

# Establishment of local adaptation in partly self-fertilizing populations

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Bogi Trickovic, Sylvain Glémin. Establishment of local adaptation in partly self-fertilizing populations. Genetics, 2022, 220 (2), 10.1093/genetics/iyab201. hal-03467503

## HAL Id: hal-03467503 https://hal.science/hal-03467503

Submitted on 9 Dec 2021

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1	Establishment of local adaptation in partly
2	self-fertilizing populations
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12	<b>Running head:</b> local adaptation with selfing
13	
14	Keywords: branching process, local adaptation, migration-selection
15	balance, protected polymorphism, selfing
16	November 2, $2021$

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#### Abstract

Populations often inhabit multiple ecological patches and thus experience diver-18 gent selection, which can lead to local adaptation if migration is not strong enough 19 to swamp locally adapted alleles. Conditions for the establishment of a locally ad-20 vantageous allele have been studied in randomly mating populations. However, many 21 species reproduce, at least partially, through self-fertilization, and how selfing affects 22 local adaptation remains unclear and debated. Using a two-patch branching process 23 formalism, we obtained a closed-form approximation under weak selection for the prob-24 ability of establishment of a locally advantageous allele (P) for arbitrary selfing rate 25 and dominance level, where selection is allowed to act on viability or fecundity, and 26 migration can occur via seed or pollen dispersal. This solution is compared to diffu-27 sion approximation and used to investigate the consequences of a shift in a mating 28 system on P, and the establishment of protected polymorphism. We find that selfing 29 can either increase or decrease P, depending on the patterns of dominance in the two 30 patches, and has conflicting effects on local adaptation. Globally, selfing favors local 31 adaptation when locally advantageous alleles are (partially) recessive, when selection 32 between patches is asymmetrical and when migration occurs through pollen rather 33 than seed dispersal. These results establish a rigorous theoretical background to study 34 heterogeneous selection and local adaptation in partially selfing species. 35

### 36 1 Introduction

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Most advantageous alleles are lost from populations (Haldane, 1927), but those that escape 37 extinction are ultimately destined to fix, providing that the fitness effect of an allele remains 38 positive over space and time. However, fitness effects can vary across species' range, so that 39 an allele that is advantageous in one ecological patch might be deleterious in another. Two 40 mutually exclusive outcomes are then possible: a locally advantageous allele is maintained by 41 divergent selection as polymorphism, or the allele with the best overall performance across 42 the patches becomes fixed. Since ranges of essentially all species are spread across hetero-43 geneous environments, it is of some interest to understand the conditions under which these 44 outcomes are materialized. Although previous works investigated these conditions for ran-45 domly mating populations in both a deterministic (Bulmer, 1972, Felsenstein, 1976, Levene, 46 1953, Maynard Smith, 1970) and a stochastic setting (Tomasini and Peischl, 2018, Yeaman 47 and Otto, 2011), conditions for maintenance of local adaptation in partially self-fertilizing 48 populations remain unexplored. Partial selfing is widespread among eukaryotes and well-49 described in plants (Igic and Kohn, 2006), animals (Jarne and Auld, 2006), algae (Hanschen 50 et al., 2018), and fungi (Billiard et al., 2012), and considering its effect on spatially hetero-51 geneous selection is especially relevant for at least two reasons. First, partial selfing is more 52 frequently found among sessile or less mobile organisms, for which landscape heterogeneity 53 directly translates into local selective pressures because of the absence of the homogenizing 54 effect of movements across the environment. Second, partial selfing likely influences the con-55 ditions for local adaptation by altering the effective population size and effective migration 56 rate, hence the genetic structure of a population, but also by reducing the role of heterozy-57 gotes' fitness in the dynamics of allelic frequencies. 58

In a single population, selfing exerts two opposing effects on the fixation probability of an 60 advantageous allele (Pollak (1987), Pollak and Sabran (1992), Charlesworth (1992), Caballero 61 and Hill (1992)). Firstly, it increases the rate at which a rare advantageous allele spreads 62 through the population. As the selfing rate increases, homozygotes appear more quickly so 63 that the spread of an advantageous allele becomes increasingly decoupled from the fitness 64 of the heterozygote. In other words, selfing increases the effective dominance coefficient: 65 the rate of spread in a partially selfing population with dominance coefficient h, would be 66 equal to the rate of spread in a randomly mating population with dominance coefficient 67  $\tilde{h} = F + (1 - F)h$  (where F is the equilibrium population inbreeding coefficient). Secondly, 68 since alleles making up the progeny are not independently sampled, selfing also reduces the 69 efficacy of selection by reducing the effective population size, N, by a factor of 1 + F (Gale 70

(1990)). These two opposing effects cancel out when an advantageous allele is codominant 71 (h = 0.5), implying that the fixation probability of a codominant advantageous allele is in-72 variant across populations with different selfing rates. If an advantageous allele is partially 73 recessive (h < 0.5), then the effect of increased efficacy of selection through increased ef-74 fective dominance outweights the reduction in  $\tilde{N}$  yielding an increase in the establishment 75 probability. Conversely, partially dominant advantageous alleles (h > 0.5) are less likely to 76 fix because the reduced efficiency due to lower effective population size trumps increased 77 efficacy of selection due to increased homozygosity. These predictions are altered for male 78 and fecundity selection. Under selfing, no selection occurs on the male function, but the 79 strength of selection on the female function is doubled because two gametes are transmitted 80 for one selected parent (Damgaard, 2000). 81

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The evolutionary dynamic becomes further elaborated in structured populations with di-83 vergent selection. The simplest scenario involves two patches with an invading allele being 84 advantageous in one but deleterious in the other patch. The dynamic of local adaptation 85 then further depends on the effect that selfing has on gene flow. Partial selfing reduces the 86 effective haploid migration rate due to the reduction in the number of female gametes that 87 can be sired by immigrating male gametes, for individuals in the selfing population will have 88 already fertilized themselves to a large extent. This reduction in gene flow has been pro-89 posed to prevent the spread of maladaptive alleles from neighboring populations and thus 90 to promote local adaptation (Linhart and Grant, 1996), but two meta-analyses of reciprocal 91 transplant experiments reported the absence of correlation between local adaptation and the 92 mating system (Hereford, 2010, Leimu and Fischer, 2008). However, it is not immediately 93 clear how the interplay between the mating system, migration, and selection modes affects 94 the propensity for local adaptation. When local reproduction is panmictic, maintenance of 95 local polymorphism roughly requires that local selection is stronger than migration. On the 96 one hand, selfing reduces effective migration. On the other hand, it may either increase or 97 decrease the efficacy of local selection, depending on the balance between the effect of in-98 creasing effective dominance and increasing genetic drift. In addition, in diploids, conditions 99 where alleles are (partially) dominant when locally beneficial and (partially) recessive when 100 locally deleterious are especially favorable to the maintenance of polymorphism (Yeaman 101 and Otto, 2011). By unmasking recessive alleles, selfing is expected to reduce the range of 102 applicability of those conditions. Overall, we still lack correct theoretical predictions, which 103 makes it difficult to interpret the empirical results such as in Leinu and Fischer (2008) and 104 Hereford (2010). 105

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<sup>107</sup> In the present work, we extend the results of previous theoretical models of local adaptation <sup>108</sup> to partially self-fertilizing populations. We first derive a closed-form approximation for the <sup>109</sup> probability that a locally advantageous allele escapes extinction. We then use this result <sup>110</sup> to examine how previously described effects of selfing affect (1) the probability that allele <sup>111</sup> escapes extinction, (2) conditions required for the establishment of protected polymorphism, <sup>112</sup> and (3) the dependence of these properties on the mode of selection and migration.

### 113 2 Methods

We work with a hermaphroditic population that is divided into two patches connected by 114 bidirectional migration. Migration can occur during both the haploid and the diploid phase. 115 In the following, we will use the example of a plant life cycle, but results can readily be 116 transposed to other life cycles. Thus, only male migration, pollen dispersal, occurs during 117 the haploid phase, and diploid migration corresponds to seed dispersal. Fitness is controlled 118 by a single biallelic locus, with allele A favored in the first patch and allele a favored in the 119 other patch. These patches are referred to as favored and disfavored patch, respectively. The 120 life cycle of the modeled organism is composed of the following sequential stages: (1) male and 121 female meiosis leading to to the production of male gametophyte (pollen containing sperm 122 cell) and female gametophyte (embryo sac, containing egg cell), (2) pollen dispersal, (3) 123 mating (including selfing) and seed formation, (4) seed dispersal, and (5) seed establishment 124 and development, which yields adults of the next generation. To make the model general, 125 we allow selection to operate on viability and on male and female fecundity. More precisely, 126 adults in patch i with genotype k (AA, Aa, or aa) produce  $W_{i,k}^{Q}$  female and  $W_{i,k}^{Q}$  male 127 gametophytes. We do not consider haploid selection, but this could readily be included 128 in the model setting. Finally, each offspring with genotype k survives to maturity with 129 probability  $V_{i,k}$ . The population selfing rate, S, is defined as the proportion of individuals in 130 the population that self-fertilize and is equal across patches. Following previous works (ex: 131 Hartfield and Glémin, 2016, Hössjer and Tyvand 2016) we assume that the population reaches 132 equilibrium for inbreeding coefficient F and genotypic composition on a much shorter time-133 scale than the change in allelic frequencies (separation of time scale argument). Within each 134 patch, we can thus write genotype frequencies directly as a function of allelic frequencies and 135 F. If selection is not too strong, we can also use the neutral expectation: F = S/(2-S). 136 This assumption is relaxed in simulations. Mathematical symbols and their meaning are 137 outlined in Table 1. 138

#### <sup>139</sup> 2.1 Deriving the difference equation for allele frequency

Using the preceding definitions, one can derive the difference equations for allele frequencies in each patch. Let  $X_i$  and  $Y_i$  be the frequencies of genotypes AA and Aa, and  $x_i$  be the frequency of allele A in  $i^{th}$  patch. Our system has two degrees of freedom, given that there are three genotype frequencies and they must add up to unity. Thus, we keep track of frequencies of genotypes AA and Aa, while the frequency of aa genotype is by definition  $1-X_i - Y_i$ . Adult genotype frequencies in generation t in  $i^{th}$  patch are:

$$X_i = x_i^2(t) + Fx_i(t)(1 - x_i(t))$$
(1a)

$$Y_i = 2x_i(t)(1 - x_i(t))(1 - F)$$
(1b)

Adult genotypes may produce different number of male and female gametophytes. Let  $W_{i,k}^{\mathcal{O}}$ and  $W_{i,k}^{\mathcal{Q}}$  be the number of male and female gametophytes that an adult with genotype k(AA, Aa and aa) produces in patch *i*. Thus, the frequency of female and male gametophyte A in *i*<sup>th</sup> patch are, respectively:

$$x_i^{\mathcal{Q}} = \left( W_{i,AA}^{\mathcal{Q}} X_i + W_{i,Aa}^{\mathcal{Q}} \frac{Y_i}{2} \right) / \overline{W}_i^{\mathcal{Q}}$$
(2a)

$$x_{i}^{\mathcal{O}} = \left( W_{i,AA}^{\mathcal{O}} X_{i} + W_{i,Aa}^{\mathcal{O}} \frac{Y_{i}}{2} \right) / \overline{W}_{i}^{\mathcal{O}}$$
(2b)

where  $\overline{W}_{i}^{Q} = X_{i}W_{i,AA}^{Q} + Y_{i}W_{i,Aa}^{Q} + (1 - X_{i} - Y_{i})W_{i,aa}^{Q}$  and  $\overline{W}_{i}^{\mathcal{O}} = X_{i}W_{i,AA}^{\mathcal{O}} + Y_{i}W_{i,Aa}^{\mathcal{O}} + (1 - X_{i} - Y_{i})W_{i,aa}^{\mathcal{O}}$ . After pollen migration, the frequency of allele A in pollen in  $i^{th}$  patch is:

$$g_i^{O'} = (1 - m_{ij})x_i^{O'} + m_{ij}x_j^{O'}$$
(3)

where  $m_{ij}$  is the fraction of pollen in  $i^{th}$  patch that come from  $j^{th}$  patch. Pollen dispersal is followed by mating, which yields offspring genotypes:

$$X'_{i} = (1 - S)x_{i}^{\varphi}g_{i}^{\mathcal{O}} + S\left(\frac{W_{i,AA}^{\varphi}}{\overline{W}_{i}^{\varphi}}X_{i} + \frac{Y_{i}}{4}\frac{W_{i,Aa}^{\varphi}}{\overline{W}_{i}^{\varphi}}\right)$$
(4a)

$$Y'_{i} = (1-S)\left(x_{i}^{\mathcal{Q}}(1-g_{i}^{\mathcal{O}}) + (1-x_{i}^{\mathcal{Q}})g_{i}^{\mathcal{O}}\right) + S\frac{W_{i,Aa}^{\mathcal{Q}}}{\overline{W}_{i}^{\mathcal{Q}}}\frac{Y_{i}}{2}$$
(4b)

<sup>154</sup> Seed migration changes the genotype frequency to:

$$X''_{i} = (1 - M_{ij})X'_{i} + M_{ij}X'_{j}$$
(5a)

$$Y''_{i} = (1 - M_{ij})Y'_{i} + M_{ij}Y'_{j}$$
(5b)

where  $M_{ij}$  is the fraction of seed in patch *i* originating from patch *j*. Genotype *j* in patch *i* has probability  $V_{i,j}$  to survive to maturity, so the frequency of allele *A* in the generation t + 1 is:

$$x_i(t+1) = \left( V_{i,AA} X_i'' + V_{i,Aa} \frac{Y_i''}{2} \right) / \overline{V}_i$$
(6)

where  $\overline{V}_i = X''_i V_{i,AA} + Y''_i V_{i,Aa} + (1 - X''_i - Y''_i) V_{i,aa}.$ 

Equation (6) is our difference equation that expresses the frequency of allele A in the next generation in terms of its frequency in the current generation.

#### <sup>162</sup> 2.2 Analysis of the deterministic model

We first analyze the deterministic model that gives the conditions for a protected polymor-163 phism. This extends results of Bulmer (1972) to partial selfing and more general forms of 164 selection. Given that investigation of the consequences of an arbitrary selection, regime is 165 prohibitively complicated, the proceeding analysis is restricted to a few special cases. We are 166 ultimately interested in three selection scenarios: (1) when selection operates on differential 167 survival to maturity and when selection operates on (2) female and (3) male fecundity. For 168 each of these scenarios, we first consider seed migration only, as in Bulmer (1972) initial 169 model (also as in Yeaman and Otto, 2011). In addition to the comparison with previous 170 models, it allows analyzing the effect of selfing on selection only, as selfing does not affect 171 seed migration. Then, we consider pollen migration thus analyzing the joint effect of selfing 172 on both selection and migration. In total, we examine six categories of scenarios. 173

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<sup>175</sup> We use the standard approach to obtain conditions for stable polymorphism by considering <sup>176</sup> the conditions for which both monomorphic equilibria are unstable. Let both patches be fixed <sup>177</sup> for allele *a* and allele *A* acts as an invader. Equivalent results can be obtained by considering <sup>178</sup> patches fixed for allele *A* and *a* acting as the invader. The logic of derivation is the same <sup>179</sup> in all cases, wherein we linearize equations (6) around  $\vec{x} = [0, 0]^T$  to obtain the system of <sup>180</sup> linear difference equations, where **J** is the associated Jacobian. While **J** captures the invasion dynamics for an arbitrary mode of selection and migration, it is difficult to analyze, so we focus on special population genetic cases outlined above. Each of these scenarios will have an associated Jacobian  $\mathbf{J}^{\{k\}}$ :

$$\begin{bmatrix} x_1(t+1) \\ x_2(t+1) \end{bmatrix} = \mathbf{J}^{\{k\}} \begin{bmatrix} x_1(t) \\ x_2(t) \end{bmatrix}, \quad (J_{ij}^{\{k\}}) = \begin{cases} k = \circ, & M_{ij} \Delta V_{0,i} \\ k = \wp, & M_{ij} \Delta W_{0,j}^{\wp} \\ k = \sigma', & M_{ij} \Delta W_{0,j}^{\sigma'} \end{cases}$$
(7)

Terms  $\Delta V_{0,i}$ ,  $\Delta W_{0,i}^{Q}$ , and  $\Delta W_{0,i}^{Q}$  are the intergenerational change in frequency of A in  $i^{th}$ 184 patch due to selection on a particular fitness component, and  $M_{ij}$  accounts for migration 185 between patches, with  $M_{i,i} = 1 - M_{i,j}$ , with  $j \neq i$ . In the case of viability selection, the 186 frequency change of A in the patch 1 reflects either the contribution of alleles A that stay in 187 patch 1  $(1 - M_{12})$  and survives to adulthood  $(\Delta V_{0,1})$ , or the contribution of alleles A that 188 migrate from patch 2  $(M_{12})$  and then survive to adulthood  $(\Delta V_{0,1})$ . Similar logic holds for 189 female and male fecundity selection but off-diagonal selection terms are exchanged because 190 selection occurs prior to migration: note the j indices in  $\Delta W$  terms instead of i in the 191  $\Delta V$  term in equation (7). Selection terms for the three scenarios are obtained by keeping 192 constant the two fitness components not involved in the scenarios in the general recursion 193 equations. Thus, under seed migration the three selection terms are: 194

$$\Delta V_{0,i} = \frac{FV_{i,AA} + (1-F)V_{i,Aa}}{V_{i,aa}}$$
(8a)

$$\Delta W_{0,i}^{Q} = \frac{(1-F)(W_{i,aa}^{Q} + (1+3F)W_{i,Aa}^{Q}) + F(1+3F)W_{i,AA}^{Q}}{2(1+F)W_{i,aa}^{Q}}$$
(8b)

$$\Delta W_{0,i}^{\vec{O}} = \frac{(1-F)((1-F)W_{i,Aa}^{\vec{Q}} + FW_{i,AA}^{\vec{O}}) + (1+3F)W_{i,aa}^{\vec{O}}}{2(1+F)W_{i,aa}^{\vec{O}}}$$
(8c)

These expressions can be made more intuitive by parameterizing fitnesses relative to geno-195 type *aa*, where  $s_i^{\circ}$ ,  $s_i^{\circ}$ ,  $s_i^{\circ}$  are the reproductive advantage of AA homozygote relative to 196 aa homozygote when selection acts on viability, female, and male fecundity, respectively. 197 Parameters  $\tilde{h}_i^{\circ}$ ,  $\tilde{h}_i^{\circ}$ ,  $\tilde{h}_i^{\circ}$  represent the effective dominance of the heterozygote in  $i^{th}$  patch 198 for the three respective selection modes. These are composite parameters that depend on F199 and the actual dominance and are introduced to capture the fact that selfing increases the 200 effective dominance of invading heterozygote due to contribution of mutant homozygotes to 201 the invasion process. For the three cases of viability, female, and male fecundity effective 202

<sup>203</sup> dominances are respectively:

$$\tilde{h}_i^\circ = (1 - F)h_i^\circ + F \tag{9a}$$

$$\tilde{h}_{i}^{Q} = \frac{(1+3F)}{2(1+F)} (F + (1-F)h_{i}^{Q}) = \frac{1}{2}(1+S)(F + (1-F)h_{i}^{Q})$$
(9b)

$$\tilde{h}_{i}^{\vec{O}} = \frac{(1-F)}{2(1+F)} (F + (1-F)h_{i}^{\vec{O}}) = \frac{1}{2}(1-S)(F + (1-F)h_{i}^{\vec{O}})$$
(9c)

These forms capture the fact that selfing increases the effective dominance of invading 204 mutants: the invader has dominance  $h_i$  when it invades in a heterozygous form (that is, 205 1 - F fraction of time), and dominance of one when it invades in a homozygous form (that 206 is, F fraction of time). Selfing also affects the global selection intensity on male and female 207 fecundity. The 1/2 factor captures the fact that selection acts only on half of the gametes 208 produced by each genotype, the 1 - S factor that selection on male fecundity only operates 209 under outcrossing and the 1+S factor that under selfing an individual contribute two alleles 210 through seed production (female fitness). Taken together: 211

$$\Delta V_{0,i} = 1 + \tilde{h}_i^{\circ} s_i^{\circ} \tag{10a}$$

$$\Delta W^{\mathcal{Q}}_{0,i} = 1 + \tilde{h}^{\mathcal{Q}}_i s^{\mathcal{Q}}_i \tag{10b}$$

$$\Delta W_{0,i}^{\mathcal{O}} = 1 + \tilde{h}_i^{\mathcal{O}} s_i^{\mathcal{O}}$$
(10c)

The fitness of the mutant always take the same form as in a haploid model with an effective selective advantage  $\tilde{s} = \tilde{h}s$ .

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The preceding approach can be readily extended to the selective scenarios where migration occurs solely via pollen. One can still use the Jacobian in (7), albeit with the modified migration rate to account for the facts that (a) pollen is haploid and thus do not contribute in the same way as diploid seed to the gene pool of the next generation, and (b) that in all three cases migration operates prior to selection rather than after:

$$(J_{ij}^{\{k\}}) = \begin{cases} k = \circ, & \tilde{M}_{ij}^{\circ} \Delta V_{0,i} \\ k = \varphi, & \tilde{M}_{ij}^{\varphi} \Delta W_{0,i}^{\varphi} \\ k = \sigma^{\circ}, & \tilde{M}_{ij}^{\sigma^{\circ}} \Delta W_{0,i}^{\sigma^{\circ}} \end{cases}$$
(11)

<sup>220</sup> Selection terms are still parameterized according to equations (10a–10c), but effective mi-

221 gration is given by:

$$\tilde{M}_{ij}^{\circ} = (1 - S) \frac{m_{ij}}{2} \frac{1 + h_i^{\circ} s_i^{\circ}}{1 + \tilde{h}_i^{\circ} s_i^{\circ}}$$
(12a)

$$\tilde{M}_{ij}^{Q} = (1-S)\frac{m_{ij}}{2}\frac{1}{1+\tilde{h}_{i}^{Q}s_{i}^{Q}}$$
(12b)

$$\tilde{M}_{ij}^{\vec{O}} = (1-S)\frac{m_{ij}}{2} \frac{1 + \frac{\tilde{h}_j^{\vec{O}} s_j^{\vec{O}}}{(1-S)/2}}{1 + (1-m_{ij})\tilde{h}_i^{\vec{O}} s_i^{\vec{O}} + m_{ij}\tilde{h}_j^{\vec{O}} s_j^{\vec{O}}}$$
(12c)

Viability effective migration rate (12a) can be intuitively understood by noting that 1 - S222 corresponds to the fraction of pollen that is exchanged between the patches,  $m_{ij}/2$  corrects 223 for the fact that haploid phase contributes two-fold less alleles to the gene pool of the 224 next generation relative to the diploid progeny dispersal, and the relative fitness ratio (1 +225  $h_i^{\circ} s_i^{\circ})/(1 + \tilde{h}_i^{\circ} s_i^{\circ})$  accounts for the fold increase in invader frequency in the patch of origin 226 due to the inhibitory effect of selfing on gene flow. Similar interpretation holds for (12b) 227 and male fecundity selection (12c), except that fitness ratio now corrects for selection acting 228 prior to migration. Note that for weak selection, the three effective migration rates reduce to 229  $(1-S)\frac{m_{ij}}{2}$ . The only complication is that when selection acts on the male fitness component, 230 one has to modify the effective dominance along with the effective migration rate. More 231 precisely,  $\Delta W_{0,i}^{\mathcal{O}} = 1 + \omega \tilde{h}_i^{\mathcal{O}} s_i^{\mathcal{O}}$ , where  $\omega$ : 232

$$\omega = 1 - m_{ij} \left( 1 - \frac{\tilde{h}_j^{\mathcal{O}'} s_j^{\mathcal{O}'}}{\tilde{h}_i^{\mathcal{O}'} s_i^{\mathcal{O}'}} \right)$$
(13)

Overall, a simple parameterization procedure allows the exploration of a wide breadth of population genetic scenarios.

#### 235 2.3 Branching process approximation

By analyzing the stability of system 7, one can only examine conditions necessary for the 236 invading allele to escape extinction. However, we also want to know the probability of the 237 escape. We pursue this by representing the change in the number of invading allele as 238 a multi-type branching process. Selection is thus assumed to be stronger than drift (i.e., 239  $|N\tilde{h}_i^{\{k\}}s_i^{\{k\}}| \gg 1$ ). We work with two types, each tracking the number of mutant alleles 240 in one of the two patches. The number of the mutant alleles is represented by the vector 241  $\vec{N}(t) = [N_1(t), N_2(t)]^T$ , where  $N_1(t)$  and  $N_2(t)$  are the number of mutants in patch 1 and 2 in 242 generation t, respectively. Let  $f_i$  be the probability generating function (PGF) of offspring 243

number of mutant alleles of type *i*. The ultimate probability of extinction of type *i*  $(1 - P_i)$ is given by the smallest positive root of the following system of equations (Haccou *et al.* (2005)):

$$1 - P_1 = f_1(1 - P_1, 1 - P_2) \tag{14a}$$

$$1 - P_2 = f_2(1 - P_1, 1 - P_2) \tag{14b}$$

As we can assume that the number of offspring that types *i* and *j* leave are uncorrelated, then  $f_k(1-P_1, 1-P_2) = f_{k,1}(1-P_1)f_{k,2}(1-P_2)$ , with  $k = \{1, 2\}$ . Intuitively, the probability that mutant goes extinct conditioning on appearance in patch 1 is the probability that all of its offspring left in patch 1 ultimately go extinct  $(f_{1,1}(1-P_1))$ , and the probability that all offspring left in patch 2 via migration  $(f_{1,2}(1-P_2))$  are ultimately lost. A similar explanation holds when mutant originates in patch 2. To solve the system, one needs to obtain the  $f_{i,j}(z)$ PGFs.

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In the Wright-Fisher model with random mating, the number of mutant offspring is ap-255 proximately Poisson-distributed with mean  $\Delta \mathcal{W}_{0,i}$ , where  $\mathcal{W}$  stands for the different form of 256 selection as described above. Partial self-fertilization affects the mutant offspring distribu-257 tion in two ways. First, it increases the mean number of offspring by inflating the effective 258 dominance coefficient (see above). Second, selfing increases the variance in offspring number 259 by the factor 1 + F relative to the randomly mating population (Caballero and Hill, 1992, 260 Pollak, 1987). Therefore, offspring number should follow a distribution with mean  $\Delta \mathcal{W}_{0,i}$ 261 and variance  $\Delta W_{0,i}(1+F)$ . To our knowledge, the full distribution has never been obtained. 262 even in single populations, probably because only the two first moments are needed for 263 branching process and diffusion approximations. In appendix, we derive the exact probabil-264 ity generating function (PGF) of the distribution in different cases. In a single population 265 we have: 266

$$f_{\phi}(z) = (1 - F) \underbrace{e^{-(1-z)\left((1-S)\frac{W_{Aa}^{\varphi} + W_{Aa}^{\mathcal{O}}}{2}V_{Aa} + \frac{S}{2}W_{Aa}^{\varphi}V_{Aa}\right)}}_{\text{Transmitted in } Aa} \underbrace{e^{-\frac{1}{2}(1-z^{2})\frac{S}{2}W_{Aa}^{\varphi}V_{AA}}}_{\text{Transmitted in } AA \text{ (only selfing)}} + F \underbrace{e^{-(1-z)\left((1-S)\frac{W_{Aa}^{\varphi} + W_{Aa}^{\mathcal{O}}}{2}V_{Aa}\right)}}_{\text{Transmitted in } Aa \text{ (only outcrossing)}} \underbrace{e^{-\frac{1}{2}(1-z^{2})SW_{Aa}^{\varphi}V_{AA}}}_{\text{Transmitted in } AA \text{ (only selfing)}}$$
(15)

<sup>267</sup> The first term in equation (15) corresponds to a A parental allele coming from an Aa individ-

ual (probability 1-F) and the second term to an AA individual (probability F). Offspring 268 can be transmitted either in AA offspring, which occurs only through selfing (because we 269 consider a rare mutant) or in Aa offspring, which can occur either through outcrossing or 270 through selfing when the parent is Aa (so with a probability S/2). Note that fecundity selec-271 tion depends on parent genotypes whereas viability selection depends on offspring genotype. 272 Using the properties of PGFs we easily retrieve that the mean of the distribution is  $\Delta \mathcal{W}_i$ 273 obtained in the deterministic analysis and the variance is  $\Delta W_i(1+F)$ . For F=0, equation 274 (15) boils down to the PGF of a Poisson distribution. Hereafter, as for the deterministic 275 analysis, we consider the different forms of selection separately by setting constant the other 276 fitness components. 277

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For the two-patch model we need to include migration in the  $f_{i,j}(z)$  PGFs. For seed migration, we show that:

$$f_{i,j}(z) = (1-F)e^{-(1-z)\left((1-S)\frac{W_{Aa,i}^{Q}+W_{Aa,i}^{Q}}{2}M_{i,j}V_{Aa,j}+\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{Aa,j}\right)}e^{-\frac{1}{2}(1-z^{2})\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{AA,j}} + Fe^{-(1-z)\left((1-S)\frac{W_{AA,i}^{Q}+W_{AA,i}^{Q}}{2}M_{i,j}V_{Aa,j}\right)}e^{-\frac{1}{2}(1-z^{2})SW_{AA,i}^{Q}M_{i,j}V_{AA,j}}$$
(16)

recalling that  $M_{i,i} = 1 - M_{i,j}$  with  $j \neq i$ . Note that fecundity selection occurs in patch i, 281 before seed migration, whereas viability selection occurs in patch j, after seed migration. 282 However, the different orderings of migration and selection yield the same results (see *Math*-283 *ematica* notebook). We also retrieve that the mean of the four distributions are given by the 284 Jacobian terms obtained above,  $M_{i,j} \Delta W_{i,j}$  and the variance is also inflated by 1 + F. For 285 pollen migration the form is slightly different because migrants can only contribute to the 286 next generation through outcrossing and male gametes (whereas selfed seeds can migrate). 287 The form of the PGF is thus different for the resident and migrant contribution. We have: 288

$$f_{i,i}(z) = (1-F)e^{-(1-z)\left((1-S)\frac{W_{Aa,i}^{Q} + W_{Aa,i}^{Q}(1-m_{i,j})}{2}V_{Aa,i} + \frac{S}{2}W_{Aa,i}^{Q}V_{Aa,i}\right)}e^{-\frac{1}{2}(1-z^{2})\frac{S}{2}W_{Aa,i}^{Q}V_{AA,i}} + Fe^{-(1-z)\left((1-S)\frac{W_{AA,i}^{Q} + W_{AA,i}^{Q}(1-m_{i,j})}{2}V_{Aa,i}\right)}e^{-\frac{1}{2}(1-z^{2})SW_{AA,i}^{Q}V_{AA,i}}$$
(17a)

$$f_{i,j}(z) = (1-F)e^{-(1-z)(1-S)\frac{W_{Aa,i}^{O'}m_{i,j}}{2}V_{Aa,j}} + Fe^{-(1-z)(1-S)\frac{W_{AA,i}^{O'}m_{i,j}}{2}V_{Aa,j}} \quad \text{for } j \neq i$$
(17b)

As expected, the mean of the distributions are still given by the Jacobian terms with the

appropriate effective migration rates,  $\tilde{M}_{i,j} \Delta \mathcal{W}_{i,j}$  (see above). However, the variances are not 290 inflated by 1 + F. For migrant alleles, equation (17b) boils down to a Poisson distribution 291 because the contribution is only through outcrossing. In contrast for resident allele, the 292 variance is inflated by more than 1 + F (see appendix for details). The reason is that for a 293 given selfing rate, only alleles produced by outcrossing can be exported to the other patch, 294 which increase the proportion of resident offspring contributed by selfing, hence the variance. 295 Note, however, that the difference in PGFs between the two migration modes only affects 296 high-order terms of selection and migration so has no effect on branching process approxi-297 mation results, which can all be expressed with the same form using appropriate effective 298 parameters as defined in previous section (see *Mathematica* notebook). 299

300

Previous section also showed that  $\Delta \mathcal{W}_{0,i}$  always has the form of  $1 + \tilde{s}_i$ , where  $\tilde{s}_i$  is the effective 301 advantage of an invading mutant in patch i, while  $M_{ij}$  represents the effective migration rate 302 between patches i and j. Thus, one can derive  $P_i$  for this generic case and then parameterize 303 migration and selection to reflect the specific population genetic case. Since we cannot obtain 304 the exact solution for extinction probabilities, we approximate to weak selection using the 305 approach of Tomasini and Peischl (2018), which is based on the approximation for slightly 306 supercritical multitype branching processes (Haccou et al., 2005). All model parameters 307 are rescaled by  $\tilde{s}_1$  such that  $M_{ij} := \chi_{ij}\tilde{s}_1$  and  $\tilde{s}_2 := \zeta \tilde{s}_1$ . By linearizing around  $\tilde{s}_1 = 0$ 308 and neglecting higher-order terms, we obtain a closed-form solution for the probability of 309 establishment conditioning on the patch in which locally advantageous allele appeared. All 310 analytical solutions are compared to simulated data using the method described in Appendix 311 D. Simulations were conducted with the help of GNU Parallel (Tange, 2011). 312

#### 313 2.4 Diffusion process approximation

An alternative way of incorporating stochastic transmission of alleles across generations is by approximating frequency change to diffusion. This approach has been originally developed for the two-patch model in an outcrossing population by Sakamoto and Innan (2019) in the case of wholly outcrossing population. Here, we re-capitulate their derivation and extend it to the case of partial selfing. The establishment probability satisfies the Kolmogorov backward equation (KBE):

$$0 = \sum_{i=1}^{2} \mu_i \frac{\partial P(x_1, x_2)}{\partial x_i} + \sum_{i=1}^{2} \frac{\sigma_i}{2} \frac{\partial^2 P(x_1, x_2)}{\partial x_i^2}$$
(18)

where  $\mu_i$  and  $\sigma_i$  are drift and diffusion coefficients for patch *i*, and are given by:

$$\mu_i = \tilde{s}_i x_i (1 - x_i) + \tilde{M}_{ij} (x_j - x_i), \quad \sigma_i = \frac{x_i (1 - x_i)}{2N_1 / (1 + F)}$$
(19)

Note that  $\tilde{s}$  corresponds to effective selective advantage of mutant, and  $M_{ij}$  is the effective migration rate; These were derived in section 2.2. Diffusion coefficient is inflated by the factor of 1 + F as described previously. Unfortunately, we could not find neither the explicit nor approximate solution to this partial differential equation. Following treatment in Barton (1987), the problem is simplified by focusing on the first phase of fixation when mutant allele is rare. Thus, one can approximate coefficients as:

$$\sigma_i = \frac{x_i}{2N_1/(1+F)} + o(x_i^2), \quad \mu_i = \tilde{s}_i x_i + \tilde{M}_{ij}(x_j - x_i) + o(x_i^2)$$
(20)

<sup>327</sup> which leads to the simplified KBE:

$$0 = \left(\tilde{s}_{1}x_{1} + \tilde{M}_{12}(x_{2} - x_{1})\right) \frac{\partial P(x_{1}, x_{2})}{\partial x_{1}} + \left(\tilde{s}_{2}x_{2} + \tilde{M}_{21}(x_{1} - x_{2})\right) \frac{\partial P(x_{1}, x_{2})}{\partial x_{2}} + \frac{x_{1}}{4N_{1}/(1 + F)} \frac{\partial^{2} P(x_{1}, x_{2})}{\partial x_{1}^{2}} + \frac{x_{2}}{4N_{2}/(1 + F)} \frac{\partial^{2} P(x_{1}, x_{2})}{\partial x_{2}^{2}}$$
(21)

Because the invading allele is rare, the mutants in patch i go extinct independently of one another with probability  $e^{-l_i}$ , which means that the establishment probability takes the form:

$$P(x_1, x_2) = 1 - e^{-2\left(\frac{N_1}{1+F}x_1l_1 + \frac{N_2}{1+F}x_2l_2\right)}$$
(22)

Substituting eqn. 22 into 21 results in an algebraic equation which captures the establishment probability for an arbitrary number of initial mutants across two patches. We are interested in two special cases, when mutant either starts in favored  $(x_1 = 1/(2N_1) \text{ and } x_2 = 0)$  or disfavored patch  $(x_1 = 0 \text{ and } x_2 = 1/(2N_2))$ . With this parameterization, we obtain the system of two non-linear equations:

$$0 = 2\tilde{M}_{21}N_2l_2 + 2N_1l_1\tilde{s}_1 - N_1l_1(2\tilde{M}_{12} + l_1)$$
(23)

$$0 = 2\tilde{M}_{12}N_1l_1 + 2N_2l_2\tilde{s}_2 - N_2l_2(2\tilde{M}_{12} + l_2)$$
(24)

<sup>335</sup> By solving these for  $l_1$  and  $l_2$ , taking the real root, and substituting into eqn. 22, one retrieves <sup>336</sup> a closed-form solution for the establishment probability (see *Mathematica* notebook). With <sup>337</sup> all of the simplifying assumptions above, the diffusion approximation works in the same regime when  $N_e s \gg 1$ , as is the case with branching approximation. As will be shown later in the text, the comparison of two solutions reveals that diffusion approximation performs identically when the allele starts in the favored patch and slightly better when it originates in the disfavored one. Because branching process approximation is easier to work with (e.g., series expansion readily yields intuitive special cases), we use this solution throughout our analysis and note that the diffusion approach yields marginally better precision.

#### 344 **3** Results

#### <sup>345</sup> 3.1 Probability of establishment of a mutant

#### 346 3.1.1 General equations

The probability of establishment of a new allele is non-zero if the branching process is supercritical, which means that the leading eigenvalue of the mean reproductive matrix must be larger than unity (Haccou *et al.*, 2005). For the invasion of allele A under viability selection, it corresponds to:

$$\frac{M_{12}}{\frac{((1-F)V_{1,Aa}+FV_{1,AA})-V_{1,aa}}{(1-F)V_{1,Aa}+FV_{1,AA}}} + \frac{M_{21}}{\frac{((1-F)V_{2,Aa}+FV_{2,AA})-V_{2,aa}}{(1-F)V_{2,Aa}+FV_{2,AA}}} < 1$$
(25)

The denominator is the relative reproductive advantage of invading mutant against the 351 resident allele. The invading population is a combination of mutant heterozygotes (when the 352 two gene copies of an individual are not identical by descent, 1 - F fraction of time) and 353 homozygotes (when the two gene copies are identical by descent, F fraction of time). So the 354 whole term  $((1 - F)V_{i,Aa} + FV_{i,AA})$  gives the fitness of the invading mutant weighted by the 355 contribution of invading genotypes. In an outcrossing population (F = 0), condition (25) 356 reduces to  $M_{12}/(1 - V_{1,aa}/V_{1,Aa}) + M_{21}/(1 - V_{2,aa}/V_{2,Aa}) < 1$ , which is identical to Bulmer's 357 inequality. The same inequality with re-parameterized selection holds for fecundity and male 358 sexual selection (see Appendix C). The full equations for the establishment probabilities are 359 too long and not very informative and are thus reported in the appendix (see equations 360 (A16) and (A17)). Without loss of generality, consider that allele A is advantageous in 361 patch 1 but deleterious in patch 2  $(s_1 > 0 > s_2)$ ; in the case of symmetrical migration 362  $(M_{12} = M_{21} = M/2)$  and migration prior to selection the general probability of establishment 363

of allele A in either patch 1 or 2 is given by:

$$P_{1} = \max\left[\frac{1}{1+F}\frac{2\sigma(\sigma+\Delta)(\tilde{h}_{1}s_{1}+\tilde{h}_{2}s_{2}+\sigma-M)}{2\Delta(\sigma+\Delta)+M^{2}+M(\sigma-\Delta)},0\right]$$
(26)

$$P_{2} = \max\left[\frac{1}{1+F}\frac{2M\sigma(\tilde{h}_{1}s_{1}+\tilde{h}_{2}s_{2}+\sigma-M)}{2\Delta(\sigma+\Delta)+M^{2}+M(\sigma-\Delta)},0\right]$$
(27)

where  $\Delta = \tilde{h}_1 s_1 - \tilde{h}_2 s_2$  and  $\sigma = \sqrt{\Delta^2 + M^2}$  with  $\tilde{h}$  as defined above for viability, female and male fecundity selection. These resemble – but are not equal – to equations (4) and (5) in (Tomasini and Peischl, 2018), who obtained an inexact result because of a typo in their application of Haccou et al.'s theorem. Initially the typo came from Aeschbacher and Bürger (2014) and was independently detected by Pontz and Bürger (2021) (see their Appendix A). Interestingly, the correct solutions are more complicated and less elegant than the ones of Tomasini and Peischl (2018).

#### 372 3.1.2 Limiting cases and comparison with previous results

Despite the complexity of the general equations, useful insights can be obtained from simple 373 limit conditions. In the limit of no migration  $(M_{12} = M_{21} = 0)$ , we get back to the single-374 patch scenario where selection favors allele A in patch 1:  $P_1 = 2\frac{h_1s_1}{1+F}$ . This is equivalent 375 to Charlesworth (1992) and Caballero and Hill (1992) for viability selection. For male and 376 female fecundity selection, the result is similar to the one intuited in Damgaard (2000), except 377 that we also accounted for the reduction in P due to increased variance of offspring number. 378 Conversely, in the limit of full migration we obtain  $P_1 = P_2 = \frac{\tilde{h}_{1s_1+\tilde{h}_{2s_2}}}{1+F}$ , which is equivalent 379 to Nagylaki (1980), with the appropriate rescaling for dominance and partial selfing. The 380 probability of establishment is simply the average over the two patches. Interestingly, the fact 381 that the effects of selfing on viability selection cancel out for codominant alleles  $(h_1 = h_2 =$ 382 1/2) is no longer true with intermediate migration, even for seed migration that is not affected 383 by selfing. In the limit of weak symmetrical migration, we obtain  $P_1 = s_1 - \frac{M}{1+F}$  and  $P_2 =$ 384  $\frac{Ms_1}{(1+F)(s_1-s_2)}$  and in the limit of strong migration (i.e.  $M >> s_i$ ):  $P_1 = \frac{s_1+s_2}{2} + (1+F)\frac{s_1(s_1-s_2)}{4M}$ 385 and  $P_2 = \frac{s_1 + s_2}{2} - (1 + F)\frac{s_2(s_1 - s_2)}{4M}$ . Thus, unlike in a single population a locally advantageous 386 allele that is codominant in both patches is more likely to escape extinction in selfers than 387 in outcrossers. The relation between F and  $P_2$  is more complicated, and the allele can either 388 be more likely, for high migration rates, or less likely, for low migration rates, to escape 389 extinction. The effects of selfing under codominance only vanish either for no migration or 390 full migration. 391

#### <sup>392</sup> 3.1.3 Comparison with simulations

In general, our approximation for viability shows good correspondence with simulations 393 across different selfing rates (Figure 1). This also holds true across different dominance co-394 efficients, and when selection or migration are asymmetrical (Figure 2). Correspondence is 395 better in cases where the invading allele initially appears in the favored rather than in the 396 disfavored patch. Diffusion approximation gives identical results when allele starts in the 397 favored, and slightly better results when in the case of the disfavored patch. The improve-398 ment only occurs when the migration rate is low, and this pattern persists across dominances 399 and modes of selection. A possible reason for the slightly worst accuracy of the branching 400 process approach in the disadvantageous patch with low migration is that the rescaling of 401 the model assumes that selection and migration parameters are of the order of  $\tilde{s}_1$ . For low 402 migration, we can have  $m_{21} \ll \tilde{s}_1$ , so that migration could not be sufficient to introduce 403 the allele in the favored patch before it goes extinct in the disfavored one. 404



Figure 1: Comparison of analytical solution to simulated data across different selfing rates (corresponding to different equilibrium F). Dashed lines are diffusion approximation. Left panel: the probability of establishment when the allele emerges in the favored patch; Right panel: the probability of establishment when the allele emerges in the disfavored patch. Parameters:  $h_1^{\circ} = h_2^{\circ} = 1/2$ ,  $s_1^{\circ} = -s_2^{\circ} = 0.01$ ,  $M_{12} = M_{21} = M$ .



Figure 2: Simulations of different selection regimes. Going from left to right, the examined scenarios are as follows. Dashed lines denote diffusion approximation. First column: dominant case  $(h_1^{\circ} = h_2^{\circ} = 3/4, s_1^{\circ} = -s_2^{\circ} = 0.01, M_{12} = M_{21} = M)$ ; Second column: recessive case  $(h_1^{\circ} = h_2^{\circ} = 1/4, s_1^{\circ} = -s_2^{\circ} = 0.01, M_{12} = M_{21} = M)$ ; Third column: Asymmetric selection case  $(s_1^{\circ} = 0.01, s_2^{\circ} = -0.0125, h_1^{\circ} = h_2^{\circ} = 1/2, M_{12} = M_{21} = M)$ ; Fourth column: asymmetric migration  $(s_1^{\circ} = -s_2^{\circ} = 0.01, h_1^{\circ} = h_2^{\circ} = 1/2, M_{12} = M, and M_{21} = 1.25M)$ .

 $P_1$  is a monotonically decreasing function in M, because strong migration causes the spread-405 ing of the locally advantageous allele to become swamped by the resident from the disfa-406 vored patch.  $P_2$  is non-monotonic function in M. Increasing migration initially increases the 407 probability that an invading allele escapes from the disfavored patch before it goes extinct. 408 However, at large migration rates, the spreading allele escapes the disfavored patch but is 409 swamped due to a large influx of deleterious residents from the disfavored patch. For male 410 fecundity selection, the analytical solutions for  $P_1$  and  $P_2$  are slightly worse against the sim-411 ulations (Figure A11) than those provided for viability selection. Note, however that as the 412 selfing rate tends towards 1, the effective selection coefficient on male function vanishes so 413 that the strong selection condition for branching process approximation is not met anymore. 414 Slight discrepancies are also observed when selection or migration are asymmetrical (Figures 415 A12, and A13). 416

417

We also varied F continuously to obtain a fine-grained view of the analytic performance. 418 Three insights emerge. First, there is a good agreement between simulated data and ana-419 lytical solution, although deviations increase as the migration rate increases. Second, the 420 branching process poorly captures the dynamics of the invasion when mutants are partially 421 recessive. For example, in the limit of complete recessivity (h = 0), the mutant does not 422 have any reproductive advantage (i.e., equations 10a–10c reduce to unity). We clearly see 423 this in Figure 3, where the analytical solution underestimates P when the allele is partially 424 recessive (first column). However, this discrepancy disappears as F increases, as homozy-425

gotes increasingly contribute to the invading process. Third, diffusion approximation yields a better fit when mutant starts in the favored patch, but this improvement generally works only when M is low.



Figure 3: Simulations of different selection regimes. Going from left to right, the examined scenarios are as follows. Dashed lines denote diffusion approximation. Each column denotes the establishment probability for a set of dominance coefficients noted above the panel. Lines correspond to different migration rates (see legend box below). Other parameters:  $s_1^{\circ} = -s_2^{\circ} = 0.01$ ,  $M_{12} = M_{21} = M$ ). The axes are on logarithmic scale and error bars are excluded.

## 3.2 Decomposing the effects of selfing on the establishment prob ability

Selfing impedes the spread of an invading beneficial allele by reducing the effective population 431 size and by increasing the effective dominance in the disfavored patch. On the other hand, 432 selfing also facilitates the invasion process by increasing the effective dominance in the favored 433 patch and reducing the gene flow when dispersal occurs through pollen. In this section, we 434 ask: are the impeding effects generally more important than facilitating effects? When 435 does the introduction of selfing increase P? To this end, we introduce an indicator  $\beta_i(y)$ 436 which denotes the effect that selfing has on  $P_i$  solely via parameter y. For example,  $P_i^{\{\bar{h}_1\}}$ 437 corresponds to the establishment probability in patch i, if selfing only exerted its effect by 438

<sup>439</sup> inflating favored dominance. More generally:

$$\beta_i(y) = \left(\frac{dP_i^{\{y\}}}{dF}\right)\Big|_{F=0}, \qquad y \in \{\tilde{h}_i, \tilde{N}, \tilde{M}\}, \quad i \in \{1, 2\}$$
(28)

Consider decomposing the effects of selfing on the establishment of an allele affecting viability. 440 For example, the indicator  $\beta_1(\tilde{h}_1^\circ)$  tells us whether a shift to selfing increases  $P_1$ , if selfing 441 solely acted through an increase in the effective dominance in the favored patch. This allows 442 us to examine the effect of each factor separately and assess when one outweighs the other. 443 The indicator is obtained by taking equation A16 and sequentially setting: (1) F = 0 which 444 eliminates selfing's effect on  $\tilde{N}$ , then (2) parameterizing  $\tilde{s}_1^\circ := s_1^\circ \tilde{h}_1^\circ$  which introduces the 445 effect of selfing on favored dominance, and finally, (3) setting  $\tilde{s}_2^\circ := s_2^\circ h_2^\circ$  which excludes the 446 effect of selfing on the effective dominance in the disfavored patch. The outlined method is 447 also applicable to other selection and migration scenarios, and the general procedure is given 448 in Appendix F. 449

#### 450 3.2.1 Emergence in the favored patch

We focus on the establishment conditioning on allele emerging in the favored patch. Consider 451 viability selection first (see Figure 4). Given our interest in knowing whether selfing increases 452 or decreases the establishment probability, we only focus on the region of parameter space 453 where allele can become established in fully outcrossing population (right of the solid line in 454 Figure 4). When the invading allele is partially recessive in favored and partially dominant 455 in the disfavored patch (white region), the criterion for escaping extinction is not satisfied, 456 and a shift to selfing can only have a promoting effect on the establishment in this region of 457 parameter space. 458

459

Under seed dispersal, selfing only affects selection via effective dominance and the effective 460 population size. One can recognize three regions of selfing effects (Figure 4). Firstly, when 461 the invading mutant is partially recessive in the favored and partially dominant in the dis-462 favored patch, selfing increases  $P_1$  via the inflation of  $\tilde{h}_1^{\circ}$  (blue region). More formally, this 463 will be the outcome when  $\beta_k(\tilde{h}_1^\circ) > -(\beta_k(\tilde{h}_2^\circ) + \beta_k(\tilde{N}))$  (dark blue region). This is because 464 the mutant is already dominant in the disfavored patch so selfing does not significantly 465 increase the rate of purging, but it does increase the rate of spread owing to the mutant 466 being partially recessive in the favored patch. Thus, the net effect is increased  $P_1$ . Secondly, 467 when the mutant is partially dominant in the favored and partially recessive in the disfa-468 vored patch, selfing decreases  $P_1$  via inflation of  $\tilde{h}_2^{\circ}$  (darker red region). This happens when 469

 $\beta_k(\tilde{h}_1^\circ) < -\beta_k(\tilde{h}_1^\circ)$  (dark red region). The effect is opposite to the first regime: selfing has 470 a larger effect on the increase in purging from the disfavored patch (since the dominance in 471 the disfavored patch is low) than on the increase in spreading in the favored patch (because 472 dominance in the favored patch is already high). The net effect is a decrease in  $P_1$ . The 473 region of parameter space that lies between these two zones corresponds to cases when the 474 facilitating effect of selfing (via dominance in the favored patch) roughly cancels out the 475 impeding effect (via dominance in the disfavored patch) so that the net effect on  $P_1$  is deter-476 mined by the reduction in effective population size and the net effect of selfing is to decrease 477  $P_1$ . 478

479

Under pollen dispersal, we also found the same three regions but with different boundaries 480 (Figure 4). In addition, selfing also affects pollen dispersal by reducing the effective number of 481 migrants, so in the intermediate zone the effect of selfing on  $P_1$  depends both on the reduction 482 in effective population size and effective migration rate, which creates a fourth region – the 483 region for which all parameter combinations where  $\beta_k(\tilde{h}_1^\circ) + \beta_k(\tilde{M}) > -(\beta_k(\tilde{h}_2^\circ) + \beta_k(\tilde{N}))$ 484 (light blue region). It corresponds to conditions where the reduction in effective migration 485 rate overwhelms the impeding effects of selfing. Overall, selfing increases the establishment 486 of new alleles under broader conditions under pollen than under seed dispersal. Note that 487 selection coefficients are an order of magnitude lower in the right panel of Figure 4, and the 488 region where selfing has a net-positive effect is comparable (if not larger) to the blue region 489 in the left panel. 490



Figure 4: Four zones of selfing's effects on the establishment probability when mutant originates in the favored patch. White region denotes parameter space where the mutant cannot establish under outcrossing. Selection act only on viability, and migration occurs only via pollen (left), or only via seed (right). Blue and red regions correspond to parameter space where selfing facilitates and impedes  $P_1$ , respectively. Lines in the left panel are as follows. Solid black line:  $P_1 = 0$ ; Dashed black line:  $\beta_k(\tilde{h}_1^\circ) = -(\beta_k(\tilde{h}_2^\circ) + \beta_k(\tilde{N}))$ ; Dotted black line:  $\beta_k(\tilde{h}_1^\circ) = -\beta_k(\tilde{h}_2^\circ)$ . Lines in the right panel are as follows. Solid black line:  $P_1 = 0$ ; Dashed black line:  $\beta_k(\tilde{h}_1^\circ) = -(\beta_k(\tilde{h}_2^\circ) + \beta_k(\tilde{N}))$ ; Dotted black line:  $\beta_k(\tilde{h}_1^\circ) = -\beta_k(\tilde{h}_2^\circ)$ ; Dashdotted line:  $\beta_k(\tilde{h}_1^\circ) + \beta(\tilde{M}) = -(\beta_k(\tilde{h}_2^\circ) + \beta_k(\tilde{N}))$ ; Dotted line:  $\beta_k(\tilde{h}_1^\circ) + \beta(\tilde{M}) = -\beta_k(\tilde{h}_2^\circ)$ . Parameters for the left panel:  $s_1^\circ = -s_2^\circ = 0.01$ ,  $h_1^\circ = h_2^\circ = 1/2$ ,  $M_{12} = M_{21} = 0.01$ . Parameters for the right panel:  $s_1^\circ = -s_2^\circ = 0.001$ ,  $h_1^\circ = h_2^\circ = 1/2$ ,  $M_{12} = M_{21} = 0.005$ .

Although qualitatively similar results holds for two other modes of selection (Figure 5), one notices that the region where the selfing exerts its effect solely via effective dominance is significantly expanded. This is because an increase in the selfing rate diminishes the male component's relevance and increases the importance of the female component. The relative sizes of these regions vary based on parameter values, so more general quantitative statements are hard to make.



Figure 5: Zones of selfing's effect on  $P_1$  under female fecundity (upper row ), and on male fecundity (lower row). Color code as in Figure 4. Migration via seed is depicted in the left column, and via pollen in the right column. Black lines as in the previous figure. Depending on selection and migration scenario, parameters are either:  $h_1^{\varphi} = h_2^{\varphi} = 1/2$  or  $h_1^{\varsigma^{*}} = h_1^{\sigma^{*}} = 1/2$ ,  $s_1^{\varphi} = -s_2^{\varphi} = 0.01$  or  $s_1^{\sigma^{*}} = -s_2^{\sigma^{*}} = 0.01$ , and  $M_{12} = M_{21} = 0.01$  or  $m_{12} = m_{21} = 0.01$ .

#### <sup>497</sup> 3.2.2 Emergence in the disfavored patch

Similar conclusions are reached if one considers emergence of mutant in the disfavored patch (Figure A16). However, under pollen dispersal, selfing reduces the effective migration rate, which can have either positive or negative effect on  $P_2$  depending on the parameters of the model. This phenomenon arises due to  $P_2$  being a non-monotonic function of m (see Figure 2). More specifically, if migration is much stronger than selection, then a mutant can escape to favored patch where it can spread, but the influx of maladapted allele is also high, thus having a net impeding effect on invading allele. This means that introduction of selfing will reduce the effective migration rate, and thus increase  $P_2$ . Put differently, increasing F has the same kind of effect on  $P_2$  as decreasing m. However, if the migration rate is already low enough, the introduction of selfing further depresses m and, thus, prevents invader from successfully escaping into the favored patch.

## <sup>509</sup> 3.3 Consequence of selfing on the establishment of protected poly <sup>510</sup> morphism

Once the allele A escapes extinction, it can either fix across both patches or segregate 511 at intermediate frequencies for a finite but large number of generations due to divergent 512 selection. Because both patches are of finite size, one of the two alleles will ultimately fix 513 but this quasi-stationary behavior corresponds to protected polymorphism in deterministic 514 models. We wish to delineate the effects of selfing on these two outcomes. Given that an 515 invading allele can appear in any of the two patches where the favored patch accounts for z516 fraction of the total population across both patches, the global probability of alleles A and 517 a becoming established is: 518

$$P^{(A)} = zP_1^{(A)} + (1-z)P_2^{(A)}$$
<sup>(29)</sup>

$$P^{(a)} = zP_1^{(a)} + (1-z)P_2^{(a)}$$
(30)

where  $P_i^{(A)}$  and  $P_i^{(a)}$  are probabilities that A and a become established, conditioning on 519 initially appearing in patch *i*. For the sake of simplicity, we will further assume that patches 520 are of equal size (z = 1/2), and migration is symmetrical. Probability that allele A is es-521 tablished is computed by parameterizing equations (26) and (27) where selection coefficients 522 were determined from Jacobian associated with boundary  $\vec{x} = [0, 0]^T$ , while the establish-523 ment probability of a was calculated with elements of Jacobian associated with boundary 524  $\vec{x} = [1, 1]^T$ . For example, if selective advantage of invading heterozygote Aa relative to ho-525 mozygote aa in patch i is  $s_ih_i$ , then the advantage of invading Aa relative to homozygote 526  $AA \text{ is } -s_i(1-h_i)/(1+s_i).$ 527

#### 528 3.3.1 Conditions for protected polymorphism and critical migration rates

<sup>529</sup> Polymorphism is protected if both  $P^{(A)} > 0$  and  $P^{(a)} > 0$ , that is for the conditions under <sup>530</sup> which the branching processes for the invasion of A and for the invasion of a are supercritical. <sup>531</sup> This boils down to the extension of Bulmer's inequality given by equation (25) directly obtained from the Jacobian matrix, which must also be satisfied with genotypes AA and aa shifted (corresponding to the supercriticality for the invasion of allele a). From this, we can define critical migration rates above which polymorphism is lost and the allele with the highest marginal fitness invades as in Yeaman and Otto (2011). Without loss of generality we can assume that  $s_1 > -s_2 > 0$ . For seed dispersal and viability selection  $M_c$  is then given by:

$$M_{c} = \begin{cases} 1, & \text{if } \frac{(1+(1-F)h_{1}s_{1})(1+(1-F)h_{2}s_{2})}{(1+s_{1})(1+s_{2})} > 1\\ -\frac{(1-(1-F)h_{1})(1-(1-F)h_{2})s_{1}s_{2}}{(1-(1-F)h_{1})s_{1}+(1-(1-F)h_{2})s_{2}+(1-F)(h_{1}+h_{2}-2(1-F)h_{1}h_{2})s_{1}s_{2}}, & \text{otherwise} \end{cases}$$
(31)

For F = 0, (31) reduces to equation (5) in Yeaman and Otto (2011) and for F = 1 to  $M_c = -\frac{s_1s_2}{s_1+s_2}$ . The first condition corresponds to a form of dominance reversal where the allele is dominant when advantageous and recessive when deleterious. Under such a condition, polymorphism can be maintained even under full migration.

542

Depending on dominance, selfing thus has two opposite effects. On the one hand, by unmask-543 ing recessive alleles, selfing makes selection stronger relative to migration and so enlarges 544 the conditions for the maintenance of protected polymorphism. On the other hand, selfing 545 makes dominance reversal conditions less likely as selection mainly operates on homozygotes, 546 and so restricts the conditions for protected polymorphism. Figure 6 shows the dominance 547 conditions under which selfing increases or decreases the critical migration rate. We de-548 termined these conditions in two ways: either when  $M_c$  is higher under full selfing than 549 under full outcrossing (i.e.,  $M_c|_{F=0} < M_c|_{F=1}$ ) or whether introduction of selfing in an oth-550 erwise outcrossing population increases  $M_c$ , that is  $\frac{\partial M_c}{\partial F}\Big|_{F=0} > 0$ . For symmetrical selection 551  $(s_2 = -s_1)$ , selfing increases migration rate if  $h_2 > h_1$ . Under the opposite condition, the 552 critical migration is 1 and local adaptation is always maintained under outcrossing. As se-553 lection becomes more asymmetrical, selfing favors local adaptation for a broader range of 554 dominance coefficients. Note that the effect of selfing on the migration rate is not monotonic 555 for a narrow range of conditions (light blue region in Figure 6), where little selfing disfavors 556 local adaption  $\left(\frac{\partial M_c}{\partial F}\Big|_{F=0} < 0\right)$  but high selfing increases it  $(M_c|_{F=0} < M_c|_{F=1})$ . Finally, it is 557 worth noting that when selfing favors local adaptation, the effect is rather weak (blue curves 558 on Figure 6). On the contrary, under dominance reversal conditions, above a given threshold, 559 selfing dramatically reduces the migration rate from 1 to  $-\frac{s_1s_2}{s_1+s_2}$  under full selfing. Similar 560 results are obtained for fecundity selection but with selfing favoring local adaption under 561 broader conditions for female fecundity and for narrower conditions for male fecundity (see 562 Appendix). 563



Figure 6: Effect of selfing on the critical migration rate. The three first panels show dominance conditions under which selfing increases (blue regions) or decreases (red regions) the critical migration rate,  $M_c$ . Selection is symmetrical in the first panel ( $s_1 = -s_2 = 0.01$ ), and asymmetrical in the second ( $s_1 = 0.02$  and  $s_2 = -0.01$ ) and third panels ( $s_1 = 0.05$  and  $s_2 = -0.01$ ). In the light blue region,  $M_c$  is not monotonic with F: introduction of selfing in an outcrossing population decreases  $M_c$  ( $\frac{\partial M_c}{\partial F}|_{F=0} < 0$ ) but above a given selfing rate,  $M_c$  becomes higher than in an outcrossing population and we always have  $M_c|_{F=0} < M_c|_{F=1}$ . In the dark blue region, selfing always increases  $M_c$  ( $M_c|_{F=0} < M_c|_{F=1}$ ). In the dark red region,  $M_c = 1$  in outcrossing populations and  $M_c < 1$  in the light red region. The last panel illustrates how  $M_c$  varies with F in the four regions, corresponding to the black dots of the second panel. For all curves  $s_1 = 0.02$  and  $s_2 = -0.01$ . Dark blue:  $h_1 = 0.4$  and  $h_2 = 0.4$ ; light blue:  $h_1 = 0.55$  and  $h_2 = 0.4$ ; light red:  $h_1 = 0.65$  and  $h_2 = 0.4$ ; light red:  $h_1 = 0.65$  and  $h_2 = 0.4$ ; light blue:  $h_1 = 0.4$ . Note that  $M_c$  is in log-scale.

- The picture is different under pollen dispersal. Under full selfing, effective migration is zero 564 so selection can act independently in each patch and polymorphism is always maintained. As 565 a consequence, there is always a threshold selfing rate above which the critical migration rate 566
- is higher than in an outcrossing population. Here, we thus concentrate on the effect of the 567
- introduction of selfing in an outcrossing population, so the conditions for which  $\frac{\partial M_c}{\partial F}\Big|_{F=0} > 0.$
- 568
- Under symmetrical selection, the conditions are the same as for seed migration. However, 569 for asymmetrical selection, selfing increases  $M_c$  for a much broader range of parameters.



Figure 7: Same legend and same parameters as in Figure 6 but with pollen dispersal instead of seed dispersal.

570

#### 3.3.2Establishment and maintenance of protected polymorphism 571

The above analysis showed how selfing affects the critical migration rate, hence the conditions 572 for local adaptation. However, when local adaptation is possible, selfing also affects the 573 probability of establishment and maintenance of polymorphism. This can be analyzed by 574

quantifying how selfing affects  $P^{(A)}$  and  $P^{(a)}$ , which is given by:

$$b_k = \left(\frac{dP^{(k)}}{dF}\right)\Big|_{F=0} > 0 \quad \text{where } k = \{A, a\}$$
(32)

Four outcomes are possible upon the introduction of selfing. First,  $P^{(A)}$  increases, and  $P^{(a)}$ 576 decreases, meaning that allele A is more likely to fix across both patches in selfers than 577 in outcrossers. Second and conversely,  $P^{(A)}$  decreases, but  $P^{(a)}$  increases, implying that 578 selfers are less likely to fix A compared to an outcrossing population. Third, both  $P^{(A)}$ 579 and  $P^{(a)}$  increase upon shift to selfing, meaning that selfing increases the probability that 580 protected polymorphism is established. Fourth and final, both  $P_A$  and  $P_a$  decrease, making 581 the protected polymorphism less likely to become established in the selfing population. Some 582 examples are given for different migration rates with symmetrical or asymmetrical selection 583 (Figure 8). 584



(a) Symmetrical selection

(b) Asymmetrical selection

Figure 8: Effect of selfing on the establishment of protected polymorphism under symmetrical (a) and asymmetrical selection (b). Five regions can be distinguished: blue:  $b_A > 0$  and  $b_a > 0$ , red:  $b_A < 0$  and  $b_a < 0$ , dark purple  $b_A > 0$  and  $b_a < 0$ , light purple  $b_A < 0$  and  $b_a > 0$ , and white: polymorphism cannot be maintained under outcrossing. The dotted lines correspond to the limiting conditions for which selfing increases the critical migration rate (above the line) as in Figure 6. (a)  $s_1 = 0.01$  and  $s_2 = -0.01$ ; m = 0.0001, 0.001, 0.01, 0.01 from top left to bottom right. (b)  $s_1 = 0.05$  and  $s_2 = -0.01$ ; m = as in (a).

One can intuitively understand these outcomes by noting that dominance reverses when the alternative allele invades. So, if invader A is dominant, then invader a will be recessive.

The dominant allele A is likely to escape extinction when invading but unlikely to result 587 in protected polymorphism because allele a is recessive and thus likely to go extinct. This 588 appears clearly in the limit of low migration, where probabilities of emergence tend toward 589 single population predictions, with four quadrants corresponding to the four dominance 590 conditions (Figure 8). Importantly, these four regions vary with the amount of migration, 591 and they do not directly align with the conditions given by the critical migration rates. The 592 reason is that the sign of  $P^{(A)}$  and  $P^{(a)}$  only depends on the effect of selfing through the 593 effective dominance, whereas the absolute value also depends on the reduction in effective 594 size. Here, we only consider the two-fold reduction in  $N_e$  caused by selfing, but the linked 595 selection can further reduce the effective size of the local population under selfing (Roze, 596 2016). This will not affect the critical migration rate but can strongly reduce probabilities of 597 emergence hence the establishment of local adaptation. Following this rationale, Yeaman and 598 Otto (2011) considered a critical migration rate above which the probability of emergence of 590 both alleles is higher than  $1/(4N_e)$ . High local drift under selfing can thus strongly reduce 600 the conditions for the establishment of local adaptation. 601

#### 602 4 Discussion

We investigated the effect of selfing on the establishment of an allele in a population sub-603 divided into two patches, where only one locus determines the fitness of an organism. By 604 representing the spread of an invading allele as a branching process, we obtained a closed-605 form analytical solution for the probability of establishment of the locally advantageous 606 allele for an arbitrary population selfing rate. This extends the work of Tomasini and Peis-607 chl, 2018 to include diploidy, dominance, and partial selfing. We also corrected for a typo in 608 the derivation of their equations but which surprisingly lead to less elegant results. Below, 609 we discuss the implication for adaptation in partially selfing species. 610

611

A well-known result is that selfing favors the establishment (and fixation) of recessive alleles 612 but disfavors the establishment of dominant ones, with no effect under exact codominance 613 (h = 1/2) (Caballero and Hill, 1992, Charlesworth, 1992). The pattern is more complex in 614 a subdivided population with heterogeneous selection. First, the codominant allele has a 615 higher probability of becoming established in the selfing population than in the outcrossing 616 population if it emerges in the favored patch and generally smaller probability if it emerges 617 in the disfavored patch. Therefore, the probability of establishment of a codominant allele is 618 not independent of the mating system, as was the case for a single partly selfing population 619 (Charlesworth (1992)). Second, assuming that migration and selection are symmetrical, self-620

ing will increase the establishment probability when the invading mutant is recessive in the favored patch (resulting in a maximal increase in  $\tilde{h}_1$ ) and dominant in the disfavored patch (yielding a minimal increase in  $\tilde{h}_2$ ). If the two dominances are roughly equal, the opposed effects of selfing on effective dominances cancel each other out, and the net effect is set by the interplay between the positive effect of reduced effective migration and the negative effect of the reduction in  $N_e$ .

627

Once the invading allele escapes extinction, it can either fix in both populations, thus one 628 population is fixed for a maladaptive allele, or segregate at intermediate frequencies, thus 629 contributing to protected polymorphism, and both populations can be considered as locally 630 adapted. It is usually thought that selfers are better locally adapted because of the reduced 631 gene flow between patches with different selection demands (Linhart and Grant (1996)). 632 However, selfing affects in a complex way three key parameters determining local adaptation 633 - selection, drift, and gene flow. By separately considering seed and pollen migration, we 634 were able to distinguish the straightforward effect of reducing gene flow from the more subtle 635 effects of altering genotypic frequencies and drift induced by selfing. 636

637

Under seed dispersal only, selfing does not affect gene flow but still alters the propensity 638 for local adaptation. The conditions under which selfing favors local adaptation strongly 639 depend on the dominance of alleles in the two patches. Under outcrossing, the most fa-640 vorable condition for local adaptation is under dominance reversal, that is, when the allele 641 is dominant when locally beneficial and recessive when locally deleterious. If so, protected 642 polymorphism can be maintained even under full migration  $(M_c = 1)$ , which corresponds to 643 conditions for polymorphism in Levene (1953)'s model. Under this condition, selfing desta-644 bilizes polymorphism, which cannot be maintained under full dispersal: above a given selfing 645 rate, the critical migration rate strongly decreases (Figure 6, and see also Glémin, 2021, for 646 the Levene's model with selfing). Conversely, under most other conditions, especially when 647 selection is asymmetrical, selfing tends to increase the critical migration rate, hence favors 648 local adaptation. What dominance patterns across heterogeneous habitat are the most fre-649 quent in natural populations is unknown. However, dominance reversal is maybe not as 650 unlikely as it may seem because it can naturally arise in simple fitness landscape models 651 (Connallon and Chenoweth, 2019). If we now consider pollen dispersal, selfing enhances 652 local adaptation by reducing gene flow. Under dominance reversal conditions, this leads to 653 non-monotonic behaviors where local adaptation can be the most easily maintained, either 654 under outcrossing or under high selfing (Figure 7). Characterizing the pollination and seed 655 dispersal modes and their quantitative impacts on gene flow appears thus crucial to make 656

proper predictions on the effect of selfing. Finally, if we also consider the effect of linked selection that reduces local effective size beyond the two-fold level in selfing populations (Roze, 2016), selfing reduces the possibility of local adaptation, which requires stronger selection as exemplified by Hodgins and Yeaman (2019) who simulated local adaptation in selfing populations with and without background selection. Overall, the complex and contradictory effects of selfing on local adaptation may explain why no general empirical pattern has emerged so far (Hereford, 2010, Leimu and Fischer, 2008).

664

Despite the large uncertainties about the global effect of selfing on local adaptation, the 665 analysis of the model yields some predictions about the genetic architecture of local adap-666 tation in selfing versus outcrossing species. In outcrossing species, the global adaptation 667 from de novo mutations is predicted to be biased towards dominant mutations, the so-called 668 Hadane's sieve (Haldane, 1927, Ronfort and Glémin, 2013), and local adaptation to benefi-669 cial dominant/deleterious recessive mutations (Yeaman and Otto, 2011). On the contrary, 670 no sieve related to dominance is expected under high selfing. As for other forms of selection, 671 we also predict that local adaptation should be more prominent on female traits because 672 selfing reinforces selection on female fecundity components at the cost of male fecundity 673 components. A similar conclusion was reached by Olito et al. (2018) from a model including 674 male/female antagonism and heterogeneous habitat with full dispersal. Finally, beyond the 675 current work, simulations showed that local adaptation genes tend to aggregate into clusters 676 in outcrossers (Yeaman and Whitlock, 2011) whereas the genetic architecture tends to be 677 more diffuse in selfers (Hodgins and Yeaman, 2019, Le Thierry d'Ennequin et al., 1999). 678 Thus, a natural extension of the model would be to consider local adaptation at two loci to 679 dissect the additional effect of selfing on genetic linkage. However, using the same formalism 680 would require following a multi-type branching process in a higher dimension (at least six), 681 which remains highly challenging. 682

### 683 5 Data availability

Supplemental files are available at https://github.com/BogiTrick/local\_adaptation\_ single\_locus and at figshare (https://doi.org/10.25386/genetics.16664650). These entries contain: *Mathematica* notebook required for reproduction of all reported theoretical results and figures; C+ + source code of the custom simulator used for generation of simulated data for comparison with analytics; Shell scripts for the bulk run of the simulator; and R scripts used to process the raw simulated data for plotting in the above-mentioned notebook.

### 6 6 Acknowledgements

We are thankful to Guillaume Martin and two anonymous reviewers for helpful comments, especially for suggesting to formally derive the offspring distribution and to alternatively solve our main problem by diffusion approximation. We also thank Matthew Hartfield for the critical reading of the manuscript.

## <sup>696</sup> 7 Funding

B. T. was supported by Erasmus Mundus Joint Masters Degree Scholarship awarded by
 Erasmus+ programme. S.G. was supported by the Agence National de la Recherche (ANR
 SEAD-ANR-13-ADAP-0011).

#### 700 8 Competing interests

<sup>701</sup> Authors declate no competing interests.

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Symbol	Meaning
$x_i(t)$	Frequency of allele A in patch $i$ at the start of the life cycle (generation $t$ )
$x_i^{Q}$	Frequency of allele A in patch $i$ after female fecundity selection
$x_i^{o^*}$	Frequency of allele A in patch $i$ after male fecundity selection
$g_i^{O^{\uparrow}}$	Frequency of allele A in patch $i$ after pollen migration
$X_i$	Frequency of genotype $AA$ at the start of the life cycle
$Y_i$	Frequency of genotype $Aa$ at the start of the life cycle
$X'_i$	Frequency of genotype $AA$ after mating
$Y_i'$	Frequency of genotype $Aa$ after mating
$X_{i}^{\prime\prime}$	Frequency of genotype $AA$ after seed migration
$Y''_i$	Frequency of genotype $Aa$ after seed migration
$N_i^*$	Population size in patch $i$
$N_i$	The number of invading alleles in patch $i$
$\tilde{N}$	The effective population size
$M_{ij}$	The fraction of seed (or the probability of seed) in patch $i$ originating from patch $j$
$m_{ij}$	The fraction of pollen (or the probability of pollen) in patch $i$ originating from patch $j$
$\Delta \mathcal{W}_{0,i}$	The intergenerational $A$ frequency change in patch $i$ , when $A$ rare (generic selection)
$\Delta V_{0,i}$	The intergenerational $A$ frequency change in patch $i$ , when $A$ rare (only viability selection)
$\Delta W^{Q}_{0,i}$	The intergenerational $A$ frequency change in patch $i$ , when $A$ rare (only female fecundity selection)
$\Delta W^{\rm O}_{0,i}$	The intergenerational $A$ frequency change in patch $i$ , when $A$ rare (only male fecundity selection)
$V_{i,k}$	The progeny number left by genotype $k$ ( $k \in \{AA, Aa, aa\}$ ) that survives to maturity in patch $i$
$W_{i,k}^{Q}$	Number of female gametophytes produced by genotype $k \ (k \in \{AA, Aa, aa\})$ in patch $i$
$W_{i,k}^{O^{\uparrow}}$	Number of male game tophytes produced by genotype $k~(k \in \{AA, Aa, aa\})$ in patch i
$\overline{V}_i$	Mean population viability fitness in patch $i$
$\overline{W}_i^{Q}$	Mean population fecundity fitness in patch $i$
$\overline{W}_i^{O^*}$	Mean population male sexual fitness in patch $i$
F	Equilibrium population inbreeding coefficient. Set to $S/(2-S)$
S	Fraction of the population that reproduces by selfing (i.e., the population selfing rate)
$s_i^{\{k\}}$	The relative selective advantage of invading A, with selection via $k^{th}$ $(k \in \{V, F, M\})$ fitness component
$h_i^{\{k\}}$	The dominance coefficient of allele $A$ , when selection acts only via $k^{th}$ fitness component
$\tilde{M}_{ij}$	The effective fraction of seed (or the probability of seed) in patch $i$ that originates from patch $j$
$\tilde{h}_i^{\{k\}}$	The effective dominance coefficient of allele $\vec{A}$ , when selection acts only via $k^{th}$ fitness component
ω	Correction for the effective dominance coefficient for male selection and pollen dispersal
$\tilde{s}_i^{\{k\}}$	The effective selective advantage of invading allele $A$ with selection via $k^{th}$ fitness component

**Table 1:** List of symbols used in the text. As a general rule, parameters with tilde signify an effective parameter. Upper-case symbols are reserved for processes affecting the diploid phase of a life cycle, whereas the lower-case represents the process of the haploid phase.

## 775 Appendices

# A Deriving the PGF of the distribution of allele off spring number

#### 778 A.1 Single population

We first derive the full probability generating function (PGF) of the number of mutant alleles 779 under partial selfing in a single population. When the A mutant is rare, it can be found either 780 in a Aa individual with probability 1 - F and in a AA individual with probability F. The 781 PGF can thus be written as  $(1-F)f_{Aa}(z) + Ff_{AA}(z)$  where  $f_{Aa}$  and  $f_{AA}$  are the PGF for the 782 parent allele being in each genotype, respectively. We can then decompose the total number 783 of alleles,  $G_i$ , contributed by one individual of genotype i as the sum of alleles transmitted 784 through outcrossed ovule,  $N_{i,o}$ , through exported pollen,  $N_{i,p}$ , and through selfed ovule,  $N_{i,s}$ . 785 Because the mutant is rare, it can only be transmitted in heterozygote after outcrossing, so 786 in a single copy. After selfing, two copies are always transmitted if the parent is AA and 787 either two or one copies are transmitted if the parent is Aa. In this last case we note  $N_{i,s}^{AA}$ 788 and  $N_{i,s}^{Aa}$  are the number of homozygote and heterozygote seeds produced under selfing. The 789 total number of offspring alleles transmitted at the next generation is thus: 790

$$G_{AA} = N_{AA,o} + N_{AA,p} + 2N_{AA,s} \tag{A1a}$$

$$G_{Aa} = N_{Aa,o} + N_{Aa,p} + 2N_{Aa,s}^{AA} + N_{Aa,s}^{Aa}$$
(A1b)

We assume that the number of exported pollen and the different numbers of seeds follow independent Poisson distributions. The different means depends on the fecundity of the parent, the viability of the seed produced and the proportion of each category:

$$\mathbb{E}[N_{Aa,o}] = \frac{1}{2}(1-S)W_{Aa}^{\mathbb{Q}}V_{Aa}$$

$$\mathbb{E}[N_{Aa,p}] = \frac{1}{2}(1-S)W_{Aa}^{\mathbb{Q}}V_{Aa}$$

$$\mathbb{E}[N_{Aa,s}] = \frac{1}{2}\frac{S}{2}W_{Aa}^{\mathbb{Q}}V_{AA}$$

$$\mathbb{E}[N_{Aa,s}] = \frac{1}{2}\frac{S}{2}W_{Aa}^{\mathbb{Q}}V_{AA}$$

$$\mathbb{E}[N_{Aa,s}] = \frac{1}{2}\frac{S}{2}W_{Aa}^{\mathbb{Q}}V_{Aa}$$

$$\mathbb{E}[N_{AA,s}] = \frac{1}{2}SW_{Aa}^{\mathbb{Q}}V_{AA}$$

$$\mathbb{E}[N_{AA,s}] = \frac{1}{2}SW_{Aa}^{\mathbb{Q}}V_{AA}$$

$$\mathbb{E}[N_{AA,s}] = \frac{1}{2}SW_{Aa}^{\mathbb{Q}}V_{AA}$$

$$\mathbb{E}[N_{AA,s}] = \frac{1}{2}SW_{Aa}^{\mathbb{Q}}V_{AA}$$

The factor 1/2 corresponds to the fact that the focal A is chosen with probability 1/2. Put another way, on average each individual transmits two alleles so the contribution for a single allele must be halved. Finally, we use the property that the PGF of 2X is  $f(z^2)$  where f(z)is the PGF of X and that the PGF of the sum of independent variables is the product of the PGFs. Noting  $g(\lambda, z) = e^{-(1-z)\lambda}$ , the PGF of a Poisson distribution with mean  $\lambda$ , we have:

$$f_{\phi}(z) = (1 - F)g(\mathbb{E}[N_{Aa,o}], z)g(\mathbb{E}[N_{Aa,p}], z)g(\mathbb{E}[N_{Aa,s}], z)g(\mathbb{E}[N_{Aa,s}], z^2) + Fg(\mathbb{E}[N_{AA,o}], z)g(\mathbb{E}[N_{AA,p}], z)g(\mathbb{E}[N_{AA,s}], z^2)$$
(A3)

which yields equation (15) of the main text.

From the properties of PGFs we can easily obtain the moments of the distribution for the different forms of selection (see *Mathematica* notebook):

$$\mathbb{E}_{\phi} = f'_{\phi}(1)$$

$$= 1 + \tilde{h}s \tag{A4a}$$

$$\mathbb{V}_{\phi} = f_{\phi}''(1) + f_{\phi}'(1) - f_{\phi}'(1)^{2} 
= (1+F)(1+\tilde{h}s) + o(s)$$
(A4b)

So we retrieved the well known result that selfing increases variance in allele offspring number by 1 + F. Interestingly, the full distribution presents a peculiar non-monotonic behavior for high selfing, with an excess (resp. a deficit) in even (resp. odd) numbers. Note also that the full distributions are not exactly the same under the different modes of selection.

#### <sup>806</sup> A.2 Two-patch model

We need to derive the distribution of the number of mutant alleles issued from one patch 807 and staying in the same patch, with PGF  $f_{i,i}(z)$ , and the distribution of those establish-808 ing in the other patch, with PGF  $f_{i,j}(z)$ . Assuming that the distribution of resident and 809 migrant alleles are independent, the total number of alleles produced by patch i has PGF: 810  $f_i(z) = f_{i,i}(z) f_{i,j}(z)$ . The  $f_{i,j}(z)$  can be obtained using the same equations as for a single 811 population by paying attention to the order of events to correctly set indices: male fecundity 812 selection, pollen migration, female fecundity selection, reproduction, seed migration and vi-813 ability selection. Under seed migration, fecundity selection occurs in patch i but viability 814

selection in patch j. The means given in equation (A2) become:

$$\mathbb{E}[N_{Aa,o,ij}] = \frac{1}{2}(1-S)W_{Aa,i}^{Q}M_{i,j}V_{Aa,j} \\
\mathbb{E}[N_{Aa,p,ij}] = \frac{1}{2}(1-S)W_{Aa,i}^{Q}M_{i,j}V_{Aa,j} \\
\mathbb{E}[N_{Aa,s,ij}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{AA,j} \\
\mathbb{E}[N_{Aa,s,ij}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{AA,j} \\
\mathbb{E}[N_{Aa,s,ij}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{Aa,j} \\
\mathbb{E}[N_{Aa,s,ij}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}M_{i,j}V_{Aa,j} \\
\mathbb{E}[N_{Aa,s,ij}] = \frac{1}{2}SW_{Aa,i}^{Q}M_{i,j}V_{Aa,j} \\
\mathbb{E}[N_{AA,s,ij}] = \frac{1}{2}SW_{AA,i}^{Q$$

with  $M_{i,j} = 1 - M_{i,i}$ . Plugging (A5) into (A3) yields equation (16) in the main text. From the corresponding PGFs we then retrieve the same mean as obtained by the deterministic analysis (see below), and variances inflated by 1 + F (see *Mathematica* notebook):

 $\mathbb{E}_{\phi,ij} = M_{i,j}(1 + \tilde{h}_i s_i) \quad \text{for fecundity selection}$ (A6a)

$$= M_{i,j}(1 + \tilde{h}_j s_j)$$
 for viability selection (A6b)

$$\mathbb{V}_{\phi,ij} = (1+F)\mathbb{E}_{\phi,ij} + o(s_i, s_j) \tag{A6c}$$

Note that in subsequent analyses the order of migration and selection terms yields the same results. Under pollen migration, the PGF for resident and migrant contribution have different forms because an allele can contribute offspring to the other patch only through outcrossing and through the male pathway. For offspring contributing to the resident patch we have:

$$\mathbb{E}[N_{Aa,o,ii}] = \frac{1}{2}(1-S)W_{Aa,i}^{Q}V_{Aa,i} \\
\mathbb{E}[N_{Aa,p,ii}] = \frac{1}{2}(1-S)W_{Aa,i}^{Q^{*}}(1-m_{i,j})V_{Aa,i} \\
\mathbb{E}[N_{Aa,s,ii}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}V_{AA,i} \\
\mathbb{E}[N_{Aa,s,ii}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}V_{AA,i} \\
\mathbb{E}[N_{Aa,s,ii}] = \frac{1}{2}\frac{S}{2}W_{Aa,i}^{Q}V_{Aa,i}$$

$$\mathbb{E}[N_{Aa,s,ii}] = \frac{1}{2}SW_{Aa,i}^{Q}V_{AA,i} \\
\mathbb{E}[N_{AA,s,ii}] \\
\mathbb{E}[N_{AA,s,ii}] = \frac{1}{2}SW_{AA,ii}^{Q}V$$

<sup>823</sup> whereas for offspring contributing to the other patch:

$$\mathbb{E}[N_{Aa,o,ii}] = 0 \qquad \mathbb{E}[N_{Aa,o,ii}] = \frac{1}{2}(1-S)W_{Aa,i}^{\mathcal{O}}m_{i,j}V_{Aa,j} \qquad \mathbb{E}[N_{AA,o,ii}] = 0 \qquad \mathbb{E}[N_{AA,o,ii}] = 0$$

Plugging (A7) and (A8) into (A3) yields equations (17a) and (17b) in the main text. The mean and variance for resident offspring are:

$$\mathbb{E}_{\phi,ii} = (1 - \tilde{M}_{i,j})(1 + \tilde{h}_i s_i) \quad \text{for viability and female fecundity selection}$$
(A9a)  
=  $(1 - \tilde{M}_{i,j})(1 + \omega \tilde{h}_i s_i) \quad \text{for male fecundity selection}$ (A9b)

$$= (1 - M_{i,j})(1 + \omega h_i s_i) \quad \text{for male recurdity selection}$$
(A9b)

$$\mathbb{V}_{\phi,ii} = \mathbb{E}_{\phi,ij} \left( 1 + \frac{F}{1 - \tilde{M}_{ij}} \right) + o(s_i, s_j) \tag{A9c}$$

<sup>826</sup> and for migrant offspring:

$$\mathbb{E}_{\phi,ij} = \tilde{M}_{i,j}(1 + \tilde{h}_j s_j) \quad \text{for viability fecundity selection}$$
(A10a)

$$= 0 \quad \text{for female fecundity selection} \tag{A10b}$$

$$= \tilde{M}_{i,j}(1 + \omega \tilde{h}_i s_i) \quad \text{for male fecundity selection}$$
(A10c)

$$\mathbb{V}_{\phi,ij} = \mathbb{E}_{\phi,ij} + o(s_i, s_j) \tag{A10d}$$

where  $\tilde{M}_{i,j} \approx m_{i,j}(1-S)/2$  are effective migration rates as defined in the main text (equations 827 12a to 12c) and  $\omega$  is a correcting factor defined in equation (13). Compared to seed migration, 828 the variance is not uniformly increased by 1 + F. As migrant offspring can only be produced 829 through outcrossing, the distribution is simply Poisson and the variance equal to the mean. 830 On the contrary, because the proportion of outcrossed offspring contributing to the resident 831 patch is reduced due to pollen migration, the variance is inflated by more than 1 + F. 832 However, the difference between the two modes of migration does not affect the following 833 approximations for weak selection. 834

## <sup>835</sup> B The establishment probability approximated to weak <sup>836</sup> selection

Following the procedure outlined in Haccou *et al.* (2005) (Section 5.6.2) and previously adapted for a similar problem by Tomasini and Peischl (2018), we seek to approximate P by working with slightly supercritical process. Let  $\rho$  be the leading eigenvalue and  $\mathbf{u} = [u_1, u_2]^T$ and  $\mathbf{v} = [v_1, v_2]^T$  normed left and right eigenvectors of the mean reproductive matrix  $\mathbf{M}$ . <sup>841</sup> Eigenvectors are normalized such that:

$$u_i > 0, \quad v_i > 0, \quad i \in \{1, 2\}$$
  
 $\sum_i u_i v_i = \sum_i u_i = 1$ 

We choose a parameter  $\epsilon$  in the model, such that the process is slightly supercritical when  $\epsilon$ is small. All other parameters in the model are rescaled by  $\epsilon$ . More formally:

$$\rho(\epsilon) \to 1 \quad \text{as} \quad \epsilon \to 0$$

Eigenvalues and eigenvectors of **M** are dependent on  $\epsilon$ . Probability of establishment starting from a single copy of allele in patch *i* is given by:

$$P_i = 2(\rho(\epsilon) - 1)\frac{v_i(\epsilon)}{B(\epsilon)} + o(\epsilon)$$
(A11)

$$B(\epsilon) = \sum_{i} u_i(\epsilon) \operatorname{Var}\left(\phi_{ij} \sum_{j} v_j(\epsilon)\right) + (\rho(\epsilon)(\rho(\epsilon) - 1)) \sum_{j} u_j(\epsilon) v_j(\epsilon)^2$$
(A12)

As  $\epsilon \to 0$ ,  $\rho$  approaches unity and the second term in B (equation (A12)) can be neglected. As per equation 5.85 in Haccou *et al.* (2005), we take that  $B(\epsilon) \to B(0)$  and  $v_i(\epsilon) \to v_i(0)$ :

$$P_k \approx 2(\rho(\epsilon) - 1)\frac{v_i(0)}{B(0)} \tag{A13}$$

$$B(0) \approx \sum_{k} u_i(0) \operatorname{Var}\left(\phi_{ij} \sum_{j} v_j(0)\right)$$
(A14)

Recall that  $\tilde{s}_i$  is the advantage of an allele in patch *i* accounting for the effect of selffertilization. Assuming weak selective advantage,  $\tilde{s}_1$  is taken as  $\epsilon$ . All other parameters are expressed in terms of  $\tilde{s}_1$ :

$$\tilde{M}_{ij} = \tilde{s}_1 \chi_{ij}, \quad \tilde{s}_2 = \zeta \tilde{s}_1$$

The leading eigenvalue of **M** can be written as  $\rho = 1 + \tilde{c}\tilde{s}_1 + o(\tilde{s}_1^2)$ . Dropping the higher-order terms in  $\tilde{s}_1$ , we retrieve the expression for  $\tilde{c}$ :

$$\tilde{c} = \frac{1}{2} \left( \sqrt{\left(\zeta + \chi_{12} - 1\right)^2 + 2\chi_{21} \left(-\zeta + \chi_{12} + 1\right) + \chi_{21}^2} + \zeta - \chi_{12} - \chi_{21} + 1 \right)$$

By taking only the zeroth term of  $v_i$  and B in Taylor expansion about  $\tilde{s}_1 = 0$ , we obtain the

approximation of the probability of establishment conditioning on a single mutant appearing in patch i:

$$P_k \approx 2\tilde{c} \frac{v_k(0)}{B(0)} \tilde{s}_1 \tag{A15}$$

Transforming back to original variables  $\tilde{M}_{ij}$  and  $\tilde{s}_i$  and letting

$$= \sqrt{2\tilde{M}_{12}\left(\tilde{M}_{21} - \tilde{s}_1 + \tilde{s}_2\right) + \left(\tilde{M}_{21} + \tilde{s}_1 - \tilde{s}_2\right)^2 + \tilde{M}_{12}^2}$$

<sup>857</sup> we have:

$$P_{1} = \frac{\left(-\tilde{M}_{12}\left(-2\tilde{M}_{21}+2\tilde{s}_{1}-2\tilde{s}_{2}+\psi\right)+\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}\right)\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}+\psi\right)+\tilde{M}_{12}^{2}\right)\left(-\tilde{M}_{12}+\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}+\psi\right)\left(-\tilde{M}_{12}-\tilde{M}_{21}+\tilde{s}_{1}+\tilde{s}_{2}+\psi\right)}{(A16)}$$

$$P_{2} = \frac{\tilde{M}_{12}\left(-\tilde{M}_{12}\left(-2\tilde{M}_{21}+3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)-\tilde{M}_{12}\left(\tilde{M}_{21}\left(3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)+\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}\right)\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}+\psi\right)+\tilde{M}_{12}^{2}\right)\left(-\tilde{M}_{12}-\tilde{M}_{21}+\tilde{s}_{1}+\tilde{s}_{2}+\psi\right)}{(F+1)\left(\tilde{M}_{12}^{2}\left(2\tilde{M}_{21}+3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)-\tilde{M}_{12}\left(\tilde{M}_{21}\left(3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)+\left(\tilde{s}_{1}-\tilde{s}_{2}\right)\left(3\tilde{s}_{1}-3\tilde{s}_{2}+2\psi\right)\right)+\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}\right)^{2}\left(\tilde{M}_{21}+\tilde{s}_{1}+\tilde{s}_{2}+\psi\right)}{(F+1)\left(\tilde{M}_{12}^{2}\left(2\tilde{M}_{21}+3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)-\tilde{M}_{12}\left(\tilde{M}_{21}\left(3\tilde{s}_{1}-3\tilde{s}_{2}+\psi\right)+\left(\tilde{s}_{1}-\tilde{s}_{2}\right)\left(3\tilde{s}_{1}-3\tilde{s}_{2}+2\psi\right)\right)+\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}\right)^{2}\left(\tilde{M}_{21}+\tilde{s}_{1}-\tilde{s}_{2}+\psi\right)-\tilde{M}_{12}^{3}\right)}{(A17)}$$

858

When migration is symmetrical  $(\tilde{M}_{12} = \tilde{M}_{21} = \tilde{M}), \psi$  reduces to  $\sqrt{4\tilde{M}^2 + (\tilde{s}_1 - \tilde{s}_2)}$ , pre-859 viously defined as the scaled measure of the heterogeneity in selection and migration. Set-860 ting F = 0, the equations (A16) and (A17) behave similarly to those derived previously 861 (Tomasini and Peischl (2018)). Comparing the analytical solution against simulations, one 862 can see that the solution reported here fits simulations slightly better than the Tomasini-863 Peischl result (Figure A9). The discrepancy is probably caused by the latter's use of B term 864 from Aeschbacher and Bürger (2014) (see their equation S22), which neglects to square ele-865 ments of the eigenvectors after factoring them out of the variance. We, on the other hand, 866 computed B directly from Haccou et al. (2005), which does not suffer from this error. Cu-867 riously, the Tomasini-Peischl approximation is much more elegant as the denominator can 868 be interpreted as the measure of the heterogeneity of migration and selection. Relative to 869 the result reported in Sakamoto and Innan (2019), our solution had identical performance in 870 the favored patch, and worse performance in the disfavored patch (pink dashed lines). This 871 discrepancy occurs only when the migration rate is low. 872



Figure A9: Comparison of analytical solution to simulated data and previous results. Comparison to approximation Tomasini and Peischl (2018) (left), and comparison to the single-patch heuristic under fecundity selection Damgaard (2000) (right). All equations parameterized with  $h_1^{\circ} = h_2^{\circ} = h_1^{\circ} = -h_2^{\circ} = 1/2$ ,  $s_1^{\circ} = -s_2^{\circ} = s_1^{\circ} = -s_2^{\circ} = 0.01$ ,  $M_{12} = M_{21} = M$ .

## <sup>873</sup> C The criterion for escaping extinction

#### <sup>874</sup> C.1 Seed dispersal

If the selective disadvantage in the disfavored patch is too large or migration is too strong, the spreading locally advantageous allele can be swamped by its deleterious counterpart. The range of parameters that are necessary but not sufficient for a successful invasion are obtained by linearizing the system about  $\vec{x} = [0, 0]^T$  and investigating the conditions required for this equilibrium to be locally unstable. If migration occurs prior to selection – which is the case when seed disperses and selection acts on viability, then Jacobian **J** is:

$$\mathbf{J} = \begin{bmatrix} (1 - M_{12})\Delta \mathcal{W}_{0,1} & M_{12}\Delta \mathcal{W}_{0,1} \\ M_{21}\Delta \mathcal{W}_{0,2} & (1 - M_{21})\Delta \mathcal{W}_{0,2} \end{bmatrix}$$
(A18)

$$\Delta W_{0,i} = (F\mathcal{W}_{i,AA} + (1-F)\mathcal{W}_{i,Aa})/\mathcal{W}_{i,aa}$$
(A19)

Symbol  $\mathcal{W}$  is a place-holder for any of the three selection modes  $(V, W^{\heartsuit}, \text{ or } W^{\heartsuit})$ . If selection occurs prior to migration – which happens when seed disperses and selection acts on sexual components– then Jacobian is:

$$\mathbf{J} = \begin{bmatrix} (1 - M_{12})\Delta \mathcal{W}_{0,1} & M_{12}\Delta \mathcal{W}_{0,2} \\ M_{21}\Delta \mathcal{W}_{0,1} & (1 - M_{21})\Delta \mathcal{W}_{0,2} \end{bmatrix}$$
(A20)

However, the eigenvalues of these two matrices are identical, so we here use (A18). The equilibrium is locally unstable whenever the leading eigenvalue of  $\mathbf{J}$  is greater than unity:

$$\rho = \frac{1}{2} \left( (1 - M_{12}) \Delta \mathcal{W}_{0,1} + (1 - M_{21}) \Delta \mathcal{W}_{0,2} + \sqrt{4(M_{12} + M_{21} - 1) \Delta \mathcal{W}_{0,1} \Delta \mathcal{W}_{0,2} + ((M_{21} - 1) \Delta \mathcal{W}_{0,1} + (M_{21} - 1) \Delta \mathcal{W}_{0,2})^2} \right)$$
(A21)

Term  $\Delta W_{0,i}$  can be thought of as the rate of spread of A allele in  $i^{th}$  patch. Then  $\Delta W_{0,1} > 1$ (because A is advantageous in the first patch), and  $0 < \Delta W_{0,2} < 1$  (because A is deleterious in the second patch). It is important to note that these inequalities hold regardless of the mode of selection. More formally:

$$\Delta V_{0,1} > 1, \quad 1 > \Delta V_{0,2} > 0 \tag{A22}$$

$$\Delta W_{0,1}^{Q} > 1, \quad 1 > W_{0,2}^{Q} > 0 \tag{A23}$$

$$\Delta W_{0,1}^{\mathcal{O}} > 1, \quad 1 > W_{0,2}^{\mathcal{O}} > 0 \tag{A24}$$

Substituting (A19) in (A21), and rearranging (see *Mathematica* notebook for details), we find that  $\rho > 1$  when:

$$\frac{M_{12}}{\frac{((1-F)\mathcal{W}_{1,Aa}+F\mathcal{W}_{1,AA})-\mathcal{W}_{1,aa}}{(1-F)\mathcal{W}_{1,Aa}+F\mathcal{W}_{1,AA}}} + \frac{M_{21}}{\frac{((1-F)\mathcal{W}_{2,Aa}+F\mathcal{W}_{2,AA})-\mathcal{W}_{2,aa}}{(1-F)\mathcal{W}_{2,Aa}+F\mathcal{W}_{2,AA}}} < 1$$
(A25)

Terms in denominators of inequality A25 represent the relative fitness of the invading allele *A*. Letting F = 0 and parameterizing such that  $\mathcal{W}_{i,AA} = 1 - s_1^{\circ}$ ,  $\mathcal{W}_{i,Aa} = 1$ , and  $\mathcal{W}_{i,aa} = 1 - t_1^{\circ}$ , we retrieve Bulmer's inequality  $M_{12}/t_1^{\circ} + M_{21}/t_2^{\circ}$ . Parameterizing according to our fitness scheme ( $\mathcal{W}_{i,AA} = 1 + s_i^{\circ}$ ,  $\mathcal{W}_{i,Aa} = 1 + s_i^{\circ}\tilde{h}_i^{\circ}$ , and  $\mathcal{W}_{i,aa} = 1$ ) yields:

$$\frac{\left(1+s_1^{\circ}\tilde{h}_1^{\circ}\right)M_{12}}{s_1^{\circ}\tilde{h}_1^{\circ}} + \frac{\left(1+s_2^{\circ}\tilde{h}_2^{\circ}\right)M_{21}}{s_2^{\circ}\tilde{h}_2^{\circ}}$$
(A26)

<sup>896</sup> Conversely to the previous case,  $0 < \Delta W_{1,1} < 1$  (as invading allele *a* is deleterious in the <sup>897</sup> first patch) and  $\Delta W_{1,2} > 1$  (given that *a* is beneficial in the second patch). Once the allele *A* <sup>898</sup> has escaped extinction, it can either fix in both patches or be maintained for finite number <sup>899</sup> of generations by divergent selection. Thus, the criterion for protected polymorphism is that <sup>900</sup> both allele *A* and *a* can escape extinction. By linearizing the system of replicator equations about  $\vec{x} = [1, 1]^T$  we obtain Jacobian:

$$\mathbf{J} = \begin{bmatrix} (1 - M_{12})\Delta \mathcal{W}_{1,1} & M_{12}\Delta \mathcal{W}_{1,1} \\ M_{21}\Delta \mathcal{W}_{1,2} & (1 - M_{21})\Delta \mathcal{W}_{1,2} \end{bmatrix}$$
(A27)

$$\Delta \mathcal{W}_{1,i} = (F\mathcal{W}_{i,aa} + (1-F)\mathcal{W}_{i,Aa})/\mathcal{W}_{i,AA}$$
(A28)

 $_{902}$  Therefore, allele *a* is allowed to invade whenever:

$$\frac{M_{12}}{\frac{((1-F)\mathcal{W}_{1,Aa}+F\mathcal{W}_{1,aa})-\mathcal{W}_{1,AA}}{(1-F)\mathcal{W}_{1,Aa}+F\mathcal{W}_{1,aa}}} + \frac{M_{21}}{\frac{((1-F)\mathcal{W}_{2,Aa}+F\mathcal{W}_{2,aa})-\mathcal{W}_{2,AA}}{(1-F)\mathcal{W}_{2,Aa}+F\mathcal{W}_{2,aa}}} < 1$$
(A29)

which reduces to  $M_{12}/s_1^\circ + M_{21}/s_2^\circ$  with fitness notation of Bulmer.

#### 904 C.2 Pollen dispersal

The analysis is more complicated for the three selection scenarios when pollen disperses because one has to re-parameterize migration rate in addition to dominance coefficients. We use Jacobian of the form:

$$\mathbf{J} = \begin{bmatrix} (1 - \tilde{M}_{12})\Delta \mathcal{W}_{0,1} & \tilde{M}_{12}\Delta \mathcal{W}_{0,1} \\ \tilde{M}_{21}\Delta \mathcal{W}_{0,2} & (1 - \tilde{M}_{21})\Delta \mathcal{W}_{0,2} \end{bmatrix}$$
(A30)

 $_{908}$  The leading eigenvalue of (A30) is:

$$\rho = \frac{1}{2} \left( (1 - \tilde{M}_{12}) \Delta \mathcal{W}_{0,1} + (1 - \tilde{M}_{21}) \Delta \mathcal{W}_{0,2} + \sqrt{4(\tilde{M}_{12} + \tilde{M}_{21} - 1) \Delta \mathcal{W}_{0,1} \Delta \mathcal{W}_{0,2} + \left((\tilde{M}_{21} - 1) \Delta \mathcal{W}_{0,1} + (\tilde{M}_{21} - 1) \Delta \mathcal{W}_{0,2}\right)^2} \right), \quad (A31)$$

where  $\Delta W$  and  $\tilde{M}$  are parameterized as outlined in Section 2.2. Given that  $1/2 \ge \tilde{M}_{ij} \ge 0$ for all *i* and *j*, and

$$\Delta V_{0,1} > 1, \quad 1 > \Delta V_{0,2} > 0 \tag{A32}$$

$$\Delta W_{0,1}^{Q} > 1, \quad 1 > W_{0,2}^{Q} > 0, \tag{A33}$$

<sup>911</sup> the same inequalities hold as in the case of seed dispersal. However, under male fecundity

<sup>912</sup> selection migration rates have to be:

$$m_{ij} < \frac{W_{j,aa}^{\mathcal{O}} \left( W_{i,aa}^{\mathcal{O}} - (1-F) W_{i,Aa}^{\mathcal{O}} - F W_{i,AA}^{\mathcal{O}} \right)}{W_{i,aa}^{\mathcal{O}} \left( (1-F) W_{j,Aa}^{\mathcal{O}} + F W_{j,AA}^{\mathcal{O}} \right) - W_{j,aa}^{\mathcal{O}} \left( (1-F) W_{i,Aa}^{\mathcal{O}} + F W_{i,AA}^{\mathcal{O}} \right)},$$
(A34)

913 for both  $m_{12}$  and  $m_{21}$ , or:

$$m_{ij} > \frac{W_{j,aa}^{\mathcal{O}} \left( W_{i,aa}^{\mathcal{O}} - (1-F) W_{i,Aa}^{\mathcal{O}} - F W_{i,AA}^{\mathcal{O}} \right)}{W_{i,aa}^{\mathcal{O}} \left( (1-F) W_{j,Aa}^{\mathcal{O}} + F W_{j,AA}^{\mathcal{O}} \right) - W_{j,aa}^{\mathcal{O}} \left( (1-F) W_{i,Aa}^{\mathcal{O}} + F W_{i,AA}^{\mathcal{O}} \right)},$$
(A35)

for both  $m_{12}$  and  $m_{21}$ . The conditions (A34) and (A35) are identical to saying that  $\omega_i > 0$ for all *i*, or  $\omega_i < 0$  for all *i*. A possible intuitive explanation for these conditions is as follows. If migration from favored to disfavored patch is too high, the mutant alleles are transferred to a disfavored patch where they are purged, thus causing the mutant to go extinct. If, on the other hand, migration from disfavored to favored patch is high, then the spreading mutant is swamped by the influx of deleterious residents from the opposite patch.

#### <sub>920</sub> D Simulation method

Selection and migration are assumed to alter genotype frequencies deterministically. Genetic drift is implemented by randomly drawing genotypes from multinomial distribution right after reproduction. We relax the assumption that the population has to reach equilibrium in the inbreeding coefficient F. Each simulation run terminates in a successful or failed invasion and is composed of the following four steps:

1. Inject a single heterozygote containing allele A in a population that is fixed for a allele. When interested in  $P_i$ , the mutant is injected in  $i^{th}$  patch.

- <sup>928</sup> 2. Update genotype frequencies by applying equations (2a)-(4b); This emulates selection
   on sexual components, pollen dispersal, and reproduction (including selfing).
- 3. Sample the genotypes from multinomial distribution to determine the genotype frequencies after the reproduction step:  $\mathbf{MN}([X_i, Y_i, Z_i], N_i^*)$ , where  $N_i^*$  is the size of  $i^{th}$ patch.
- 4. Update genotype frequencies due to seed dispersal by implementing (5a) and (5b).
- 5. Compute the number of each genotype after viability selection as  $X_i^* := X_i'' V_{i,AA}$ ,  $Y_i^* := Y_i'' V_{i,Aa}$ , and  $Z_i^* := 1 - X^* - Y^*$ .

6. Is the number of invading mutant alleles larger than 1000? If not, convert genotype numbers to genotype frequencies by dividing drawn genotype numbers with the total patch size and begin the new generation by going to step 2. If yes, count it as a successful invasion and terminate the simulation run.

If the mutant allele does not invade in 10,000 generations, we count the simulation run as a failed invasion. The establishment probability is obtained by running 10,000 simulations and computing the fraction of runs that ended in the successful invasion. All error bars in the figures correspond to the standard deviation of this metric. The chosen number for invasion threshold is well over  $1/s_1$ , given that we use  $s_1 = 0.01$ . Both patches contain 10,000 individuals, and populations are always in  $|Ns| \gg 1$  regime.

# <sup>946</sup> E Simulations under various selection and migration <sup>947</sup> modes

Our approximation gives a good fit for simulated data under female and male fecundity, 948 although the fit is not excellent as in the case of viability selection (Figures A10–A13). In 949 the case of male fecundity selection under complete selfing (S = 1), the male component 950 does not contribute to the fitness, and the allele is expected to behave neutrally. One can see 951 that this occurs because the probability that the invading allele reaches the threshold that 952 we use to determine whether the invasion is successful is inversely proportional to the size 953 of the threshold,  $1/N_{\text{thres}}$ , (grey dashed line in figures below). The figures below compare 954 the analytics to simulated data, with upper row denoting the case when allele originates in 955 the favored patch, and bottom row depicts the same dynamic but when allele appears in 956 the disfavored patch. From left to right, columns show codominant, partially dominant, and 957 partially recessive case, respectively. 958



Figure A10: Comparison of analytical solution to simulations when selection acts on the female fecundity and only seed disperses. Left column: codominant case  $(h_1^{\varphi} = h_2^{\varphi} = 1/2)$ ; Middle column: dominant case  $(h_1^{\varphi} = h_2^{\varphi} = 3/4)$ ; Right column: recessive case  $(h_1^{\varphi} = h_2^{\varphi} = 1/4)$ . Upper and lower panels depict the establishment probability conditioning on allele emerging in favored and disfavored patch, respectively. Parameters:  $s_1^{\varphi} = -s_2^{\varphi} = 0.01$ ,  $M_{12} = M_{21} = M$ .



Figure A11: Comparison of analytical solution to simulations when selection acts on male fecundity and only seed disperses. Left column: codominant case  $(h_1^{\mathcal{O}} = h_2^{\mathcal{O}} = 1/2)$ ; Middle column: dominant case  $(h_1^{\mathcal{O}} = h_2^{\mathcal{O}} = 3/4)$ ; Right column: recessive case  $(h_1^{\mathcal{O}} = h_2^{\mathcal{O}} = 1/4)$ . Upper and lower panels depict the establishment probability conditioning on allele emerging in favored and disfavored patch, respectively. Parameters:  $s_1^{\mathcal{O}} = -s_2^{\mathcal{O}} = 0.01$ ,  $M_{12} = M_{21} = M$ .



Figure A12: Comparison of analytical solution to simulations when selection acts on the female fecundity, only seed disperses, and selection or migration are asymmetrical. Left column: asymmetric selection  $(s_1^{\varphi} = 0.01, s_2^{\varphi} = -0.02, h_1^{\varphi} = h_2^{\varphi} = 1/2)$ ; Right column: asymmetric migration  $(s_1^{\varphi} = -s_2^{\varphi} = 0.01, h_1^{\varphi} = h_1^{\varphi} = 1/2, M_{12} = M, \text{ and } M_{21} = 1.25M)$ .



Figure A13: Comparison of analytical solution to simulations when selection acts on the male fecundity, only seed migrates, and selection or migration are asymmetrical. Left column: asymmetric selection  $(s_1^{\mathcal{O}} = 0.01, s_2^{\mathcal{O}} = -0.02, h_1^{\mathcal{O}} = h_2^{\mathcal{O}} = 1/2)$ ; Right column: asymmetric migration  $(s_1^{\mathcal{O}} = -s_2^{\mathcal{O}} = 0.01, h_1^{\mathcal{O}} = 1/2, M_{12} = M, \text{ and } M_{21} = 1.25M)$ .



Figure A14: Comparison of analytical solution to simulations when only pollen disperses. Allele starts in the favored patch. Top row: viability selection; Middle row: female fecundity selection; Bottom row: Male fecundity selection. Dominances reported in panels. Other parameters: corresponding seelection coefficients are always  $s_1 = -s_2 = 0.01$ , and  $m_{12} = m_{21} = m$ .



Figure A15: Same as above, but allele starts in the disfavored patch.

## **F** Procedure for computing $\beta$ indicators

Suppose one wants to derive  $\beta$  indicator when selection operates on  $j^{th}$  fitness component (where  $j \in \{V, F, M\}$ ) in  $k^{th}$  patch (where  $k \in \{1, 2\}$ ). Selfing affects the establishment probability through three factors: the effective population size  $(\beta_k(\tilde{N}))$ , effective favored and disfavored dominance  $(\beta_k(\tilde{h}_1) \text{ and } \beta_k(\tilde{h}_2))$ , and the effective migration rate  $(\beta_k(\tilde{M}))$ . Starting from equations (A16) and (A17), expressions for  $\beta$  are obtained using the following steps in a sequential manner:

•  $\beta_k(\tilde{N})$ : Parameterize migration according to eqns. 12a–12c, and then set F = 0 to exclude the effect via  $\tilde{M}$ . Let  $\tilde{s}_i^{\{j\}} = s_i^{\{j\}} \tilde{h}_i^{\{j\}}$  for  $i \in \{1, 2\}$ . Next, set F = 0 to exclude the effect on dominances. Take a derivative in F and evaluate at F = 0.

•  $\beta_k(\tilde{h}_1)$ : Parameterize migration according to eqns. 12a–12c, and then set F = 0 to exclude the effect via  $\tilde{M}$ . Set F = 0 to exclude the effect via  $\tilde{N}$ . Let  $\tilde{s}_2^{\{j\}} = s_2^{\{j\}} \tilde{h}_2^{\{j\}}$ and then set F = 0 to exclude the effect via  $\tilde{h}_2$ . Let  $\tilde{s}_1^{\{j\}} = s_1^{\{j\}} \tilde{h}_1^{\{j\}}$ . Take a derivative in F and evaluate at F = 0.



Figure A16: Zones of selfing's effect on the probability of establishment across viability (left panel), female fecundity (middle panel), and male fecundity (right panel), conditioning on allele appearing in the disfavored patch. Only seed migrates. Parameters are identical to those used in Figure 4. Upper row: scenarios with seed migration; Bottom row: scenarios with pollen migration.

•  $\beta_k(\tilde{h}_2)$ : Parameterize migration according to eqns. 12a–12c, and then set F = 0 to exclude the effect via  $\tilde{M}$ . Set F = 0 to exclude the effect via  $\tilde{N}$ . Let  $\tilde{s}_1^{\{j\}} = s_1^{\{j\}} \tilde{h}_1^{\{j\}}$ and then set F = 0 to exclude the effect via  $\tilde{h}_1$ . Let  $\tilde{s}_2^{\{j\}} = s_2^{\{j\}} \tilde{h}_2^{\{j\}}$ . Take a derivative in F and evaluate at F = 0.

•  $\beta_k(\tilde{M})$ : Set F = 0 to exclude the effect via  $\tilde{N}$ . Let  $\tilde{s}_i^{\{j\}} = s_i^{\{j\}} \tilde{h}_i^{\{j\}}$  for  $i \in \{1, 2\}$ . Then set F = 0 to exclude the effect via  $\tilde{h}_1$ , and  $\tilde{h}_2$ . Next, parameterize migration according to eqns. 12a-12c. Take a derivative in F and evaluate at F = 0.

Parameters  $\tilde{h}_i^{\circ}$ ,  $\tilde{h}_i^{\circ}$ , and  $\tilde{h}_i^{\circ}$  are given by equations (9a)–(9c). Whenever a  $\beta_i(x)$  is greater than zero, a shift to selfing increases the probability that an allele becomes established, conditioning on starting in patch *i*. Evaluating the derivative in point other than F = 0 will change the results quantitatively, but not qualitatively.

## <sup>984</sup> G The consequences of shift to selfing on local adap-<sup>985</sup> tation

Where fecundity selection is examined, the establishment probability equations were parameterized with  $s_i^{\varphi}$ , and  $h_i^{\varphi}$ , while selection on male fitness component was done by parameterizing with  $s_i^{\mathcal{O}}$ , and  $h_i^{\mathcal{O}}$ . Other than that, parameters were quantitatively identical to the viability selection case. Migration rates were also kept constant across different scenarios, and only the migration type has changed.



Figure A17: The consequences of a shift to selfing on establishment of local adaptation under female fecundity selection and seed dispersal. Color-coding and parameters as in the main text and parameters as in the main text.



Figure A18: The consequences of a shift to selfing on establishment of local adaptation under male fecundity selection and seed dispersal. Color-coding and parameters as in the main text and parameters as in the main text.



Figure A19: The consequences of a shift to selfing on establishment of local adaptation under viability selection and pollen dispersal.