$ . The computation of the  $p_{i,j}$ 's and the determination of the probabilities  $p_{i,1}$ 's is a work in progress by Lafitte Raschel and Tran [24]. By coupling and comparison techniques, we manage to define subcritical, critical and supercritical regimes, where there is almost sure extinction or positive probability of survival of the random walk killed at the boundary.

#### 4.1.2 Extinction probabilities: coupling approach

It is difficult to solve (4.3) or (4.4). Our purpose is to approximate the extinction probability with couplings. Lower and upper bounds are provided by the next Proposition.

**Proposition 4.2.** *Assume that  $(N_0^{11}, N_0^{12}) = (i, j)$  is a couple of positive integers. Then:*

(i) *The population gets extinct in finite time almost surely if and only if  $\bar{r} \leq d$ .*

(ii) *If  $\bar{r} > d$ , there is a strictly positive probability of survival  $1 - p_{i,j}$  when starting from any  $i, j \in \mathbb{N}^*$  and the extinction probability  $p_{i,j}$  satisfies:*

$$\left(\frac{d}{\bar{r}}\right)^{i+j} \leq p_{i,j} \leq \left(\frac{d}{\bar{r}}\right)^i + \left(\frac{d}{\bar{r}}\right)^j - \left(\frac{d}{\bar{r}}\right)^{i+j} \quad (4.5)$$

To prove this, we introduce the processes that dominate and lower bound  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  stochastically, and that allow to obtain the bounds in (4.5).

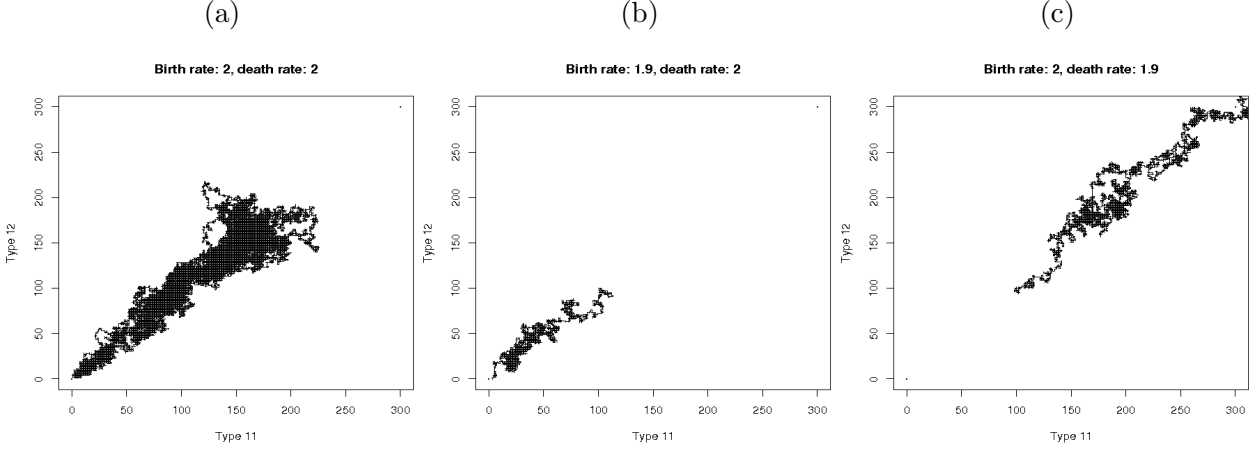


Figure 5: Simulation of the trajectories  $(N_t^{11}, N_t^{12})_{t \geq 0}$  in the critical, subcritical and supercritical cases. The number of individuals of type  $\{1, 1\}$  is in abscissa, while the number of individuals of type  $\{1, 2\}$  is in ordinate. For the three simulations, the initial condition is  $(100, 100)$ .

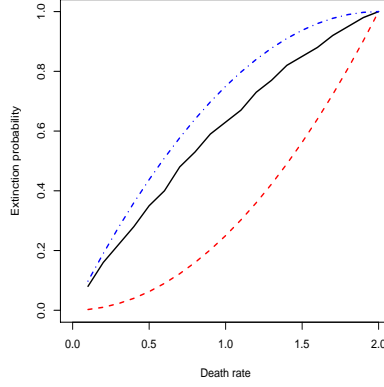


Figure 6: Simulated extinction probability for  $(N^{11}, N^{12})$  in plain line, together with the extinction probability of  $(\tilde{N}^{11}, \tilde{N}^{12})$  in dashed red line and of  $(\hat{N}^{11}, \hat{N}^{12})$  in blue dash-dots. We start with  $(N_0^{11}, N_0^{12}) = (1, 1)$ .

### 4.1.3 Stochastic domination and proof of the lower bound

The stochastic domination presented here also works for general division rates. The random walks (2.23) can be stochastically dominated by the random walks  $\tilde{N}^{11}$  and  $\tilde{N}^{12}$  with reproduction rates:

$$\frac{1}{2}(r(\tilde{N}_s^{12})\tilde{N}_s^{11} + r(\tilde{N}_s^{11})\tilde{N}_s^{12}) \text{ instead of } \frac{1}{2}(r(N_s^{12})N_s^{11} + r(N_s^{11})N_s^{12})\mathbb{1}_{N_s^{11} > 0}\mathbb{1}_{N_s^{12} > 0} \quad (4.6)$$

such that until time  $\tau$ , the processes  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  and  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  have the same paths (this can be obtained by using the same Poisson measures for  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  and  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$ , see Appendix A.2). The random walks  $\tilde{N}^{11}$  and  $\tilde{N}^{12}$  satisfy:

$$\begin{aligned} \tilde{N}_t^{11} &= N_0^{11} + \int_0^t \left( \frac{1}{2}(r(\tilde{N}_s^{12})\tilde{N}_s^{11} + r(\tilde{N}_s^{11})\tilde{N}_s^{12}) - d.\tilde{N}_s^{11} \right) ds + \tilde{M}_s^{11} \\ \tilde{N}_t^{12} &= N_0^{12} + \int_0^t \left( \frac{1}{2}(r(\tilde{N}_s^{12})\tilde{N}_s^{11} + r(\tilde{N}_s^{11})\tilde{N}_s^{12}) - d.\tilde{N}_s^{12} \right) ds + \tilde{M}_s^{12}. \end{aligned} \quad (4.7)$$

We define by  $\tilde{N}_t = \tilde{N}_t^{11} + \tilde{N}_t^{12}$  the total size of the population ruled by (4.6). As  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  and  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  coincide until time  $\tau$ , they reach the axes at the same stopping time  $\tau$ . Moreover,  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  dominates stochastically  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  since it allows rebirths of the disappeared type on the boundaries  $\{N^{11} = 0\} \cup \{N^{12} = 0\}$  provided the total population size is strictly positive.

In the case where the reproduction rate is constant,  $r(N) = \bar{r}$ , the process  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  is a particular case of bi-type Galton-Watson process (e.g. Athreya Ney [3], Chap. V) where each individual lives during an exponential time of rate  $\bar{r} + d$ . At death, a particle is replaced by:

- zero offspring with probability  $d/(\bar{r} + d)$  : this corresponds to the case of a real death.
- two offspring of the same type as their mother with probability  $\bar{r}/(2(\bar{r} + d))$  : one is the mother and the other is her daughter, of the same type.
- one offspring of type  $\{1, 1\}$  and one offspring of type  $\{1, 2\}$  with probability  $\bar{r}/(2(\bar{r} + d))$  : one is the mother and the other is her daughter with the other type.

Hence, once the trajectories have reached the abscissa axis, for instance, the extinct type  $\{1, 2\}$  may be regenerated from birth of individuals of type  $\{1, 2\}$  from individuals of type  $\{1, 1\}$ . Notice also that the total size of the population  $\tilde{N}_t = \tilde{N}_t^{11} + \tilde{N}_t^{12}$  is a continuous time birth and death process. Let:

$$\sigma = \inf\{t \geq 0, \tilde{N}_t = 0\} \quad (4.8)$$

be the extinction time of the dominating process.

**Proposition 4.3.** *Let us consider the processes  $(\tilde{N}^{11}, \tilde{N}^{12})$  starting from the (original) initial condition  $(N_0^{11}, N_0^{12})$ . We set  $N_0 = N_0^{11} + N_0^{12}$ .*

(i) *The total population is a continuous time birth and death process (e.g. Athreya and Ney [3], Chap. III) such that*

$$F(s, t) = \sum_{k=0}^{+\infty} \mathbb{P}(\tilde{N}_t = k | \tilde{N}_0 = 1) s^k = \begin{cases} \frac{d(s-1) - e^{-(\bar{r}-d)t}(\bar{r}s-d)}{\bar{r}(s-1) - e^{-(\bar{r}-d)t}(\bar{r}s-d)} & \text{if } \bar{r} \neq d \\ \frac{s - \bar{r}t(s-1)}{1 - \bar{r}t(s-1)} & \text{if } \bar{r} = d. \end{cases} \quad (4.9)$$

$$\mathbb{E}(\tilde{N}_t) = \mathbb{E}(N_0) e^{(\bar{r}-d)t}, \quad \text{and} \quad \mathbb{P}(\sigma < +\infty | \tilde{N}_0 = 1) = \lim_{t \rightarrow +\infty} F(0, t) = \begin{cases} d/\bar{r} & \text{if } \bar{r} > d \\ 1 & \text{otherwise.} \end{cases} \quad (4.10)$$

(ii) *For the population of type  $(S^1, S^2) \in \{(1, 1), (1, 2)\}$  we have:*

$$\mathbb{E}(\tilde{N}_t^{S^1 S^2}) = \frac{\mathbb{E}(N_0) e^{(\bar{r}-d)t}}{2} + \left( \mathbb{E}(N_0^{S^1 S^2}) - \frac{E(N_0)}{2} \right) e^{-d.t}. \quad (4.11)$$

*Proof.* Once that it has been noticed that  $(\tilde{N}_t)_{t \geq 0}$  is a continuous time birth and death process, the results are standard (e.g. [3], Chap. III 4-5). Notice that:

$$\begin{aligned} \mathbb{P}(\sigma \leq t) &= \mathbb{P}(\tilde{N}_t = 0) = F(0, t) = \frac{d}{\bar{r}} \left( \frac{1 - e^{-(\bar{r}-d)t}}{1 - \frac{d}{\bar{r}} e^{-(\bar{r}-d)t}} \right) & \text{if } \bar{r} > d \\ &= \frac{\bar{r}t}{1 + \bar{r}t} & \text{if } \bar{r} = d \\ &= \frac{e^{(d-\bar{r})t} - 1}{e^{(d-\bar{r})t} - \frac{\bar{r}}{d}} & \text{if } \bar{r} < d, \end{aligned}$$

from which we deduce the asymptotic extinction probability. The expectations of  $\mathbb{E}(\tilde{N}_t^{11})$ ,  $\mathbb{E}(\tilde{N}_t^{12})$  and hence  $\mathbb{E}(\tilde{N}_t)$  are obtained by noticing that  $t \mapsto (\mathbb{E}(\tilde{N}_t^{11}), \mathbb{E}(\tilde{N}_t^{12}))$  solves the system (3.4) which has been studied in a previous part. ■



In conclusion, we can distinguish three regimes:

**Proposition 4.4.** (i) In the subcritical case  $\bar{r} < d$ , the population  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \geq 0}$  gets extinct with probability 1 and so is  $(N_t^{11}, N_t^{12})_{t \geq 0}$ .

(ii) In the critical case, there is also a.s. extinction of  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \geq 0}$  and thus of  $(N_t^{11}, N_t^{12})_{t \geq 0}$ , but the expectation of the population size  $\mathbb{E}(\tilde{N}_t)$  remains constant and the extinction time is not integrable.

(iii) In the supercritical case  $\bar{r} > d$ , there is a positive probability of survival for  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$ , equal to  $(d/\bar{r})^{N_0^{11} + N_0^{12}}$  that provides the lower bound in (4.5). Moreover, in this case, the mean size  $\mathbb{E}(\tilde{N}_t)$  tends to infinity. We also have:

$$\lim_{t \rightarrow +\infty} \frac{\mathbb{E}(\tilde{N}_t^{11})}{\mathbb{E}(\tilde{N}_t)} = \frac{1}{2}.$$

*Proof.* Point (i) is clear. For Point (ii), we use that:

$$\mathbb{E}(\sigma) = \int_0^{+\infty} \mathbb{P}(\sigma > t) dt = \int_0^{+\infty} \frac{dt}{1 + \bar{r}t} = +\infty.$$

For Point (iii), we use 4.10 and the branching property. ■

#### 4.1.4 Stochastic minoration and proof of the upper bound

To obtain the upper bound in (4.5), we have to find a process that is stochastically dominated by  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$ , and for which it is possible to compute the probability to reach the axes  $\mathbb{P}(\tau < +\infty)$ . We consider the processes  $(\hat{N}_t^{11,+}, \hat{N}_t^{12,+})_{t \in \mathbb{R}_+}$  and  $(\hat{N}_t^{11,-}, \hat{N}_t^{12,-})_{t \in \mathbb{R}_+}$  with the same reproduction rates as  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  but with the following death rates: when in the state  $(i, j) \in \mathbb{N}^2$ ,

- with rate  $d(i + j)/2$ , an individual of type  $\{1, 1\}$  dies,
- with rate  $d(i + j)/2$ , an individual of type  $\{1, 2\}$  dies.

and starting with the respective following initial conditions:

$$\begin{aligned} (\hat{N}_0^{11,+}, \hat{N}_0^{12,+}) &= (\min(N_0^{11}, N_0^{12}), \max(N_0^{11}, N_0^{12})) \\ (\hat{N}_0^{11,-}, \hat{N}_0^{12,-}) &= (\max(N_0^{11}, N_0^{12}), \min(N_0^{11}, N_0^{12})). \end{aligned}$$

Since the reproduction rates of these processes are equal to the reproduction rates of  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  and since the sum of the death rates of individuals  $\{1, 1\}$  and  $\{1, 2\}$  are the same for the three processes, there exists a coupling (by choosing the same Poisson measures, see Appendix A.2) such that:

- the births and deaths occur at the same time for all the processes.
- the two processes  $(\hat{N}_t^{11,+}, \hat{N}_t^{12,+})_{t \in \mathbb{R}_+}$  and  $(\hat{N}_t^{11,-}, \hat{N}_t^{12,-})_{t \in \mathbb{R}_+}$  can be chosen to be symmetric with respect to the first bissector, and started respectively in the octant  $\{i < j\}$  and  $\{i > j\}$  of  $\mathbb{N}^2$ . Thus, they reach the axes at the same time.
- at a time  $t$  when  $N_t^{11} > N_t^{12}$  (we are in the octant  $\{i > j\}$  of  $\mathbb{N}^2$ ),
  - the births of new  $\{1, 1\}$ 's,  $\{1, 2\}$ 's and the deaths of  $\{1, 2\}$ 's for  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  give rise to the same events for  $(\hat{N}_t^{11,-}, \hat{N}_t^{12,-})_{t \in \mathbb{R}_+}$ .
  - if a death of an individual of type  $\{1, 1\}$  occurs, then:
    - \* with probability  $(N_t^{11} + N_t^{12})/(2N_t^{11})$ , an individual  $\{1, 1\}$  dies for  $(\hat{N}_t^{11,-}, \hat{N}_t^{12,-})_{t \in \mathbb{R}_+}$ ,
    - \* with probability  $1 - (N_t^{11} + N_t^{12})/(2N_t^{11}) = (N_t^{11} - N_t^{12})/(2N_t^{11})$ , this death is changed into a death of an individual  $\{1, 2\}$ .

The behaviour of  $(\widehat{N}_t^{11,+}, \widehat{N}_t^{12,+})_{t \in \mathbb{R}_+}$  is obtained by symmetry.

- at a time  $t$  when  $N_t^{11} \leq N_t^{12}$  (we are in the octant  $\{i < j\}$  of  $\mathbb{N}^2$ ),
  - the births of new  $\{1, 1\}$ 's,  $\{1, 2\}$ 's and the deaths of  $\{1, 1\}$ 's for  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  give rise to the same events for  $(\widehat{N}_t^{11,+}, \widehat{N}_t^{12,+})_{t \in \mathbb{R}_+}$ .
  - if a death of an individual of type  $\{1, 2\}$  occurs, then:
    - \* with probability  $(N_t^{11} + N_t^{12})/(2N_t^{12})$ , an individual  $\{1, 2\}$  dies for  $(\widehat{N}_t^{11,+}, \widehat{N}_t^{12,+})_{t \in \mathbb{R}_+}$ ,
    - \* with probability  $1 - (N_t^{11} + N_t^{12})/(2N_t^{12}) = (N_t^{12} - N_t^{11})/(2N_t^{12})$ , this death is changed into a death of an individual  $\{1, 1\}$ .

The behaviour of  $(\widehat{N}_t^{11,-}, \widehat{N}_t^{12,-})_{t \in \mathbb{R}_+}$  is obtained by symmetry.

From the coupling, and since the deaths and births coincide, we see that for every  $t$ ,

$$N_t^{11} + N_t^{12} = \widehat{N}_t^{11,+} + \widehat{N}_t^{12,+} = \widehat{N}_t^{11,-} + \widehat{N}_t^{12,-} \quad (4.12)$$

$$N_t^{11,+} < N_t^{11} < N_t^{11,-} \quad \text{and} \quad N_t^{12,+} > N_t^{12} > N_t^{12,-}. \quad (4.13)$$

As a consequence,

$$\begin{aligned} & \{\exists t \in \mathbb{R}_+, N_t^{11} = 0 \text{ or } N_t^{12} = 0\} \\ & \subset \{\exists t \in \mathbb{R}_+, \widehat{N}_t^{11,+} = 0 \text{ or } \widehat{N}_t^{12,+} = 0\} \cup \{\exists t \in \mathbb{R}_+, \widehat{N}_t^{11,-} = 0 \text{ or } \widehat{N}_t^{12,-} = 0\} \\ & = \{\exists t \in \mathbb{R}_+, \widehat{N}_t^{11,+} = 0 \text{ or } \widehat{N}_t^{12,+} = 0\}, \end{aligned} \quad (4.14)$$

since the two processes  $(\widehat{N}_t^{11,+}, \widehat{N}_t^{12,+})_{t \in \mathbb{R}_+}$  and  $(\widehat{N}_t^{11,-}, \widehat{N}_t^{12,-})_{t \in \mathbb{R}_+}$  reach the axes at the same time, by symmetry. To obtain the upper bound in 4.5, it thus remains to compute the r.h.s. of 4.14.

As we are interested in the asymptotic extinction probability, we focus on the discrete time skeleton of the process. We consider the following Markov chain  $(\widehat{N}_{T_k}^{11,+}, \widehat{N}_{T_k}^{12,+})_{k \in \mathbb{N}}$  with the following transitions, presented on Fig. 7: in the state  $(i, j) \in \mathbb{N}^2$  we have:

- jumps to  $(i + 1, j)$  or  $(i, j + 1)$  with probability  $\bar{r}/(2(\bar{r} + d))$ ,
- jumps to  $(i - 1, j)$  or  $(j, i - 1)$  with probability  $d/(2(\bar{r} + d))$ .

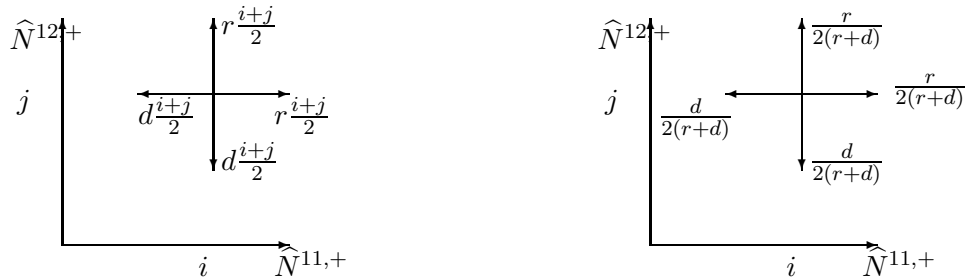


Figure 7: Rates of events (left) and transition probabilities (right) of  $(\widehat{N}_t^{11,+}, \widehat{N}_t^{12,+})_{t \in \mathbb{R}_+}$  and of its discrete time skeleton.

**Proposition 4.5.** *We have:*

$$\mathbb{P}_{ij}(\exists t \in \mathbb{R}_+, \widehat{N}_t^{11,+} = 0 \text{ or } \widehat{N}_t^{12,+} = 0) = \left(\frac{d}{\bar{r}}\right)^i + \left(\frac{d}{\bar{r}}\right)^j - \left(\frac{d}{\bar{r}}\right)^{i+j}. \quad (4.15)$$

*Proof.* First, let us notice that the two processes  $(\widehat{N}_{T_k}^{11})_{k \in \mathbb{N}}$  and  $(\widehat{N}_{T_k}^{12})_{k \in \mathbb{N}}$  move independently. Hence, the survival probability is the product of the survival probabilities of each of these processes:

$$\mathbb{P}_{ij}(\forall t \in \mathbb{R}_+, \widehat{N}_t^{11,+} > 0 \text{ and } \widehat{N}_t^{12,+} > 0) = \left(1 - \left(\frac{d}{\bar{r}}\right)^i\right) \left(1 - \left(\frac{d}{\bar{r}}\right)^j\right) \quad (4.16)$$

and hence:

$$\mathbb{P}_{ij}(\exists t \in \mathbb{R}_+, \widehat{N}_t^{11,+} = 0 \text{ or } \widehat{N}_t^{12,+} = 0) = \left(\frac{d}{\bar{r}}\right)^i + \left(\frac{d}{\bar{r}}\right)^j - \left(\frac{d}{\bar{r}}\right)^{i+j}. \quad (4.17)$$

■

This concludes the proof of Prop. 4.2

## 4.2 Fecundity selection model (Model 3) in a small population

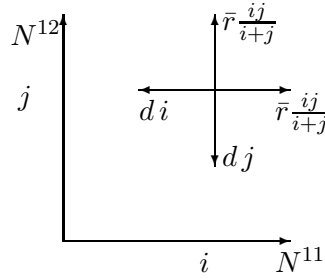


Figure 8: *Evolution of the distylous system  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  in the fecundity selection model (Model 3).*

In the case of the fecundity selection model, we will prove that the same criteria as in large population hold for separating the subcritical, critical and supercritical cases:

**Proposition 4.6.** *Assume that  $(N_0^{11}, N_0^{12}) = (i, j)$ .*

(i)  *$r \leq 2d$ , we have almost sure extinction in finite time.*

(ii)  *$r > 2d$ , we have a positive probability of survival  $1 - p_{i,j}$  such that:*

$$\left(\frac{d}{\bar{r}}\right)^{i+j} \leq p_{i,j} \leq \left(\frac{2d}{\bar{r}}\right)^{\min(i,j)}. \quad (4.18)$$

*Proof.* We begin with the proof of (i). We first assume that  $\bar{r} \leq 2d$ . When in the state  $(i, j) \in \mathbb{N}^2 \setminus \{(0, 0)\}$ , with  $i \leq j$ , the total death rate of the population is  $d(i + j)$  and the total birth rate is:

$$\begin{aligned} 2\bar{r} \frac{ij}{i+j} &= \bar{r} \frac{j}{i+j} i + \bar{r} \frac{i}{i+j} j \\ &= \bar{r} \left( \frac{1}{2} + \frac{|j-i|}{2(i+j)} \right) i + \bar{r} \left( \frac{1}{2} - \frac{|j-i|}{2(i+j)} \right) j \\ &= \frac{\bar{r}}{2} (i+j) + \frac{r}{2} \frac{|j-i|(i-j)}{i+j} \\ &\leq \frac{\bar{r}}{2} (i+j). \end{aligned}$$

Hence, it is possible to stochastically dominate the total population size by a continuous time Galton-Watson process where individuals have a death rate  $d$  and a birth rate  $\bar{r}/2$ . For  $\bar{r} \leq 2d$ , the latter process is critical or subcritical and extinction is almost sure.

We now turn to the proof of (ii), in the case where  $\bar{r} > 2d$ . Since the birth rate are upper bounded by  $\bar{r}i$  and  $\bar{r}j$ ,  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  is upper bounded by the process  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})$  of Section 4.1.3. We turn to the stochastic minoration. When  $(N_t^{11}, N_t^{12}) = (i, j)$  with  $i \leq j$ , then the birth rate for the population  $\{1, 1\}$  is:

$$\bar{r} \frac{ij}{i+j} \geq \frac{\bar{r}}{2} i.$$

Hence, as long as  $N_t^{11} \leq N_t^{12}$ ,  $N^{11}$  is stochastically lower bounded by a supercritical continuous birth and death process with individual birth and death rates  $\bar{r}$  and  $d$ . Similarly, when  $j < i$ ,  $N^{12}$  is stochastically lower bounded by the same process.

As a consequence, the total size of the population  $(N_t^{11} + N_t^{12})_{t \in \mathbb{R}_+}$  is stochastically lower bounded by the supercritical continuous time birth and death process introduced above, started at  $\min(N_0^{11}, N_0^{12})$ , and which survives with probability  $1 - (2d/\bar{r})^{\min(N_0^{11}, N_0^{12})}$  (see Prop. 4.4).  $\blacksquare$

**Remark 4.7.** Notice that the upper and lower bound in 4.18 are not tight and the couplings used in the proof are not likely to be optimal. For the lower bound, the bound 1 for  $i/(i+j)$  and  $j/(i+j)$  is rough. For the upper bound, we have only considered the less represented component in the population.

### 4.3 Compatible population without pollen limitation nor inbreeding depression (Model 4)

As a reference for the previous simulations, we provide the results for populations where there is no self-incompatibility. This corresponds to the case where  $\forall x \in \mathbb{R}^n, \Phi(x) = 0$ . In this situation, we can forget the phenotype of the individuals. This leads us to consider a population where individual reproduce with an individual rate  $r(N)$  and die with a rate  $d$ ,  $N$  being the size of the population. Notice that this corresponds to the process  $(\tilde{N}_t)_{t \geq 0}$  studied in Proposition 4.3. In absence of pollen limitation, when  $\bar{r}$  is constant,

The discrete Markov chain embedded in the continuous time branching process is the following Markov chain on  $\mathbb{N}$ , with transition probabilities  $q_{i,j}$  from  $i$  to  $j$ . For  $i > 0$ :

$$q_{i,i+1} = \frac{r(i)}{r(i)+d}, \quad q_{i,i-1} = \frac{d}{r(i)+d}, \quad q_{0,0} = 1 \quad \text{and else} \quad q_{i,j} = 0. \quad (4.19)$$

Let us denote by  $p_i$  the probability of extinction given an initial population of size  $i$ .

**Proposition 4.8.** Let  $p_1$  be given. For  $i \geq 1$ ,

$$p_{i+1} = p_1 \left( 1 + \sum_{j=1}^i \frac{d^j}{r(1) \dots r(j)} \right) - \sum_{j=1}^i \frac{d^j}{r(1) \dots r(j)}. \quad (4.20)$$

*Proof.* Using the strong Markov property at the time of the first event:

$$p_i = \frac{d}{r(i)+d} p_{i-1} + \frac{r(i)}{r(i)+d} p_{i+1}, \quad (4.21)$$

where by convention  $p_0 = 1$ . We deduce from this that:

$$p_{i+1} - p_i = \frac{d}{r(i)} (p_i - p_{i-1}) = \frac{d^i}{\prod_{j=1}^i r(j)} (p_1 - 1). \quad (4.22)$$

by recursion. The result follows from the fact that  $p_{i+1} = p_1 + \sum_{j=1}^i (p_{j+1} - p_j)$ .  $\blacksquare$

**Example 4.9.** In the case where the individual reproduction rate is constant  $r(i) = \bar{r}$ ,

$$\sum_{j=1}^i \left(\frac{d}{\bar{r}}\right)^j = \frac{d}{\bar{r} - d} \left(1 - \left(\frac{d}{\bar{r}}\right)^i\right). \quad (4.23)$$

Moreover, in this case, the process is a one-dimensional continuous time Markov branching process (e.g. [3], Chap. III) and we know that  $p_1$  is the solution of  $g(s) = s$  where  $g(s)$  is the generating function of the offspring distribution of  $(\tilde{N}_t)_{t \geq 0}$ :

$$g(s) = \frac{d}{d + \bar{r}} + \frac{\bar{r}}{d + \bar{r}} s^2.$$

This gives

$$p_1 = \frac{d}{\bar{r}} \quad \text{and hence} \quad \forall i \geq 1, p_i = \left(\frac{d}{\bar{r}}\right)^i, \quad (4.24)$$

which is expected since the branching property holds in this case, contrarily to cases where  $r(\cdot)$  is not constant and where there is interaction between the individuals.

## 5 Simulations

### 5.1 Simulation algorithm

The population dynamics described in the previous section can be simulated with the following algorithm (see [16]). Notice that the algorithm that we propose is exact (in the sense that it describes exactly the dynamics describe above without approximation scheme). Assume that the population is known at time  $t$ . Then:

1. We define the total event rate at the population level by:

$$C_t = \sum_{1 \leq u \leq v \leq n} r(\bar{N}_t^{uv}) + N_t d. \quad (5.1)$$

2. The next event time is  $t' = t + \tau$  where  $\tau$  is an independent random variable that is exponentially distributed with parameter  $C_t$ .
3. We then draw an independent uniform random variable  $\theta$ . If  $0 \leq \theta \leq \sum_{1 \leq u \leq v \leq n} r(\bar{N}_t^{uv})/C_t$  then a birth happens:
  - (a) The ovule is of type  $\{u, v\}$  with probability  $r(\bar{N}_t^{uv}) / \sum_{1 \leq u \leq v \leq n} r(\bar{N}_t^{uv})$ .
  - (b) The pollen is then of type  $\{u', v'\}$  with probability  $\bar{p}_t^{uv}(u', v')$ .
  - (c) The offspring is then of type  $\{u, u'\}$ ,  $\{u, v'\}$ ,  $\{v, u'\}$  or  $\{v, v'\}$  with probability  $1/4$ .

If  $\theta > \sum_{1 \leq u \leq v \leq n} r(\bar{N}_t^{uv})/C_t$  then an individual dies. This individual is drawn uniformly among the living individuals.

### 5.2 Simulations performed in the case of a distylous species

Each simulated curve is obtained as the average on 5000 simulations of paths  $(N_t^{11}, N_t^{12})_{t \in [0, 10000]}$ .

$$\text{Estimated extinction probability} = \frac{1}{5000} \sum_{i=1}^{50000} \mathbb{1}_{\{\text{Trajectory } i \text{ gets extinct before time } 10000\}}. \quad (5.2)$$

The simulations were run for varying number of different genotypes as initial conditions when considering Wright's model, while  $N_0^{11} = N_0^{12} = 1$  when considering the dependence model.

In Fig. 9 the extinction probability for a constant reproduction rate  $\bar{r} = 2$  is shown for an increasing death rate, for both the distylous and the self-compatible case, for different initial number of the two genotypes, under the Wright's model. Fig. 9 shows that in small population, the extinction probabilities are higher for the distylous than for the self-compatible population. As expected, the difference between the distylous and the self-compatible populations is lower when the initial population size increases, as shown in proposition 3.1 for Wright's model. The results shown in Fig. 9 for Wright's model shows the importance of the absorbing effect that increases the extinction probability for the distylous population. This figure also shows that when  $\alpha < +\infty$ , the extinction probabilities are higher than in Wright's model, both for distylous and self-compatible populations. This reflects the fact that when pollen limitation is high, it is more difficult to encounter a mate and to produce offspring.

In Fig. 10, we estimated the ratio:

$$\rho = \frac{\text{Extinction probability in the self-compatibility case}}{\text{Extinction probability in the self-incompatibility case}} \quad (5.3)$$

from our simulations results. The Fig. 10(a) shows that the ratio  $\rho$  gets smaller when the initial population size is higher, which means that the extinction probabilities for the self-compatible population decreases more rapidly when  $N$  increases than for the distylous population. This effect is even worse when the initial population is asymmetric, that is when a given genotype is more frequent than the other (compare filled with empty symbols). Once again, the differences between distylous and self-compatible populations shown in Fig. 10(a) are only due to the absorbing effects. Fig. 10(b) shows the ratio  $\rho$  for different initial conditions under the dependence model with  $\alpha = 1$  and  $\beta = 100$ . Fig. 10(c) shows similar results but for different strength of pollen limitation ( $\alpha < +\infty$ ) with  $N_0^{11} = N_0^{12} = 1$ . It is remarkable in this figure that when the strength of the pollen limitation is high ( $\alpha$  is small and  $\beta$  is large) then the ratio  $\rho$  is higher, which means that the higher the pollen limitation, the lower the difference between distylous and self-compatible populations.

## 6 Discussion

**Impact of pollen limitation versus demographic stochasticity and boundary effects** Thanks to the three relationships between the compatible population size and the reproductive rates we assumed (see 2.2 and Fig. 1), we are able to disentangle the relative effects of demographic stochasticity and pollen limitation on the fate of the populations. Indeed, when Wright's model is assumed, there is no pollen limitation. In other words all individuals of a given mating types receive enough pollen to fertilize all their ovules, as long as at least one compatible individual is present in the population. This assumption introduces a discontinuity in the individual rate of seeds production. On the other extreme, the fecundity selection model has a rate of seeds production that vanishes continuously at the boundaries. Finally, we investigated the combined effect of pollen limitation and demographic stochasticity thanks to the dependence model.

We have first studied large populations. We exhibit three different regimes, depending on the relationships between the birth and death parameters. Under the subcritical regime, the population gets extinct when  $t \rightarrow +\infty$ , while its size tends to infinity under the supercritical regime. As expected, when there is no pollen limitation, a distylous population behaves like a self-compatible population. When there exists an equilibrium, the population size is  $n^*$  in both cases. To the contrary, under the fecundity selection model, the size at equilibrium is  $2n^*$  showing that pollen limitation can have a large effect on the dynamics of distylous populations, even in large ones. In the dependence model, a

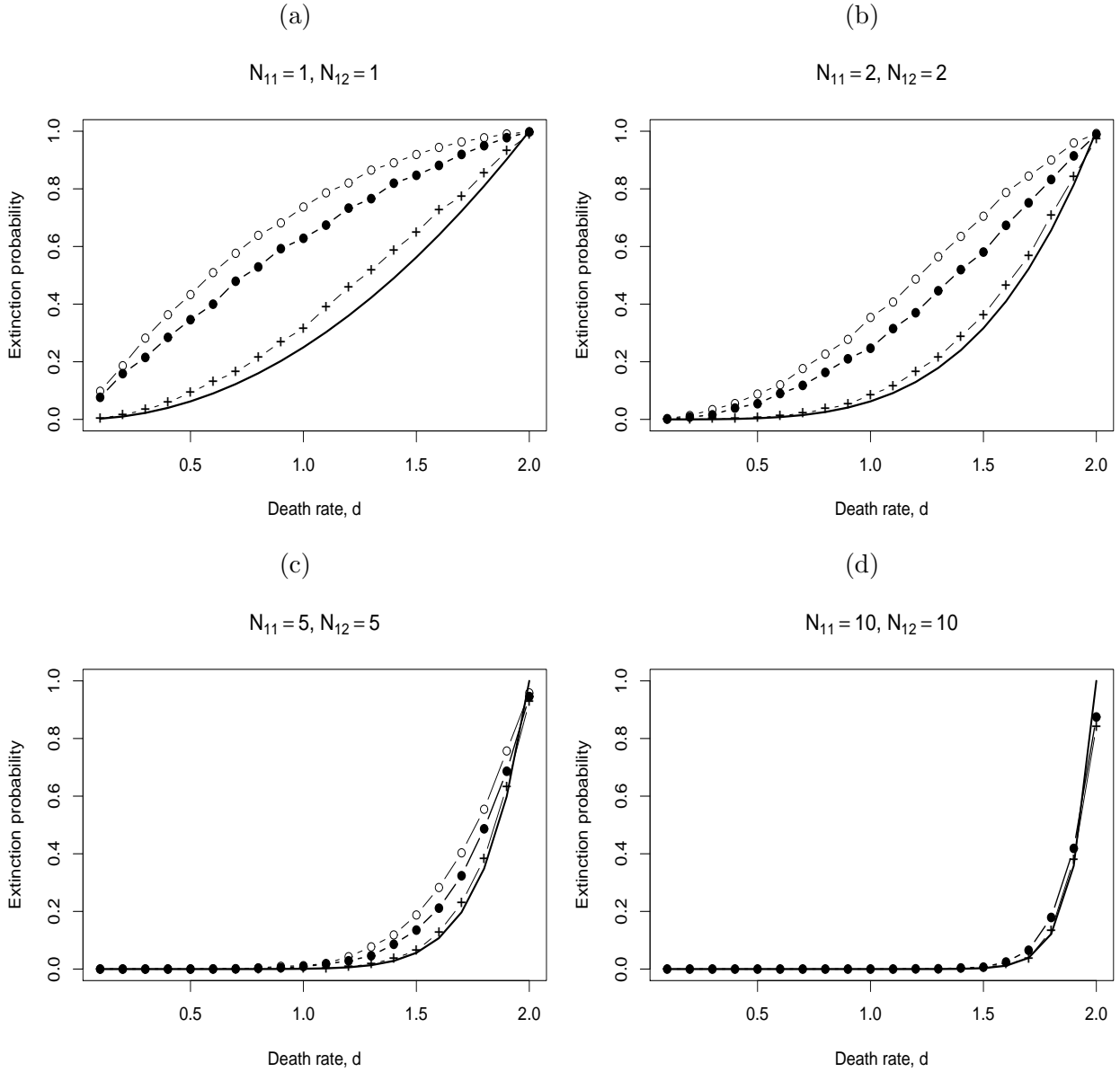


Figure 9: Comparison of the extinction probabilities of  $(N_t^{11}, N_t^{12})_{t \geq 0}$  for a constant reproduction rate  $r = 2$  when the initial number of the different genotypes varies (indicated in the top of the box). Thick line: Extinction probability in the self-compatible case (from equation 4.24); Crosses: self-compatible case with pollen limitation ( $\alpha = \beta = 1$ ); Full circles: distylous case with Wright's model; Circles: distylous case with the dependence model ( $\alpha = \beta = 1$ ).

saddle point appears that makes condition for the maintenance of the population more scarce than in Wright's model and favors populations with symmetry in the initial conditions.

In small populations, the separation into subcritical, critical or supercritical regimes is the same as for large populations. In supercritical cases, we are able to find lower and upper bounds of the probability of extinction of a distylous population under the Wright's and fecundity selection models. Again, the main difference between these models relies on the fact the critical condition for the survival of the population is twofold higher in the fecundity selection model.

Our simulations show that when pollen limitation is low ( $\alpha = 1$  and  $\beta = 1$ , see Fig. 9), the increase in the probability of extinction is small relatively to the impact of demographic stochasticity.

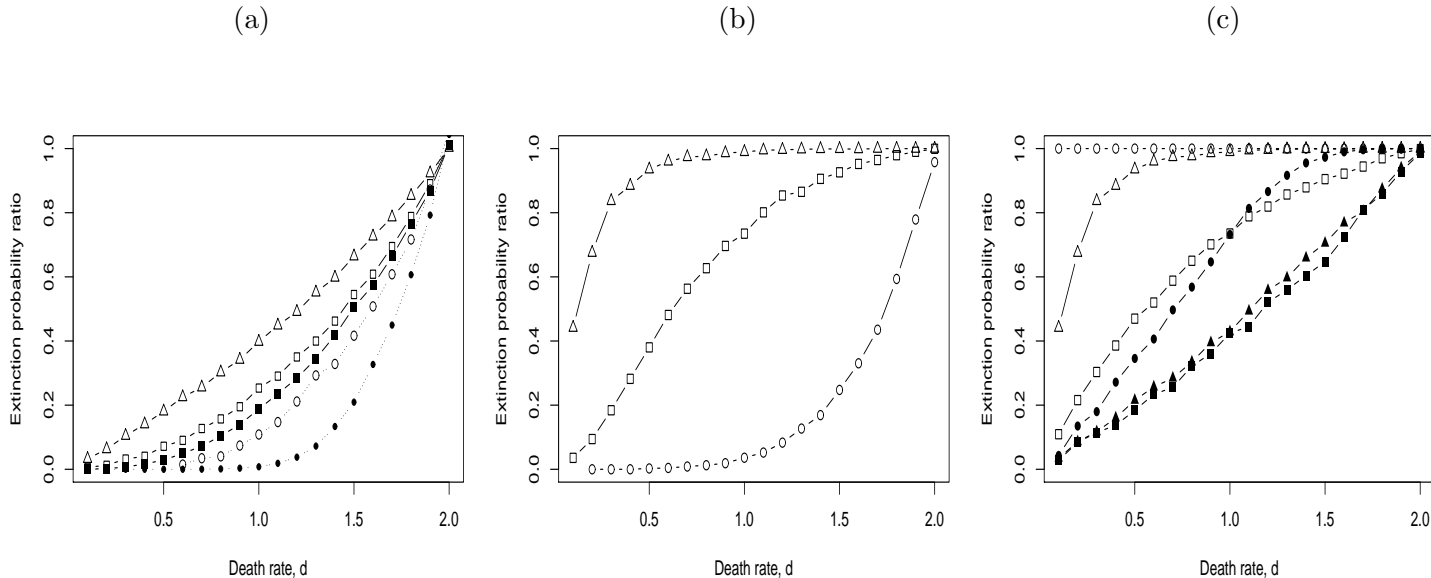


Figure 10: *Ratio of extinction probabilities in self-compatible cases over distylous case with  $\bar{r} = 2$ , varying initial conditions and varying  $\alpha$  and  $\beta$ . (a): Wright's model,  $N_0^{11} = N_0^{12} = 1$  (triangles);  $N_0^{11} = N_0^{12} = 2$  (empty squares);  $N_0^{11} = N_0^{12} = 5$  (empty circles);  $N_0^{11} = 3$  and  $N_0^{12} = 1$  (filled squares);  $N_0^{11} = 9$  and  $N_0^{12} = 1$  (filled circles). (b): Dependence model with  $\alpha = 1$  and  $\beta = 100$  and varying initial conditions:  $N_0^{11} = N_0^{12} = 1$  (triangles),  $N_0^{11} = N_0^{12} = 2$  (squares),  $N_0^{11} = N_0^{12} = 5$  (circles),  $N_0^{11} = N_0^{12} = 10$  (crosses). (c): Dependence model with  $N_0^{11} = N_0^{12} = 1$  and  $\beta = 1$  (filled symbols),  $\beta = 100$  (empty symbols),  $\alpha = 0.1$  (circles),  $\alpha = 1$  (triangles),  $\alpha = 2$  (squares).*

When we compare the extinction probabilities between a distylous and a self-compatible population by the measure  $\rho$ , we see that the higher the pollen limitation (when  $\alpha$  decreases), the lower the difference between them since  $\rho$  increases (see Fig. 10). Those results have important ecological and evolutionary consequences since they suggest pollen limitation plays a minor role in small populations relatively to demographic stochasticity, and especially the stochastic loss of one of the two mating types. When pollen limitation is very large (when  $\alpha$  is low), small populations of self-compatible and self-incompatible species tend to behave similarly. In short, our results suggest that pollen limitation plays a major role in large population only.

### Mate Finding Allee effect, inbreeding depression and the evolution of self-incompatibility

One of the most intriguing and long-standing problem in evolutionary biology resides in the existence and maintenance of SI. Indeed, the establishment probability is lower in the case of SI compared to self-compatible species since a single individual is sufficient to colonize empty spaces (the Baker's law, Pannell and Barrett [30]). Furthermore, as shown here, the extinction probability is higher for SI than for self-compatible species in absence of inbreeding depression. It has been also shown that in infinite populations, the conditions for the invasion of SI populations by a self-compatible mutant are less stringent when there is strong pollen limitation (*e.g.* [33]). The process generally invoked to explain the existence and maintenance of SI is inbreeding depression: SI can be advantageous relatively to self-compatibility when the cost of inbreeding depression caused by self-fertilization is high. Inbreeding depression can play a role in two ways: by preventing the invasion of self-compatible mutant (*e.g.* [33]), or by increasing the extinction rate of self-compatible species relatively to SI species (Lynch et al. [29]), what is suggested in data since self-compatible species are most often localised at the leaves of phylogenies, especially in plant families where distyly is present (*e.g.* in *Amsinckia* [39], in *Narcissus* [31] and in *Psychotria* [38]). Here, we proposed a very caricatural model taking into account



inbreeding depression caused by self-fertilization, to investigate if there are conditions under which the extinction probabilities are higher for SC populations than for SI populations. We found that there are some conditions in large populations where the size at equilibrium is lower in SI populations than in self-compatible populations: under strong inbreeding depression, SI populations may be less sensitive to extinction.

**What about more complex dominance networks?** Although we developed a general model for the population dynamics of SSI species, we mainly investigated the dynamics of a distylous species. Distyly is however the case where the impact of the existence of mating types is the highest since only two mating types exist. When the number of mating types increases, the proportion of compatible individuals also increases. It would be interesting to investigate the impact of the dominance relationships between allele S on the extinction of population, to check if there are dominance interaction patterns that are less sensitive to extinction than others, as highlighted by [22]: they showed that populations where all S alleles are codominant have a higher extinction rate than populations where a linear hierarchy of dominance exist between S alleles (the DOM model, see *e.g.* [8]). Our model could be used to investigate the effect of these dominance interactions more precisely.

## A SDEs and Proofs of the Section 2.3 Propositions

### A.1 SDEs

Following [16], we present a SDE describing the evolution of  $(Z_t)_{t \in \mathbb{R}_+}$ .

**Definition A.1.** Let  $Q(ds, d(u', v'), d\theta)$  be a Poisson point measure on  $\mathbb{R}_+ \times E \times \mathbb{R}_+$  with intensity  $q(ds, d(u', v'), d\theta) = ds dn(u', v') d\theta$ , where  $ds$  and  $d\theta$  are Lebesgue measures on  $\mathbb{R}_+$  and where  $dn(u', v')$  is the counting measure on  $E$ . To each atom from  $Q(ds, d(u', v'), d\theta)$  are hence associated a time of possible event  $s$ , the genotype  $(u', v')$  that either appears or dies and an auxiliary variable  $\theta$  that decides what happens (with a role similar to the variable  $\theta$  in Point 3 of the algorithm of Section 5.1):

$$Z_t(du, dv) = Z_0(du, dv) + \int_0^t \int_{E \times \mathbb{R}_+} \delta_{(u', v')}(du, dv) \left( \mathbb{1}_{\theta \leq r^{u'v'}(Z_{s-})} - \mathbb{1}_{r^{u'v'}(Z_{s-}) < \theta \leq r^{u'v'}(Z_{s-}) + d.N_s^{u'v'}} \right) Q(ds, d(u', v'), d\theta) \quad (\text{A.1})$$

Existence and uniqueness of a solution of (A.1) are stated in the next proposition, proved in appendix. Moreover, it is possible, for a given test function  $f$ , to derive from (A.1) equations for the evolution of  $(\langle Z_t, f \rangle)_{t \in \mathbb{R}_+}$ .

**Proposition A.2.** (i) If  $\mathbb{E}(N_0) < +\infty$ , then there exists a unique solution to SDE (A.1).

(ii) If additionally  $\mathbb{E}(N_0^2) < +\infty$  then for any bounded test function  $f$  on  $\mathbb{E}$ ,

$$\langle Z_t, f \rangle = \langle Z_0, f \rangle + \int_0^t \sum_{1 \leq u \leq v \leq n} (r^{uv}(Z_s) - d.N_s^{uv}) f(u, v) ds + M_t^f \quad (\text{A.2})$$

where  $(M_t^f)_{t \in \mathbb{R}}$  is a square integrable martingale starting from 0 with quadratic variation:

$$\langle M^f \rangle_t = \int_0^t \sum_{1 \leq u \leq v \leq n} (r^{uv}(Z_s) + d.N_s^{uv}) f^2(u, v) ds, \quad (\text{A.3})$$

and where  $r^{uv}(Z_t)$  has been defined in (2.9).

*Proof of the Prop. A.2.* The rate  $r^{uv}$  defined in (2.9) is bounded by a linear function in  $N_t$ . The moment condition in (i) allows us to prove that there is no explosion. The proofs then follows the ones developed in Fournier and Méléard [16] for a model of plant with asexual reproduction: see [16] Th. 3.1 and Prop. 3.4. ■

## A.2 Couplings in Wright's model for the proofs of Section 4

In this section, we give the expression of the processes  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$ ,  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  and  $(\hat{N}_t^{11}, \hat{N}_t^{12})_{t \in \mathbb{R}_+}$  that appear in Section 4.

Let us rewrite Equations (2.23) thanks to (A.1):

$$\begin{aligned} N_t^{11} = N_0^{11} + \int_0^t \int_{E \times \mathbb{R}_+} \mathbb{1}_{(u', v')=(1,1)} & \left( \mathbb{1}_{N_{s_-}^{11} > 0; N_{s_-}^{12} > 0} \mathbb{1}_{\theta \leq \frac{\bar{r}(N_{s_-}^{11} + N_{s_-}^{12})}{2}} \right. \\ & \left. - \mathbb{1}_{\frac{\bar{r}(N_{s_-}^{11} + N_{s_-}^{12})}{2} < \theta \leq \frac{\bar{r}(N_{s_-}^{11} + N_{s_-}^{12})}{2} + d \cdot N_{s_-}^{11}} \right) Q(ds, d(u', v'), d\theta) \end{aligned}$$

and similarly for  $(N_t^{12})_{t \in \mathbb{R}_+}$ .

For the stochastic domination, the process  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$  introduced in (4.6) can be rewritten as:

$$\begin{aligned} \tilde{N}_t^{11} = N_0^{11} + \int_0^t \int_{E \times \mathbb{R}_+} \mathbb{1}_{(u', v')=(1,1)} & \left( \mathbb{1}_{\theta \leq \frac{\bar{r}(\tilde{N}_{s_-}^{11} + \tilde{N}_{s_-}^{12})}{2}} \right. \\ & \left. - \mathbb{1}_{\frac{\bar{r}(\tilde{N}_{s_-}^{11} + \tilde{N}_{s_-}^{12})}{2} < \theta \leq \frac{\bar{r}(\tilde{N}_{s_-}^{11} + \tilde{N}_{s_-}^{12})}{2} + d \cdot \tilde{N}_{s_-}^{11}} \right) Q(ds, d(u', v'), d\theta) \end{aligned}$$

and similarly for  $(\tilde{N}_t^{12})_{t \in \mathbb{R}_+}$ . If we start at a point where  $(N_t^{11}, N_t^{12}) = (\tilde{N}_t^{11}, \tilde{N}_t^{12})$  then it is clear that these processes have the same births and deaths. If one of the component is null, then there is no birth  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  while there is still births in  $(\tilde{N}_t^{11}, \tilde{N}_t^{12})_{t \in \mathbb{R}_+}$ .

For the stochastic minoration, the process  $(\hat{N}_t^{11}, \hat{N}_t^{12})_{t \in \mathbb{R}_+}$  introduced in Section 4.1.4 can be chosen as follows:

$$\begin{aligned} \hat{N}_t^{11,+} = N_0^{11} + \int_0^t \int_{E \times \mathbb{R}_+} & \left[ \mathbb{1}_{(u', v')=(1,1)} \mathbb{1}_{\hat{N}_{s_-}^{11,+} > 0; \hat{N}_{s_-}^{12,+} > 0} \mathbb{1}_{\theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2}} \right] Q(ds, d(u', v'), d\theta) \\ & - \int_0^t \int_{E \times \mathbb{R}_+} \left[ \mathbb{1}_{N_{s_-}^{11} \leq N_{s_-}^{12}} \left( \mathbb{1}_{(u', v')=(1,1)} \mathbb{1}_{\frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} + d \cdot N_{s_-}^{11}} \right. \right. \\ & \quad \left. \left. + \mathbb{1}_{(u', v')=(1,2)} \mathbb{1}_{\frac{(\bar{r}+d)(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} + d \cdot N_{s_-}^{12}} \right) \right] Q(ds, d(u', v'), d\theta) \\ & - \int_0^t \int_{E \times \mathbb{R}_+} \left[ \mathbb{1}_{N_{s_-}^{11} > N_{s_-}^{12}} \left( \mathbb{1}_{(u', v')=(1,2)} \mathbb{1}_{\frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} + d \cdot N_{s_-}^{12}} \right. \right. \\ & \quad \left. \left. + \mathbb{1}_{(u', v')=(1,1)} \mathbb{1}_{\frac{(\bar{r}+d)(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} + d \cdot N_{s_-}^{11}} \right) \right] Q(ds, d(u', v'), d\theta). \\ \hat{N}_t^{12,+} = N_0^{12} + \int_0^t \int_{E \times \mathbb{R}_+} & \left[ \mathbb{1}_{(u', v')=(1,1)} \mathbb{1}_{\hat{N}_{s_-}^{11,+} > 0; \hat{N}_{s_-}^{12,+} > 0} \mathbb{1}_{\theta \leq \frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2}} \right] Q(ds, d(u', v'), d\theta) \\ & - \int_0^t \int_{E \times \mathbb{R}_+} \left[ \mathbb{1}_{N_{s_-}^{11} \leq N_{s_-}^{12}} \mathbb{1}_{(u', v')=(1,2)} \mathbb{1}_{\frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{(\bar{r}+d)(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2}} \right] Q(ds, d(u', v'), d\theta) \\ & - \int_0^t \int_{E \times \mathbb{R}_+} \left[ \mathbb{1}_{N_{s_-}^{11} > N_{s_-}^{12}} \mathbb{1}_{(u', v')=(1,1)} \mathbb{1}_{\frac{\bar{r}(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{(\bar{r}+d)(\hat{N}_{s_-}^{11,+} + \hat{N}_{s_-}^{12,+})}{2}} \right] Q(ds, d(u', v'), d\theta). \end{aligned}$$

The equations for  $\hat{N}_t^{11,-}$  and  $\hat{N}_t^{12,-}$  are similar. Notice that the process  $(N_t^{11}, N_t^{12})_{t \in \mathbb{R}_+}$  appear in the definition of  $(\hat{N}_t^{11}, \hat{N}_t^{12})_{t \in \mathbb{R}_+}$ . The first bracket corresponds to the births. The second bracket

correspond to the case where  $N_{s_-}^{11} \leq N_{s_-}^{12}$  and the third bracket to the case where  $N_{s_-}^{11} > N_{s_-}^{12}$ . We details the possibilities in the case where  $N_{s_-}^{11} \leq N_{s_-}^{12}$ . Deaths of individuals  $\{1, 2\}$  of  $N^{12}$  give death to individuals  $\{1, 2\}$  of  $\widehat{N}^{12,+}$  if

$$\frac{\bar{r}(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{(\bar{r} + d)(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})}{2}$$

which happens with probability

$$\frac{d(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})/2}{d.N_{s_-}^{12}} = \frac{N_{s_-}^{11} + N_{s_-}^{12}}{2N_{s_-}^{12}}$$

since  $N_t^{11} + N_t^{12} = \widehat{N}_t^{11,+} + \widehat{N}_t^{12,+}$ . If

$$\frac{(\bar{r} + d)(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})}{2} < \theta \leq \frac{\bar{r}(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})}{2} + d.N_{s_-}^{11}$$

which happens with probability

$$\left( d.N_{s_-}^{12} - \frac{d(\widehat{N}_{s_-}^{11,+} + \widehat{N}_{s_-}^{12,+})}{2} \right) \frac{1}{d.N_{s_-}^{12}} = \frac{N_{s_-}^{12} - N_{s_-}^{11}}{2N_{s_-}^{12}}$$

then there is a death of an individual  $\{1, 1\}$  of  $\widehat{N}^{11,+}$ . Deaths of individuals  $\{1, 1\}$  of  $N^{11}$  also give death to individuals  $\{1, 1\}$  of  $\widehat{N}^{11,+}$ . Hence individuals  $\{1, 1\}$  in  $\widehat{N}^{11,+}$  die with rate:

$$\frac{d(N_{s_-}^{12} - N_{s_-}^{11})}{2} + d.N_{s_-}^{11} = \frac{d(N_{s_-}^{11} + N_{s_-}^{12})}{2}.$$

This shows that the process  $(\widehat{N}_t^{11}, \widehat{N}_t^{12})_{t \in \mathbb{R}_+}$  has the rates announced in Section 4.1.4.

### A.3 Large population limits and proof of Proposition 2.2

*Sketch of Proof of Prop. 2.2.* We begin with (ii) by assuming existence of a solution to:

$$\langle \xi_t, f \rangle = \langle \xi_0, f \rangle + \int_0^t \left( \sum_{1 \leq u \leq v \leq n} r^{uv}(\xi_s) f(u, v) - d. \langle \xi_s, f \rangle \right) ds, \quad (\text{A.4})$$

where  $f$  is a bounded test function on  $E$ . Since all finite measures of  $\mathcal{M}_F(E)$  have the form (2.18), it remains to prove that the functions  $n^{u'v'}$  satisfy (2.19). Let us choose  $f(u, v) = \mathbb{1}_{(u', v')}(u, v)$  and integrate  $f$  with respect to  $\xi_t$ . Since  $\langle \xi_t, \mathbb{1}_{(u', v')} \rangle = n_t^{u'v'}$ , we obtain from (A.4):

$$n_t^{u'v'} = n_0^{u'v'} + \int_0^t (r^{u'v'}(\xi_s) - d.n_s^{u'v'}) ds. \quad (\text{A.5})$$

Notice that for any finite measure  $\xi$  on  $E$  of the form (2.18),  $r^{uv}(\xi)$  is the sum of terms of the form  $r(\bar{n}^{uu'}) n^{uu'} \bar{p}^{uu'}(v, v')$  for  $u, u', v, v'$  in  $E$ . In Wright's model, there may be discontinuities when several of the possible genotypes reach a size 0. Else, the function  $r^{uv}(\cdot)$  that we consider is locally Lipschitz continuous as products of locally Lipschitz continuous functions. Since  $\xi$  is continuous and since  $r^{u'v'}(\cdot)$  is continuous, the integrand in (A.5) is continuous, which entails that  $n^{u'v'}$  is of class  $\mathcal{C}^1$  and hence of class  $\mathcal{C}^\infty$  by direct recursion. Taking the derivative with respect to time gives (2.19) and achieves the proof. Moreover, the conditions on  $r^{uv}$  imply by the Cauchy-Lipschitz theorem that there exists a unique solution to (2.19) and hence to (A.4). Let us now prove existence, which is a consequence of (i).

First, let us notice that for given  $K \in \mathbb{N}^*$  and real test function  $f$  on  $E$ , the process  $(Z_t^{(K)})_{t \in \mathbb{R}_+}$  satisfies the following evolution equation:

$$\langle Z^{(K)}, f \rangle = \langle Z_0^{(K)}, f \rangle + \int_0^t \left( \sum_{1 \leq u \leq v \leq n} r^{uv}(Z_s^{(K)}) f(u, v) - d \langle Z_s^{(K)}, f \rangle \right) ds + M_s^{(K), f} \quad (\text{A.6})$$

where  $(M_t^{(K), f})_{t \in \mathbb{R}}$  is a square integrable martingale starting from 0 with quadratic variation:

$$\langle M^{(K), f} \rangle_t = \frac{1}{K} \int_0^t \left( \sum_{1 \leq u \leq v \leq n} r^{uv}(Z_s^{(K)}) f^2(u, v) + d \langle Z_s^{(K)}, f^2 \rangle \right) ds. \quad (\text{A.7})$$

Heuristically, as the quadratic variation of the martingale is of order  $1/K$ , the stochastic part of the process will disappear in the limit. Since the jumps of  $Z^{(K)}$  are of order  $1/K$ , the limiting values of  $(Z^{(K)})_{K \in \mathbb{N}^*}$  are necessarily continuous. Moreover, (2.17) implies that every one-dimensional marginal has a finite mass. The limiting values hence belong to  $\mathcal{C}(\mathbb{R}_+, \mathcal{M}_F(E))$ .

The proof of (i) separates classically in two steps. We establish tightness of the laws of  $(Z^{(K)})_{K \in \mathbb{N}^*}$ , which implies the relatively compactness for this family of probability measures (*e.g.* [14] p.104). Then, we establish that every limiting value solves (A.4) which has a unique solution.

For any  $T > 0$ , the tightness on  $\mathbb{D}([0, T], \mathcal{M}_F(E))$  is obtained by using a criterion due to Roelly [36], and since  $E$  is finite, the problem amounts to prove the tightness on  $\mathbb{D}([0, T], \mathbb{R})$  of the sequence  $(\langle Z^{(K)}, f \rangle)_{K \in \mathbb{N}^*}$  for bounded test functions  $f$ . Given the local Lipschitz continuity of  $r^{uv}(\cdot)$ , given that  $|r^{uv}(Z)| \leq C\bar{r}N_t$  and given the moment estimates (2.17) this is a classical computation which uses Aldous and Rebolledo criteria (*e.g.* [21]). See *e.g.* [16] proof of Th. 5.3.

Taking the limit in (A.6) thanks to (2.17) again allows us to identify the adherence values of  $(Z^{(K)})_{K \in \mathbb{N}^*}$  as the solution of (A.4). This provides existence of a solution to (A.4) and since we have established uniqueness, there is a unique limiting value to which the sequence converges. ■

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