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**The components of directional and disruptive selection  
in heterogeneous group-structured populations**

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## Abstract

We derive how directional and disruptive selection operate on scalar traits in a heterogeneous group-structured population for a general class of models. In particular, we assume that each group in the population can be in one of a finite number of states, where states can affect group size and/or other environmental variables, at a given time. Using up to second-order perturbation expansions of the invasion fitness of a mutant allele, we derive expressions for the directional and disruptive selection coefficients, which are sufficient to classify the singular strategies of adaptive dynamics. These expressions include first- and second-order perturbations of individual fitness (expected number of settled offspring produced by an individual, possibly including self through survival); the first-order perturbation of the stationary distribution of mutants (derived here explicitly for the first time); the first-order perturbation of pairwise relatedness; and reproductive values, pairwise and three-way relatedness, and stationary distribution of mutants, each evaluated under neutrality. We introduce the concept of individual  $k$ -fitness (defined as the expected number of settled offspring of an individual for which  $k - 1$  randomly chosen neighbors are lineage members) and show its usefulness for calculating relatedness and its perturbation. We then demonstrate that the directional and disruptive selection coefficients can be expressed in terms of individual  $k$ -fitnesses with  $k = 1, 2, 3$  only. This representation has two important benefits. First, it allows for a significant reduction in the dimensions of the system of equations describing the mutant dynamics that needs to be solved to evaluate explicitly the two selection coefficients. Second, it leads

36 to a biologically meaningful interpretation of their components. As an application of our methodology,  
37 we analyze directional and disruptive selection in a lottery model with either hard or soft selection and  
38 show that many previous results about selection in group-structured populations can be reproduced as  
39 special cases of our model.

## 40 1 Introduction

41 Many natural populations are both group-structured – with the number of individuals interacting at the  
42 local scale being finite – and heterogeneous – with different groups being subject to different demographic  
43 and environmental conditions (*e.g.*, varying group size and temperature, respectively). Understanding  
44 how evolution, and in particular natural selection, moulds phenotypic traits in such systems is compli-  
45 cated as both local heterogeneity and demographic stochasticity need to be taken into account. In order  
46 to predict the outcome of evolution in heterogeneous populations, evolutionists are generally left with  
47 the necessity to approximate the evolutionary dynamics, as a full understanding of this process is yet  
48 out of reach.

49 A standard approximation to predict evolutionary outcomes is to assume that traits are quantitative,  
50 that the details of inheritance do not matter (“phenotypic gambit”, Grafen, 1991), and that mutations  
51 have weak (small) phenotypic effects (*e.g.* Grafen, 1985; Taylor, 1989; Parker and Maynard Smith, 1990;  
52 Rousset, 2004). Under these assumptions, directional trait evolution can be quantified by a phenotypic  
53 selection gradient that captures first-order effects of selection. Thus, phenotypic change occurs in an  
54 uphill direction on the fitness landscape. This directional selection either causes the trait value to change  
55 endlessly (for instance, due to macro environmental changes or cycles in the evolutionary dynamics),  
56 or the trait value eventually approaches a local equilibrium point, a so-called *singular strategy*, where  
57 directional selection vanishes. Such a singular strategy may be locally uninvadable (“evolutionary stable”)  
58 and thus a local end-point of the evolutionary dynamics. However, when the fitness landscape is dynamic  
59 due to selection being frequency-dependent, then it is also possible that, as the population evolves uphill  
60 on the fitness landscape, this landscape changes such that the population eventually finds itself at a  
61 singular strategy that is located in a fitness valley. In this case, directional selection turns into disruptive  
62 selection, which means that a singular strategy that is an attractor of the evolutionary dynamics (and  
63 thus convergence stable) is invadable by nearby mutants and thus an *evolutionary branching point* (Metz  
64 et al., 1996; Geritz et al., 1998). Further evolutionary dynamics can then result in genetic polymorphism  
65 in the population, thus possibly favoring the maintenance of adaptive diversity in the long term (see  
66 Rueffler et al., 2006, for a review). Disruptive selection at a singular point is quantified by the disruptive  
67 selection coefficient (called quadratic selection gradient in the older literature: Lande and Arnold, 1983;  
68 Phillips and Arnold, 1989), which involves second-order effects of selection.

69 A central question concerns the nature and interpretation of the components of the selection gradient  
70 and the disruptive selection coefficient on a quantitative trait in heterogeneous populations. For the  
71 selection gradient, this question has been studied for a long time and a general answer has been given  
72 under the assumption that individuals can be in a finite number of states (summarized in Rousset, 2004).  
73 Then, regardless of the complexity of the spatial, demographic, environmental, or physiological states

74 individuals can be in or experience (in the kin-selection literature commonly referred to as class-structure,  
 75 *e.g.* Taylor, 1990; Frank, 1998; Rousset, 2004), the selection gradient on a quantitative trait depends on  
 76 three key components (Taylor, 1990; Frank, 1998; Rousset, 2004). The first component are individual  
 77 fitness differentials, which capture the marginal gains and losses of producing offspring in particular  
 78 states to parents in particular states. The second component are (neutral) reproductive values weighting  
 79 these fitness differentials. These capture the fact that offspring settling in different states contribute  
 80 differently to the future gene pool. The third component are (neutral) relatedness coefficients. These  
 81 also weight the fitness differentials, and capture the fact that some pairs of individuals are more likely to  
 82 carry the same phenotype (inherited from a common ancestor) than randomly sampled individuals. This  
 83 results in correlations between the trait values of interacting individuals. Such correlations matter for  
 84 selection (“kin selection”, *e.g.* Michod, 1982) and occur in populations subject to limited genetic mixing  
 85 and small local interaction groups. At the risk of oversimplifying, reproductive values can be thought  
 86 of as capturing the effect of population heterogeneity on directional selection, while relatedness captures  
 87 the effect of demographic stochasticity under limited genetic mixing.

88 The situation is different with respect to the coefficient of disruptive selection, *i.e.*, the second-order  
 89 effects of selection. The components of the disruptive selection coefficient have not been worked out in  
 90 general and are studied only under the assumptions of well-mixed or spatially structured populations,  
 91 but with otherwise homogeneous individuals. For the spatially structured case the effects of selection on  
 92 relatedness has been shown to matter, as selection changes the number of individuals expressing similar  
 93 trait values in a certain group (Ajar, 2003; Wakano and Lehmann, 2014; Mullon et al., 2016), resulting in  
 94 a reduced strength of disruptive selection under limited dispersal. For the general case that individuals  
 95 can be in different states one expects intuitively that disruptive selection also depends on how selection  
 96 affects the distribution of individuals over the different states. But this has not been analyzed so far  
 97 even though it is captured implicitly when second-order derivatives of invasion fitness are computed as  
 98 has been done in several previous works investigating evolutionary branching in some specific models of  
 99 class-structured populations (*e.g.* Massol et al., 2011; Rueffler et al., 2013; Massol and Débarre, 2015;  
 100 Kisdi, 2016; Parvinen et al., 2018, 2020).

101 In the present paper, we develop an evolutionary model for a heterogeneous group-structured popula-  
 102 tion that covers a large class of biological scenarios. For this model, we show that the disruptive selection  
 103 coefficient can be expressed in terms of individual fitness differentials weighted by the neutral quantities  
 104 appearing in the selection gradient. This both significantly facilitates concrete calculations under com-  
 105 plex scenarios and allows for a biological interpretation of selection. Our results contain several previous  
 106 models as special cases.

107 The remainder of this paper is organized as follows. (1) We start by describing a demographic model  
 108 for a heterogeneous group-structured population and present some background material underlying the  
 109 characterization of uninvadable (“evolutionary stable”) strategies by way of invasion fitness for this  
 110 model. We here also introduce a novel individual fitness concept – individual  $k$ -fitness – defined as the  
 111 expected number of settled offspring of an individual for which  $k - 1$  randomly chosen neighbors are  
 112 relatives (*i.e.*, members of the same lineage). This fitness concept plays a central role in our analysis. (2)

113 Assuming quantitative scalar traits, we present first- and second-order perturbations of invasion fitness  
 114 (*i.e.*, the selection gradient and disruptive selection coefficient, respectively), discuss their components  
 115 and the interpretations thereof, and finally express all quantities in terms of individual  $k$ -fitness with  
 116  $k = 1, 2, 3$ . (3) We present a generic lottery model under spatial heterogeneity for both soft and hard  
 117 selection regimes and show that the selection gradient and the disruptive selection coefficient can be  
 118 computed explicitly under any scenario falling into this class of models. We then apply these results to a  
 119 concrete local adaptation scenario where we derive conditions for evolutionary stability and convergence  
 120 stability of singular trait values, and show their dependence on migration rate and group size. In doing so,  
 121 we recover and extend previous results from the literature and show how our model connects seemingly  
 122 different approaches.

## 123 2 Model

### 124 2.1 Biological assumptions

125 We consider a population of haploid individuals that is subdivided into infinitely many groups that are  
 126 connected to each other by dispersal (*i.e.*, the infinite island model). Dispersal between groups may occur  
 127 by individuals alone or by groups of individuals as in propagule dispersal, but is always random with  
 128 respect to the destination group. We consider a discrete-time reproductive process and thus discrete  
 129 census steps. At each census, each group is in a state  $s \in \mathcal{S}$  with  $\mathcal{S} = \{s_1, s_2, \dots, s_N\}$  where  $N$  denotes  
 130 the number of possible states. The state  $s$  determines the number of individuals in a group and/or any  
 131 environmental factor determining the survival, reproduction, and dispersal of all individuals within a  
 132 group. For the sake of simplicity, we will consider only a finite number of discrete states in this paper.  
 133 The state  $s$  does not need to be a fixed property of a group but can change in time and be affected  
 134 by individual trait values and thus be determined endogenously. However, we assume that such state  
 135 changes are governed by a time-homogeneous Markov chain, meaning that there are no temporal trends  
 136 in dynamics of the group states. We denote by  $n_s$  the finite number of adult individuals in a group  
 137 in state  $s$ , which can thus change over time if the group state changes. We assume that group size is  
 138 bounded as a result of density dependence acting at the local scale (hence there is an upper bound on  
 139 group size). The described set-up includes a variety of classical models.

- 140 1. Purely spatially structured populations: The state  $s$  is identical for all groups ( $N = 1$ ) and so there  
 141 is only one group size. This is essentially the island model as developed by Wright (1943), which  
 142 has been a long-term work horse for understanding the effect of spatial structure on evolutionary  
 143 dynamics (*e.g.* Eshel, 1972; Bulmer, 1986; Rousset, 2004).
- 144 2. Stochastic population dynamics at the group level: The state  $s$  determines the number of individ-  
 145 uals in a group, which can potentially vary in time (*e.g.* Metz and Gyllenberg, 2001; Rousset and  
 146 Ronce, 2004). This case covers the situation in which each group is embedded in a community  
 147 consisting of several interacting species and where the state  $s$  determines the number of individuals  
 148 for each of the other species (*e.g.* Chesson, 1981).

- 149 3. Environmental heterogeneity: The state  $s$  determines an aspect of the within-group environment,  
 150 which affects the survival and/or reproduction of its group members. An example is heterogeneity  
 151 in patch quality or size (*e.g.* Wild et al., 2009; Massol et al., 2011; Rodrigues and Gardner, 2012).  
 152 We note that in the limit of infinite group size this coincides with models of temporal and spatial  
 153 heterogeneity as reviewed in Svardal et al. (2015).
- 154 4. Group splitting: This is a special case in which migration between groups is in fact absent but  
 155 groups can be connected to each other if they originate through splitting of a parental group. The  
 156 state  $s$  again determines the number of adults in a group. This model is inspired by compart-  
 157 mentalized replication in prebiotic evolution (stochastic corrector model, Szathmary and Demeter,  
 158 1987; Grey et al., 1995).
- 159 5. Purely physiologically structured population: In the special case with only a single individual in a  
 160 group, the state  $s$  can be taken to represent the physiological state of an individual such as age or  
 161 size or combinations thereof (*e.g.* Ronce and Promislow, 2010). In the special case of complete and  
 162 independent offspring dispersal (*i.e.*, no group dispersal) but arbitrary group size, the state  $s$  can  
 163 be taken to represent the combination of individual physiological states of all members in a group  
 164 so that the model covers within group heterogeneity.

165 Since we are mainly interested in natural selection driven by recurrent invasions by possibly different  
 166 mutants, we can focus on the initial invasion of a mutant allele into a monomorphic resident population.  
 167 Hence, we assume that at any time at most two alleles segregate in the population, a mutant allele  
 168 whose carriers express the trait value  $x$  and a resident allele whose carriers express the trait value  $y$ . We  
 169 furthermore assume that traits are one-dimensional and real-valued ( $x, y \in \mathbb{R}$ ). Suppose that initially  
 170 the population is monomorphic (*i.e.*, fixed) for the resident allele  $y$  and a single individual mutates to  
 171 trait value  $x$ . How do we ascertain the extinction or spread of the mutant?

## 172 2.2 Multitype branching process and invasion fitness

173 Since any mutant is initially rare, we can focus on the initial invasion of the mutant into the total popu-  
 174 lation and approximate its dynamics as a discrete-time multitype branching process (Harris, 1963; Karlin  
 175 and Taylor, 1975; Wild, 2011). In doing so, we largely follow the model construction and notation used  
 176 in Lehmann et al. (2016) (see section ?? in the Supplementary Material for a mathematical description  
 177 of the stochastic process underlying our model). In particular, in order to ascertain uninvasibility of  
 178 mutants into a population of residents it is sufficient to focus on the transition matrix  $\mathbf{A} = \{a(s', i' | s, i)\}$   
 179 whose entry in position  $(s', i' | s, i)$ , denoted by  $a(s', i' | s, i)$ , is the expected number of groups in state  $s'$   
 180 with  $i' \geq 1$  mutant individuals that descend from a group in state  $s$  with  $i \geq 1$  mutant individuals over  
 181 one time step in a population that is otherwise monomorphic for  $y$ . In the following, we refer to a group  
 182 in state  $s$  with  $i$  mutants and  $n_s - i$  residents as an  $(s, i)$ -group for short. The transition matrix  $\mathbf{A}$  is a  
 183 square matrix that is assumed to be primitive (we note that primitivity will obtain under all models listed  
 184 in section 2.1 but may be induced for different reasons). Thus, a positive integer  $\ell$  (possibly depending  
 185 on  $x$  and  $y$ ) exists such that every entry of  $\mathbf{A}^\ell$  ( $\ell$ th power of  $\mathbf{A}$ ) is positive. The entries  $a(s', i' | s, i)$

186 of the matrix  $\mathbf{A}$  generally depend on both  $x$  and  $y$ , but for ease of exposition we do not write these  
 187 arguments explicitly unless necessary. The same convention applies to all other variables that can in  
 188 principle depend on  $x$  and  $y$ .

189 From standard results on multitype branching processes (Harris, 1963; Karlin and Taylor, 1975) it  
 190 follows that a mutant  $x$  arising as a single copy in an arbitrary group of the population, *i.e.*, in any  
 191  $(s, 1)$ -group, goes extinct with probability one if and only if the largest eigenvalue of  $\mathbf{A}$ , denoted by  $\rho$ , is  
 192 less than or equal to one,

$$\rho \leq 1, \quad (1)$$

193 where  $\rho$  satisfies

$$\mathbf{A}\mathbf{u} = \rho\mathbf{u} \quad (2)$$

194 and where  $\mathbf{u}$  is the leading right eigenvector of  $\mathbf{A}$ . We refer to  $\rho$  as the *invasion fitness* of the mutant.  
 195 If eq.(1) holds, then we say that  $y$  is *uninvadable* by  $x$ . To better understand what determines invasion  
 196 fitness, we introduce the concept of the *mutant lineage*, which we define as the collection of descendants  
 197 of the initial mutant: its direct descendants (possibly including self through survival), the descendants of  
 198 its immediate descendants, and so on. Invasion fitness then gives the expected number of mutant copies  
 199 produced over one time step by a randomly sampled mutant from its lineage in an otherwise monomorphic  
 200 resident population that has reached demographic stationarity (Mullon et al., 2016; Lehmann et al.,  
 201 2016). The mutant stationary distribution is given by the vector  $\mathbf{u}$  with entries  $u(s, i)$  describing,  
 202 after normalization, the asymptotic probability that a randomly sampled group containing at least one  
 203 mutant is in state  $s$  and contains  $i \geq 1$  mutants. In other words, invasion fitness is the expected number  
 204 of mutant copies produced by a lineage member randomly sampled from the distribution  $\mathbf{u}$  (see eq.(??)  
 205 in the Supplementary Material and the explanation thereafter).

## 206 2.3 Statistical description of the mutant lineage

207 We use the matrix  $\mathbf{A} = \{a(s', i'|s, i)\}$  and its leading right eigenvector  $\mathbf{u}$  to derive several quantities  
 208 allowing us to obtain an explicit representation of invasion fitness, which will be the core of our sensitivity  
 209 analysis.

### 210 2.3.1 Asymptotic probabilities and relatedness of $k$ -individuals

211 We start by noting that the asymptotic probability for a mutant to find itself in an  $(s, i)$ -group is given  
 212 by

$$q(s, i) \equiv \frac{i u(s, i)}{\sum_{s' \in \mathcal{S}} \sum_{i'=1}^{n_{s'}} i' u(s', i')}. \quad (3)$$

213 From this, we can compute two state probabilities. First, the asymptotic probability that a randomly  
 214 sampled mutant finds itself in a group in state  $s$  is given by

$$q(s) \equiv \sum_{i=1}^{n_s} q(s, i). \quad (4)$$



215 Second, the asymptotic probability that, conditional on being sampled in a group in state  $s$ , a randomly  
 216 sampled mutant finds itself in a group with  $i$  mutants is given by

$$q(i|s) \equiv \frac{q(s, i)}{q(s)}. \quad (5)$$

217 Let us further define

$$\phi_k(s, i) \equiv \begin{cases} 1 & (k = 1) \\ \prod_{j=1}^{k-1} \frac{i-j}{n_s-j} & (2 \leq k \leq i) \\ 0 & (i+1 \leq k \leq n_s), \end{cases} \quad (6)$$

218 which, for  $k > 1$ , can be interpreted as the probability that, given a mutant is sampled from an  $(s, i)$ -  
 219 group,  $k-1$  randomly sampled group neighbors without replacement are all mutants. This allows us to  
 220 define the relatedness between  $k$  individuals in a group in state  $s$  as

$$r_k(s) \equiv \sum_{i=1}^{n_s} \phi_k(s, i) q(i|s). \quad (7)$$

221 This is the probability that  $k-1$  randomly sampled neighbors without replacement of a randomly sampled  
 222 mutant in state  $s$  are also mutants (*i.e.*, they all descend from the lineage founder). For example,

$$r_2(s) = \sum_{i=1}^{n_s} \frac{i-1}{n_s-1} q(i|s) \quad (8)$$

223 is the asymptotic probability of sampling a mutant among the neighbors of a random mutant individual  
 224 from a group in state  $s$  and thus provides a measure of pairwise relatedness among group members.  
 225 Likewise,

$$r_3(s) = \sum_{i=1}^{n_s} \frac{(i-1)(i-2)}{(n_s-1)(n_s-2)} q(i|s) \quad (9)$$

226 is the asymptotic probability that, conditional on being sampled in a group in state  $s$ , two random  
 227 neighbors of a random mutant individual are also mutants.

### 228 2.3.2 Individual fitness and individual $k$ -fitness

229 Consider a mutant in an  $(s, i)$ -group and define

$$w(s'|s, i) \equiv \frac{1}{i} \sum_{i'=1}^{n_{s'}} i' a(s', i'|s, i). \quad (10)$$

230 The sum on the right-hand side of eq.(10) counts the expected total number of mutants in groups in state  
 231  $s'$  produced by an  $(s, i)$ -group, and the share from a single mutant in this  $(s, i)$ -group is calculated by  
 232 dividing this lineage productivity by  $i$ . Hence,  $w(s'|s, i)$  is the expected number of offspring of a mutant  
 233 individual (possibly including self through survival), which settle in a group in state  $s'$ , given that the  
 234 mutant resided in a group in state  $(s, i)$  in the previous time period. Thus  $w(s'|s, i)$  is an individual  
 235 fitness<sup>1</sup>.

<sup>1</sup>It is important to note that the conditioning in  $w(s'|s, i)$  is only on the state of the parental generation (as emphasized by the notation) and that  $w(s'|s, i)$  depends on group transition probabilities in models in which the state  $s$  of a group can change in each generation. See eqs.(E.1–E.2) in Lehmann et al. (2016) as well as section ?? in the Supplementary Material for more details.



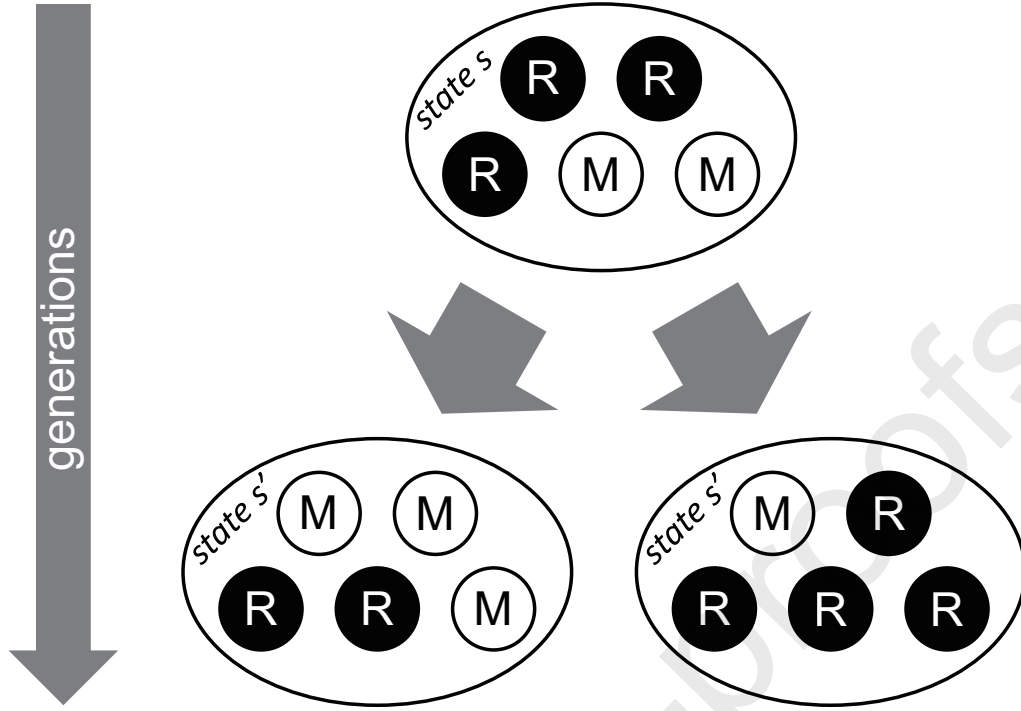


Figure 1: A schematic example for the calculation of individual  $k$ -fitness. Symbols M and R represent mutants and resident individuals, respectively. In this example, an  $(s, 2)$ -group “produced” one  $(s', 3)$ -group and one  $(s', 1)$ -group. Individual 1-fitness of each mutant in the following generation is the total number of mutants in the following generation ( $3 + 1 = 4$ ) divided by the number of mutants in the  $(s, 2)$ -group ( $= 2$ ). Thus  $w_1(s'|s, 2) = 4/2 = 2$ . For individual 2-fitness we calculate the weighted number of mutants in the following generation, where the weights are the probabilities that a random neighbor of a mutant is also a mutant, and then divide it by the number of mutants in the  $(s, 2)$ -group ( $= 2$ ). These probabilities are  $2/4$  for the  $(s', 3)$ -group and  $0/4$  for the  $(s', 1)$ -group. Thus, the weighted number of mutants is  $3 \cdot (2/4) + 1 \cdot (0/4) = 3/2$ , and the individual 2-fitness is  $w_2(s'|s, 2) = (3/2)/2 = 3/4$ . Similarly,  $w_3(s'|s, 2) = \{3 \cdot (1/6) + 1 \cdot (0/6)\}/2 = 1/4$  and  $w_4(s'|s, 2) = w_5(s'|s, 2) = 0$ .

236 We now extend the concept of individual fitness to consider a collection of offspring descending from  
 237 a mutant individual. More formally, for any integer  $k$  ( $1 \leq k \leq n_{s'}$ ) we let

$$w_k(s'|s, i) \equiv \frac{1}{i} \sum_{i'=1}^{n_{s'}} \phi_k(s', i') i' a(s', i'|s, i) \quad (11)$$

238 be the expected number of offspring produced by a single mutant individual in an  $(s, i)$ -group (possibly  
 239 including self through survival) that settle in a group in state  $s'$  and have  $k - 1$  randomly sampled group  
 240 neighbors (without replacement) that are also mutants. We refer to  $w_k(s'|s, i)$  as “individual  $k$ -fitness”  
 241 regardless of the states  $s'$  and  $(s, i)$  (see Figure 1 for an illustrative example).

242 Note that individual 1-fitness equals  $w(s'|s, i)$  as defined in eq.(10). Hence, individual  $k$ -fitness  
 243  $w_k(s'|s, i)$  is a generalization of this fitness concept. The difference between eq.(10) and eq.(11) is the  
 244 term  $\phi_k(s', i')$ , which shows that  $k$ -fitness counts an individual’s number of offspring (possibly including  
 245 self through survival) that experience a certain identity-by-descent genetic state in their group. Under  
 246 our assumption of infinitely many groups, more than one dispersing offspring can settle in the same group  
 247 only with propagule dispersal. Thus, without propagule dispersal dispersing offspring do not contribute

248 to  $k$ -fitness for  $k > 1$ .

### 249 2.3.3 Notation for perturbation analysis

250 Since our goal is to perform a sensitivity analysis of  $\rho$  to evaluate the selection gradient and disruptive  
251 selection coefficient, we assume that the mutant and resident trait values are close to each other and  
252 write

$$x = y + \delta \quad (12)$$

253 with  $\delta$  sufficiently small (*i.e.*,  $|\delta| \ll 1$ ). Thus,  $\rho$  can be Taylor-expanded with respect to  $\delta$ .

254 For invasion fitness  $\rho$ , or more generally, for any smooth function  $F$  that depends on  $\delta$ , we will use  
255 the following notation throughout this paper. The Taylor-expansion of  $F$  with respect to  $\delta$  is written as

$$F(\delta) = F^{(0)} + \delta F^{(1)} + \delta^2 F^{(2)} + \dots, \quad (13a)$$

256 where  $F^{(\ell)}$  is given by

$$F^{(\ell)} = \frac{1}{\ell!} \left. \frac{d^\ell F(\delta)}{d\delta^\ell} \right|_{\delta=0}. \quad (13b)$$

### 257 2.3.4 Properties of the monomorphic resident population

258 The zeroth-order coefficient in eq.(13) corresponds to the situation where the function  $F$  is evaluated  
259 under the supposition that individuals labelled as “mutant” and “resident” are the same. In that case,  
260 individuals in groups with the same state are assumed to be exchangeable in the sense that they have  
261 the same reproductive characteristics (the same distribution of fitnesses, *i.e.*, the same mean fitness, the  
262 same variance in fitness, and so on). This results in a neutral evolutionary process, *i.e.*, a monomorphic  
263 population.

264 We now characterize the mutant lineage dynamics under a neutral process as this plays a crucial role  
265 in our analysis. From eq.(10), the individual 1-fitness in an  $(s, i)$ -group, written under neutrality, equals

$$w_1^{(0)}(s'|s, i) = \frac{1}{i} \sum_{i'=1}^{n_{s'}} i' a^{(0)}(s', i'|s, i), \quad (14)$$

266 where each  $a^{(0)}(s', i'|s, i)$  is an entry of the matrix  $\mathbf{A}$  under neutrality. By our exchangeability assump-  
267 tion, eq.(14) does not depend on  $i$ , the number of the individuals labeled as “mutants” in this group  
268 (see section ?? (iv) in the Supplementary Material). If this would not be the case, mutants in a group  
269  $(s, i_1)$  and in a group  $(s, i_2)$  with  $i_1 \neq i_2$  would have different reproductive outputs and mutants and  
270 residents would not be exchangeable. Therefore, from now on we write  $w_1^{(0)}(s'|s, i)$  simply as  $w_1^{(0)}(s'|s)$ .  
271 We collect these neutral fitnesses in the  $N \times N$  matrix  $\mathbf{W}^{(0)} = \{w_1^{(0)}(s'|s)\}$ . Its entry  $(s', s)$  gives the  
272 expected number of descendants (possibly including self through survival) settling in groups of state  $s'$   
273 that descend from an individual residing in an  $s$ -group (mutant or resident since they are phenotypically  
274 indistinguishable).

275 The assumptions that each group is density regulated (see Section 2.1) and that the resident popula-  
276 tion has reached stationarity guarantee that the largest eigenvalue of  $\mathbf{W}^{(0)}$  equals 1 (see section ?? (v)  
277 in the Supplementary Material). This is the unique largest eigenvalue because  $\mathbf{W}^{(0)}$  is primitive due to

278 the assumption that  $\mathbf{A}$  is primitive. Thus, there is no demographic change in populations in which all  
 279 individuals carry the same trait  $y$  and that have reached stationarity.

280 The fact that under neutrality  $w_1^{(0)}(s'|s, i)$  is independent of  $i$  and  $\mathbf{W}^{(0)}$  has the unique largest  
 281 eigenvalue of 1 imposes constraints on the matrix  $\mathbf{A}^{(0)} = \{a^{(0)}(s', i'|s, i)\}$  that describes the growth  
 282 of a mutant lineage under neutrality. Let us denote the left eigenvector of  $\mathbf{W}^{(0)}$  corresponding to the  
 283 eigenvalue 1 by  $\mathbf{v}^{(0)} = \{v^{(0)}(s)\}$ , which is a strictly positive row vector of length  $N$ . Each entry  $v^{(0)}(s)$   
 284 gives the reproductive value of an individual in state  $s$ , which is the asymptotic contribution of that  
 285 individual to the gene pool. Note that  $v^{(0)}(s)$  does not depend on  $\delta$  because it is defined from  $\mathbf{W}^{(0)}$ ,  
 286 which is independent of  $\delta$ . We now construct a row vector  $\hat{\mathbf{v}}^{(0)} = \{\hat{v}^{(0)}(s, i)\}$  of length  $n \equiv \sum_{s \in \mathcal{S}} n_s$   
 287 by setting  $\hat{v}^{(0)}(s, i) = v^{(0)}(s)i$ . It has been shown that  $\hat{\mathbf{v}}^{(0)}$  is a positive left eigenvector of the matrix  
 288  $\mathbf{A}^{(0)} = \{a^{(0)}(s', i'|s, i)\}$  corresponding to the eigenvalue 1, and therefore – since  $\hat{\mathbf{v}}^{(0)}$  is strictly positive  
 289 – the Perron-Frobenius theorem implies that the largest eigenvalue of  $\mathbf{A}^{(0)}$  is  $\rho^{(0)} = 1$  (see Appendix A  
 290 in Lehmann et al., 2016, for a proof and more details). We also show that the column vector  $\{q^{(0)}(s)\}$   
 291 of length  $N$ , denoting the stable asymptotic distribution given by eq.(4) under neutrality, is the right  
 292 eigenvector of the matrix  $\mathbf{W}^{(0)}$  corresponding to the eigenvalue of 1 (see section ?? in the Supplementary  
 293 Material). There is freedom of choice for how to normalize the left eigenvector  $\mathbf{v}^{(0)}$  and here we employ  
 294 the convention that  $\sum_{s \in \mathcal{S}} v^{(0)}(s)q^{(0)}(s) = 1$ . This means that the reproductive value of a randomly  
 295 sampled mutant individual from its lineage is unity.

296 To summarize, under neutrality, the stable asymptotic distribution of mutants and the reproductive  
 297 value of individuals satisfy

$$q^{(0)}(s') = \sum_{s \in \mathcal{S}} w_1^{(0)}(s'|s)q^{(0)}(s) \quad (\mathbf{q}^{(0)} = \mathbf{W}^{(0)}\mathbf{q}^{(0)}), \quad (15a)$$

$$v^{(0)}(s) = \sum_{s' \in \mathcal{S}} v^{(0)}(s')w_1^{(0)}(s'|s) \quad (\mathbf{v}^{(0)} = \mathbf{v}^{(0)}\mathbf{W}^{(0)}), \quad (15b)$$

$$1 = \sum_{s \in \mathcal{S}} v^{(0)}(s)q^{(0)}(s) \quad (1 = \mathbf{v}^{(0)}\mathbf{q}^{(0)}), \quad (15c)$$

298 where  $\mathbf{v}^{(0)}$  is a row-vector with entries  $v^{(0)}(s)$  and  $\mathbf{q}^{(0)}$  is a column-vector with entries  $q^{(0)}(s)$ .

## 299 2.4 Invasion fitness as reproductive-value-weighted fitness

300 Equation (2) for the leading eigenvalue and eigenvector of the matrix  $\mathbf{A}$  can be left-multiplied on both  
 301 sides by any non-zero vector of weights. This allows to express  $\rho$  in terms of this vector of weights and  
 302  $\mathbf{A}$  and  $\mathbf{u}$ . If one chooses for the vector of weights the vector of neutral reproductive values  $\hat{\mathbf{v}}^{(0)}$  discussed  
 303 above, then invasion fitness can be expressed as

$$\rho = \frac{1}{V} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i=1}^{n_s} v^{(0)}(s')w_1(s'|s, i)q(i|s)q(s), \quad (16a)$$

304 where

$$V \equiv \sum_{s \in \mathcal{S}} v^{(0)}(s)q(s) \quad (16b)$$

305 (see Lehmann et al., 2016, Appendix C, eq.(C.5), for the proof). This representation of  $\rho$  is useful to  
 306 do concrete calculations. The intuition behind it is as follows. The inner sum, taken over  $i$ , represents

307 the reproductive-value-weighted average number of offspring in states  $s'$  given a parental mutant resides  
 308 in an  $s$ -group, where the average is taken over all possible mutant numbers experienced by the parental  
 309 mutant in an  $s$ -group. The middle sum takes the average over all states  $s$  in which mutants can reside in  
 310 the parental generation, and the outer sum takes the average over all possible states  $s'$  in which mutant  
 311 offspring can reside (possibly including parents through survival).

312 Hence, the numerator in eq.(16a) is the reproductive-value-weighted average individual 1-fitness of  
 313 a mutant individual randomly sampled from the mutant lineage, while the denominator  $V$  can be in-  
 314 terpreted (in force of eq.(15b)) as the reproductive-value-weighted average of the neutral 1-fitness of an  
 315 individual sampled from the asymptotic state distribution of the mutant lineage. Hence,  $\rho$  is the ratio of  
 316 the reproductive-value-weighted average fitness of a mutant individual and that of a mutant individual  
 317 under neutrality where both individuals are sampled from the same distribution. Note that in eq.(16a)  
 318 the quantities  $w_1(s'|s, i)$ ,  $q(s)$  and  $q(i|s)$  depend on  $\delta$  while  $v^{(0)}(s')$  does not.

319 Our goal is to compute from eq.(16a) the selection gradient and disruptive selection coefficients,

$$\rho^{(1)}(y) \equiv \left. \frac{\partial \rho}{\partial \delta} \right|_{\delta=0} \quad \text{and} \quad \rho^{(2)}(y) \equiv \frac{1}{2} \left. \frac{\partial^2 \rho}{\partial \delta^2} \right|_{\delta=0}. \quad (17)$$

320 These coefficients are all we need to classify singular strategies (Metz et al., 1996; Geritz et al., 1998).

321 Indeed, a singular strategy  $y^*$  satisfies

$$\rho^{(1)}(y^*) = 0. \quad (18)$$

322 This strategy is locally convergence stable (*i.e.*, a local attractor point of the evolutionary dynamics)  
 323 when

$$c(y^*) \equiv \left. \frac{d\rho^{(1)}(y)}{dy} \right|_{y=y^*} < 0. \quad (19)$$

324 Note that convergence stability hinges on mutants with small phenotypic deviation  $\delta$  invading and substi-  
 325 tuting residents (“invasion implies substitution”), which holds true when  $|\delta| \ll 1$  under the demographic  
 326 assumptions of our model (Rousset, 2004, pp. 196 and 206). Furthermore, the singular point is locally  
 327 uninvadable if

$$\rho^{(2)}(y^*) < 0. \quad (20)$$

328 A singular strategy can then be classified by determining the combination of signs of the disruptive  
 329 selection coefficient  $\rho^{(2)}(y^*)$  and the convergence stability coefficient  $c(y^*)$  at  $y^*$  (Metz et al., 1996;  
 330 Geritz et al., 1998).

### 311 3 Sensitivity analysis

#### 312 3.1 Eigenvalue perturbations

333 Using eq.(16a), as well as the normalization of reproductive values given in eq.(15c), we show in section  
 334 ?? in the Supplementary Material that the first-order perturbation of  $\rho$  with respect to  $\delta$  is given by

$$\rho^{(1)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i=1}^{n_s} v^{(0)}(s') w_1^{(1)}(s'|s, i) q^{(0)}(i|s) q^{(0)}(s). \quad (21)$$

Thus,  $\rho^{(1)}$  is simply a weighted perturbation of individual 1-fitnesses  $w_1$ . For the second-order perturbation of  $\rho$  with respect to  $\delta$ , given that  $\rho^{(1)} = 0$ , we find that

$$\rho^{(2)} = \rho^{(2w)} + \rho^{(2q)} + \rho^{(2r)} \quad (22a)$$

where

$$\rho^{(2w)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i=1}^{n_s} v^{(0)}(s') w_1^{(2)}(s'|s, i) q^{(0)}(i|s) q^{(0)}(s) \quad (22b)$$

$$\rho^{(2q)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i=1}^{n_s} v^{(0)}(s') w_1^{(1)}(s'|s, i) q^{(0)}(i|s) q^{(1)}(s) \quad (22c)$$

$$\rho^{(2r)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} \sum_{i=1}^{n_s} v^{(0)}(s') w_1^{(1)}(s'|s, i) q^{(1)}(i|s) q^{(0)}(s) \quad (22d)$$

(section ?? in the Supplementary Material). The first term, labelled  $\rho^{(2w)}$ , comes from the second-order perturbation of individual 1-fitnesses. The second term, labelled  $\rho^{(2q)}$ , comes from the first-order perturbation of the stationary distribution of mutants in the different states, and the third term, labelled  $\rho^{(2r)}$ , comes from the first-order perturbation of the stationary distribution of the number of mutants in any given state.

While eqs.(21) and (22) give some insights into how selection acts on mutants, in particular, they emphasize the role of selection on the distributions  $q(s)$  and  $q(i|s)$ , these expressions remain complicated as they involve weighted averages of fitness derivatives  $w_k^{(\ell)}(s'|s, i)$  ( $\ell = 1, 2$ ) over the neutral and perturbed mutant distributions  $q^{(1)}(i|s)$  and  $q^{(1)}(s)$ . To obtain more insightful expressions for these sensitivities, we express in the next section  $w_k(s'|s, i)$  for  $k = 1, 2, 3$  in terms of trait values. This will allow us to carry out rearrangements and simplifications of  $\rho^{(1)}$  and  $\rho^{(2)}$ .

## 3.2 Individual fitness functions

### 3.2.1 Individual 1-fitness

Consider a focal individual in a focal group in state  $s$  and denote by  $z_1$  the trait value of that individual. Suppose that the other  $n_s - 1$  neighbors adopt the trait values  $z_2, \dots, z_{n_s}$  and almost all individuals outside this focal group adopt the trait value  $z$ . Let then

$$w_{1,s'|s}(z_1, z_2, \dots, z_{n_s}, z) \quad (s', s \in \mathcal{S}, z_1, \dots, z_{n_s}, z \in \mathbb{R}) \quad (23a)$$

be the expected number of offspring in state  $s'$  that descend from a focal in state  $s$ . Equation (23a) expresses individual 1-fitness in terms of the phenotypes of all interacting individuals and will be referred to as an individual fitness function. It is a common building block of phenotypic models (see Frank, 1998; Rousset, 2004, for textbook treatments) and is the fitness that has to be considered if an exact description of a population is required, for instance, in an individual-based stochastic model, where each individual may have a different phenotype.

Because the only heterogeneity we consider are the different group states (we have no heterogeneity in individual states within groups), the individual 1-fitness function  $w_{1,s'|s}$  is invariant under permutations of  $z_2, \dots, z_{n_s}$ . With this, we can rewrite eq.(23a) as

$$w_{1,s'|s}(z_1, \mathbf{z}_{\{2, \dots, n_s\}}, z) \quad \text{or} \quad w_{1,s'|s}(z_1, \mathbf{z}_{-\{1\}}, z), \quad (23b)$$

363 where the set-subscripted vector  $\mathbf{z}_{\{2, \dots, n_s\}}$  represents a vector of length  $n_s - 1$  in which each of  $z_2, \dots, z_{n_s}$   
 364 appears in an arbitrary order but exactly once. The subscript  $-\{1\}$  is used as a shorthand notation of  
 365 the set difference  $\{1, 2, \dots, n_s\} \setminus \{1\} = \{2, \dots, n_s\}$  and used when the baseline set  $\{1, 2, \dots, n_s\}$  is clear  
 366 from the context. Therefore,  $\mathbf{z}_{-\{1\}}$  is the same as  $\mathbf{z}_{\{2, \dots, n_s\}}$ . Similarly, in the following the subscript  
 367  $-\{1, 2\}$  represents the set difference  $\{1, 2, \dots, n_s\} \setminus \{1, 2\} = \{3, \dots, n_s\}$ , and so forth. For example,  
 368  $\mathbf{z}_{-\{1, 2\}} = \mathbf{z}_{\{3, \dots, n_s\}}$  represents a vector of length  $n_s - 2$  in which each of  $z_3, \dots, z_{n_s}$  appears in an  
 369 arbitrary order but exactly once.

370 For our two allele model  $z_i, z \in \{x, y\}$ , we can write a mutant's individual 1-fitness as

$$w_1(s'|s, i) = w_{1, s'|s}(x, \underbrace{x, \dots, x}_{i-1}, \underbrace{y, \dots, y}_{n_s-i}). \quad (24)$$

371 By using the chain rule and permutation invariance, the zeroth, first, and second order perturbations of  
 372  $w_1(s'|s, i)$  with respect to  $\delta$  are

$$w_1^{(0)}(s'|s, i) = w_{1, s'|s}, \quad (25a)$$

$$w_1^{(1)}(s'|s, i) = \frac{\partial w_{1, s'|s}}{\partial z_1} + (i-1) \frac{\partial w_{1, s'|s}}{\partial z_2}, \quad (25b)$$

$$w_1^{(2)}(s'|s, i) = \frac{1}{2} \frac{\partial^2 w_{1, s'|s}}{\partial z_1^2} + \frac{i-1}{2} \frac{\partial^2 w_{1, s'|s}}{\partial z_2^2} + (i-1) \frac{\partial^2 w_{1, s'|s}}{\partial z_1 \partial z_2} + \frac{(i-1)(i-2)}{2} \frac{\partial^2 w_{1, s'|s}}{\partial z_2 \partial z_3}. \quad (25c)$$

373 Here, all functions and derivatives that appear without arguments are evaluated at the resident popu-  
 374 lation,  $(y, \dots, y)$ , a convention we adopt throughout. Note that some derivatives appearing in eqs.(25)  
 375 are ill-defined for  $n_s = 1$  and  $n_s = 2$ , but they are always nullified by the factors  $(i-1)$  and  $(i-1)(i-2)$ .  
 376 Thus, by simply neglecting these ill-defined terms, eq.(25) is valid for any  $1 \leq i \leq n_s$ .

### 377 3.2.2 Individual 2- and 3-fitness

378 Consider again a focal individual with trait value  $z_1$  in a group in state  $s$  in which the  $n_s - 1$  group  
 379 neighbors have the trait values  $\mathbf{z}_{-\{1\}} = \mathbf{z}_{\{2, \dots, n_s\}}$  in a population that is otherwise monomorphic for  $z$ .

380 For this setting, we define two types of individual 2-fitness functions. First, let

$$w_{2, s'|s}^I(z_1, \mathbf{z}_{-\{1\}}, z) \quad (s', s \in \mathcal{S}, z_1, \dots, z_{n_s}, z \in \mathbb{R}) \quad (26)$$

381 be the expected number of offspring in state  $s'$  that descend from the focal individual and that have  
 382 a random neighbor that also descends from the focal individual (see Figure 2). Intuitively speaking,  
 383  $w_{2, s'|s}^I$  measures the number of sibling pairs produced by a focal individual. Hence, when one considers  
 384 the reproductive process backward in time,  $w_{2, s'|s}^I > 0$  means that coalescence events do occur. We call  
 385  $w_{2, s'|s}^I$  the “same-parent individual 2-fitness”, because the offspring involved in it descend from the same  
 386 individual.

387 Second, for  $n_s \geq 2$  consider a neighbor of the focal individual with trait value  $z_2$ , called the *target*  
 388 individual, in a group in which the remaining  $n_s - 2$  neighbors have the trait profile  $\mathbf{z}_{-\{1, 2\}} = \mathbf{z}_{\{3, \dots, n_s\}}$ .

389 Let

$$w_{2, s'|s}^II(z_1, z_2, \mathbf{z}_{-\{1, 2\}}, z) \quad (s', s \in \mathcal{S}, z_1, \dots, z_{n_s}, z \in \mathbb{R}) \quad (27)$$

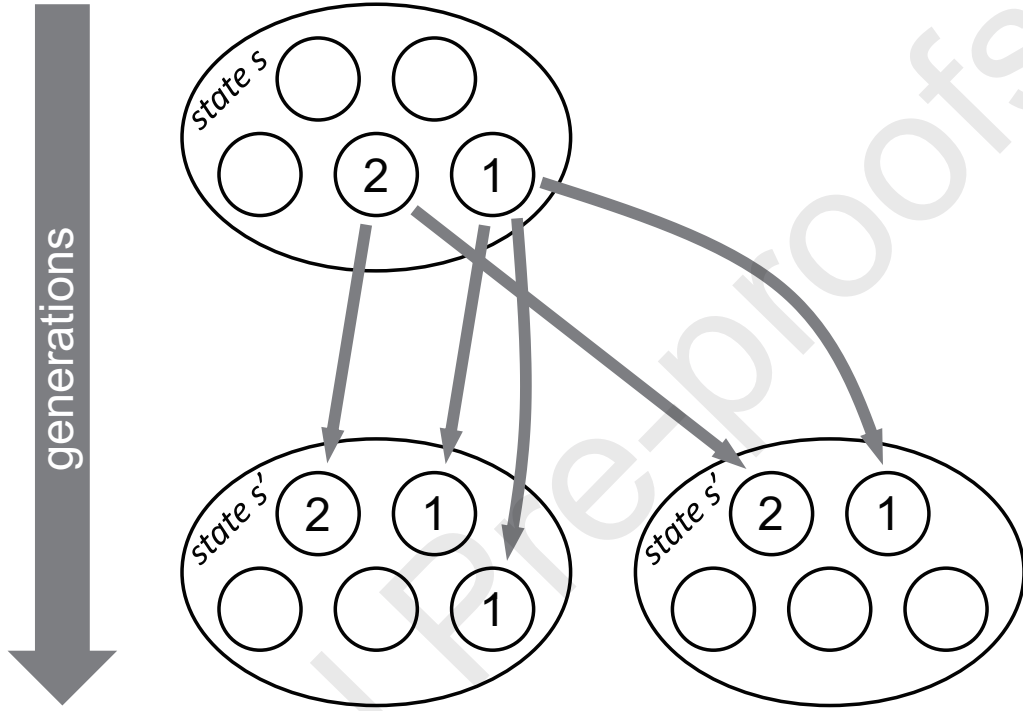


Figure 2: A schematic example of how we calculate the individual 2-fitnesses  $w_2^I$  and  $w_2^{II}$ . Gray arrows represent reproduction (or survival). We label by “1” the focal individual with trait value  $z_1$  in the parental generation and its offspring (possibly including self through survival) in the following generation. Similarly, we label by “2” the target individual with trait value  $z_2$  in the parental generation and its offspring (possibly including self through survival) in the offspring generation. Because each of the two descendants of the focal individual in the bottom-left group (those with label “1”) finds with probability  $1/4$  a random neighbor whose label is “1”, whereas the one descendant of the focal individual in the bottom-right group in the offspring generation finds no neighbors whose label is “1”, the same-parent individual 2-fitness of the focal is calculated as  $w_{2,s'|s}^I(z_1, z_{-\{1\}}, z) = 2 \cdot (1/4) + 1 \cdot (0/4) = 1/2$ . Similarly, because each of the two descendants of the focal individual in the bottom-left group finds a random neighbor whose label is “2” with probability  $1/4$ , and because the one descendant of the focal in the bottom-right group finds a random neighbor whose label is “2” with probability  $1/4$ , the different-parent individual 2-fitness of the focal is  $w_{2,s'|s}^{II}(z_1, z_2, z_{-\{1,2\}}, z) = 2 \cdot (1/4) + 1 \cdot (1/4) = 3/4$ .



390 be the expected number of offspring in state  $s'$  that descend from the focal individual with trait value  $z_1$   
 391 and that have a random neighbor that descends from the *target* individual with trait value  $z_2$  (see Figure  
 392 2). We call  $w_{2,s'|s}^{\text{II}}(z_1, z_2, \mathbf{z}_{-\{1,2\}}, z)$  the “different-parent individual 2-fitness”, because the offspring  
 393 involved in it descend from two different pre-selected individuals, which can thus collectively be thought  
 394 of as the focal set of individuals under consideration. We note that this fitness function is invariant  
 395 under the permutation of the trait values  $z_1$  and  $z_2$  of individuals from the focal set<sup>2</sup> and it is also  
 396 invariant under the permutation of the trait values in  $\mathbf{z}_{-\{1,2\}}$ . But since  $w_{2,s'|s}^{\text{II}}(z_1, z_2, \mathbf{z}_{-\{1,2\}}, z)$  counts  
 397 the offspring number (of a certain type) per individual with trait  $z_1$ ,  $w_{2,s'|s}^{\text{II}}(z_1, z_2, \mathbf{z}_{-\{1,2\}}, z)$  is a type of  
 398 individual fitness.

399 Using the notation of mutant and resident phenotypes we have for  $2 \leq i \leq n_s$  that

$$w_2(s'|s, i) = w_{2,s'|s}^{\text{I}}(x, \underbrace{x, \dots, x}_{i-1}, \underbrace{y, \dots, y}_{n_s-i}, y) + (i-1)w_{2,s'|s}^{\text{II}}(x, x, \underbrace{x, \dots, x}_{i-2}, \underbrace{y, \dots, y}_{n_s-i}), \quad (28)$$

400 because a mutant neighbor of an offspring of a focal mutant either descends from the focal itself or is an  
 401 offspring of one of the  $i-1$  mutant neighbors of the focal. The zeroth and first order perturbations of  
 402  $w_2(s'|s, i)$  with respect to  $\delta$  are given by

$$w_2^{(0)}(s'|s, i) = w_{2,s'|s}^{\text{I}} + (i-1)w_{2,s'|s}^{\text{II}}, \quad (29a)$$

$$w_2^{(1)}(s'|s, i) = \frac{\partial w_{2,s'|s}^{\text{I}}}{\partial z_1} + (i-1) \frac{\partial w_{2,s'|s}^{\text{I}}}{\partial z_2} + 2(i-1) \frac{\partial w_{2,s'|s}^{\text{II}}}{\partial z_1} + (i-1)(i-2) \frac{\partial w_{2,s'|s}^{\text{II}}}{\partial z_3}, \quad (29b)$$

403 where the derivatives  $\partial w_{2,s'|s}^{\text{II}}/\partial z_1$  and  $\partial w_{2,s'|s}^{\text{II}}/\partial z_2$  (the latter is equal to  $\partial w_{2,s'|s}^{\text{II}}/\partial z_1$  due to the per-  
 404 mutation invariance, and hence the coefficient “2” appears in eq.(29b)) involve the trait values of the  
 405 individuals of the focal set and  $\partial w_{2,s'|s}^{\text{II}}/\partial z_3$  involves the trait values of a third individual. Note that  
 406 some derivatives in eqs.(29) are ill-defined for  $n_s = 1, 2$  but they are always nullified by the factor  $(i-1)$   
 407 or  $(i-1)(i-2)$ . Thus, by simply neglecting these ill-defined terms eq.(29) is valid for any  $1 \leq i \leq n_s$ .

408 Following the same line of reasoning as for individual 1- and 2-fitness, we similarly define three differ-  
 409 ent types of individual 3-fitness. See section ?? in the Supplementary Material for more detailed expla-  
 410 nations. Specifically,  $w_{3,s'|s}^{\text{I}}(z_1, \mathbf{z}_{-\{1\}}, z)$  is defined as the expected number of offspring in state  $s'$  that  
 411 descend from a focal individual in state  $s$  with trait value  $z_1$  and that have two random neighbors sampled  
 412 without replacement both descending from the focal individual. Furthermore,  $w_{3,s'|s}^{\text{II}}(z_1, z_2, \mathbf{z}_{-\{1,2\}}, z)$  is  
 413 defined as the expected number of offspring in state  $s'$  that descend from the focal individual in state  $s$   
 414 with trait value  $z_1$  and with two random neighbors sampled without replacement both descending from  
 415 a target individual with trait value  $z_2$ . Finally,  $w_{3,s'|s}^{\text{III}}(z_1, z_2, z_3, \mathbf{z}_{-\{1,2,3\}}, z)$  is defined as the expected  
 416 number of offspring in state  $s'$  that descend from the focal individual in state  $s$  with trait value  $z_1$  with  
 417 two random neighbors sampled without replacement, one of which descends from a first target individual

<sup>2</sup>This can be seen by noting that when the focal and target individual from the focal set leave a realized number of  $A_1$  and  $A_2$  offspring, respectively, in the same group of size  $n_s$ , then this group contributes to the focal’s 2-fitness  $w_2^{\text{II}}$  with  $A_1$  (the number of focal’s offspring) times  $A_2/(n_s-1)$  (the probability that a random neighbor of focal’s offspring is the target’s offspring), which equals to  $A_1 A_2/(n_s-1)$ . Since  $A_1 A_2/(n_s-1)$  is symmetric with respect to  $A_1$  and  $A_2$ , changing the roles of the focal and target individual does not alter the realized fitness count. The same logic applies when the focal and target individuals leave offspring to different groups, because in this case the counts per group are simply summed over all groups. A single individual’s  $w_2^{\text{II}}$  is the expectation of such counts over all realizations of offspring number in the same and different groups (where the expectation is taken over all single generation stochastic events affecting reproduction and survival), and the invariance holds because it holds for each realization.

with trait value  $z_2$  and the other descends from a second target individual with trait value  $z_3$ . With these definitions, we show in section ?? in the Supplementary Material that the zeroth-order perturbation of 3-fitness  $w_3(s'|s, i)$  with respect to  $\delta$  is given by

$$w_3^{(0)}(s'|s, i) = w_{3,s'|s}^I + 3(i-1)w_{3,s'|s}^{II} + \frac{(i-1)(i-2)}{2}w_{3,s'|s}^{III}, \quad (30)$$

where  $w_{3,s'|s}^I, w_{3,s'|s}^{II}, w_{3,s'|s}^{III}$  are those three different individual 3-fitness functions evaluated in a resident monomorphic population,  $(y, \dots, y)$ .

### 3.3 Sensitivity results

We now write  $\rho^{(1)}$  and  $\rho^{(2)}$  from Section 3.1 in terms of the just defined derivatives of the individual fitness functions.

#### 3.3.1 Selection gradient

By substituting eq.(25b) into eq.(21) we obtain

$$\rho^{(1)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^{(0)}(s') \left[ \frac{\partial w_{1,s'|s}}{\partial z_1} + \sum_{i=1}^{n_s} (i-1) \frac{\partial w_{1,s'|s}}{\partial z_2} q^{(0)}(i|s) \right] q^{(0)}(s), \quad (31)$$

and by applying eq.(8) to the second term in square brackets we obtain

$$\rho^{(1)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^{(0)}(s') \left[ \frac{\partial w_{1,s'|s}}{\partial z_1} + (n_s - 1) \frac{\partial w_{1,s'|s}}{\partial z_2} r_2^{(0)}(s) \right] q^{(0)}(s). \quad (32)$$

Thus, in order to be able to evaluate  $\rho^{(1)}$  it is sufficient to compute the neutral pairwise relatedness  $r_2^{(0)}(s)$  while the explicit evaluation of the  $q^{(0)}(i|s)$  distribution is not needed. It is indeed a well-known result that the selection gradient  $\rho^{(1)}$  can be expressed in terms of reproductive values and relatedness-weighted fitness derivatives (see Frank, 1998; Rousset, 2004, for textbook treatments) and where  $q^{(0)}(s)$  and  $v^{(0)}(s)$  are given by eq.(15) with  $w_{1,s'|s} = w_1^{(0)}(s'|s)$ .

Equation (32) can be interpreted as the expected first-order effect of all members of a lineage changing to expressing the mutant allele on the fitness of a focal individual that is a random member of this lineage. The recipient is sampled from state  $s$  with probability  $q^{(0)}(s)$  and the derivative in the first term in the square brackets of  $\rho^{(1)}$  is the effect of the focal changing its own trait value on its individual fitness. The derivative in the second term in the square brackets describes the effect of the group neighbors of the focal changing their trait value on the focal's individual fitness. This term is weighted by pairwise neutral relatedness since this is the likelihood that any such neighbor carries the same allele as the focal in the neutral process. Equation (32) is the inclusive fitness effect of mutating from the resident to the mutant allele for a demographically and/or environmentally structured population and the term in brackets can be thought of as the state- $s$ -specific inclusive fitness effect on offspring in state  $s'$ . Equation (32) has previously been derived by Lehmann et al. (2016, Box 2) and is in agreement with eqs.(26) and (27) of Rousset and Ronce (2004), who derived the first-order perturbation  $\rho^{(1)}$  in terms of other quantities under the assumptions of fluctuating group size.

447 We show in section ?? in the Supplementary Material that by substituting eq.(29a) into eq.(??),  
448 pairwise relatedness (eq.(8)) under neutrality satisfies the recursion

$$r_2^{(0)}(s') = \frac{1}{q^{(0)}(s')} \sum_{s \in \mathcal{S}} \left[ w_{2,s'|s}^I + (n_s - 1) w_{2,s'|s}^{II} r_2^{(0)}(s) \right] q^{(0)}(s). \quad (33)$$

449 This expression for  $r_2^{(0)}(s)$ , formulated in terms of individual 2-fitnesses, is novel but is in full agreement  
450 with previous results. In particular, eq.(29) of Rousset and Ronce (2004) can be shown to reduce to  
451 eq.(33) (see section ?? in the Supplementary Material for a proof of this connection).

452 In summary, consistent with well established results, we present a biologically meaningful represen-  
453 tation of  $\rho^{(1)}$ . The ingredients in this representation can be obtained from the three systems of linear  
454 equations defined by eqs.(15a), (15b) and (33). This system of equations is fully determined once the  
455 individual  $k$ -fitnesses functions for  $k = 1, 2$ , namely,  $w_{1,s'|s}$ ,  $w_{2,s'|s}^I$ , and  $w_{2,s'|s}^{II}$  are specified for a resident  
456 population, and the  $k$ -fitness functions can usually be evaluated once a life-cycle has been specified. The  
457 dimension of this combined equation system has maximally three times the number of states  $N$ . This is  
458 significantly lower than the dimension of the matrix  $\mathbf{A}$  we began with, especially, if group size  $> 10$ . In  
459 the next section, we extend these results to the disruptive selection coefficient.

### 460 3.3.2 Disruptive selection coefficient

461 Assuming that  $\rho^{(1)} = 0$  and substituting eq.(25) into eq.(22), rearrangements given in section ?? in the  
462 Supplementary Material show that

$$\begin{aligned} \rho^{(2w)} = \frac{1}{2} \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^{(0)}(s') & \left[ \frac{\partial^2 w_{1,s'|s}}{\partial z_1^2} + (n_s - 1) \frac{\partial^2 w_{1,s'|s}}{\partial z_2^2} r_2^{(0)}(s) \right. \\ & \left. + 2(n_s - 1) \frac{\partial^2 w_{1,s'|s}}{\partial z_1 \partial z_2} r_2^{(0)}(s) + (n_s - 1)(n_s - 2) \frac{\partial^2 w_{1,s'|s}}{\partial z_2 \partial z_3} r_3^{(0)}(s) \right] q^{(0)}(s) \end{aligned} \quad (34a)$$

$$\rho^{(2q)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^{(0)}(s') \left[ \frac{\partial w_{1,s'|s}}{\partial z_1} + (n_s - 1) \frac{\partial w_{1,s'|s}}{\partial z_2} r_2^{(0)}(s) \right] q^{(1)}(s) \quad (34b)$$

$$\rho^{(2r)} = \sum_{s' \in \mathcal{S}} \sum_{s \in \mathcal{S}} v^{(0)}(s') \left[ (n_s - 1) \frac{\partial w_{1,s'|s}}{\partial z_2} r_2^{(1)}(s) \right] q^{(0)}(s). \quad (34c)$$

463 Equation (34a) depends on four different types of qualitative effects on the fitness of a focal individual:  
464 (i) The second-order effect on own fitness of the focal changing its trait value, which is positive, and then  
465 contributes to disruptive selection, if fitness is convex in own phenotype. (ii) The second-order effect  
466 resulting from the neighbors of the focal changing their trait values, which is positive if the focal's fitness  
467 is convex in phenotype of group neighbors. This contributes to disruptive selection proportionally to  
468 pairwise relatedness  $r_2^{(0)}(s)$ , since this is the likelihood that a random neighbor carries the same allele as  
469 the focal individual. (iii) The joint effect of the focal individual and any of its neighbors changing their  
470 trait value, which is positive if the effect of increased trait values of own and others complement each  
471 other. This again contributes to disruptive selection in proportion to the likelihood that any neighbor  
472 is a mutant. (iv) The joint effect of pairs of neighbors of the focal changing their trait values, which is  
473 positive if the effect of increased trait values in neighbors complement each other. This contributes to  
474 disruptive selection with the probability  $r_3^{(0)}(s)$  that a pair of neighbors carry the the same allele as the  
475 focal individual.

Equation (34b) depends, for each state, on the product of the state specific inclusive fitness effect (recall the term in brackets in eq.(32)) multiplied with the perturbation  $q^{(1)}(s)$  of the group state probability. A contribution to disruptive selection occurs if the mutant allele increases its probability to be in a given state while simultaneously increasing the individual fitness of its carriers in that state. Similarly, eq.(34c) depends, for each state, on the product of the state specific indirect effect of others on own fitness (recall the second term in brackets in eq.(32)) and the relatedness perturbation  $r_2^{(1)}(s)$ . This contributes to disruptive selection if the mutant allele increases the probability that a focal has mutant neighbors while simultaneously increasing the individual fitness of those neighbors. Finally, we note that in the presence of a single state (*i.e.*, no state heterogeneity among groups)  $\rho^{(2q)} = 0$ . This is the case in all previously published expressions for the disruptive selection coefficient (Day, 2001; Ajar, 2003; Wakano and Lehmann, 2014; Mullan et al., 2016), which therefore reduce to  $\rho^{(2w)} + \rho^{(2r)}$  as defined by eqs.(34a) and (34c).

In order to compute  $\rho^{(2)}$  we need, in addition to eqs.(15a), (15b) and (33), expressions for  $q^{(1)}(s)$ ,  $r_3^{(0)}(s)$ , and  $r_2^{(1)}(s)$ . In section ?? in the Supplementary Material, we derive the corresponding recursions for  $\rho^{(1)} = 0$ . In particular, we show that  $q^{(1)}(s)$  satisfies

$$q^{(1)}(s') = \sum_{s \in \mathcal{S}} \left[ \frac{\partial w_{1,s'|s}}{\partial z_1} + (n_s - 1) \frac{\partial w_{1,s'|s}}{\partial z_2} r_2^{(0)}(s) \right] q^{(0)}(s) + \sum_{s \in \mathcal{S}} w_{1,s'|s} q^{(1)}(s) \quad (35)$$

and that  $r_3^{(0)}(s)$  satisfies

$$r_3^{(0)}(s') = \frac{1}{q^{(0)}(s')} \sum_{s \in \mathcal{S}} \left[ w_{3,s'|s}^I + 3(n_s - 1) w_{3,s'|s}^{II} r_2^{(0)}(s) + \frac{(n_s - 1)(n_s - 2)}{2} w_{3,s'|s}^{III} r_3^{(0)}(s) \right] q^{(0)}(s). \quad (36)$$

Finally, we show that  $r_2^{(1)}(s)$  satisfies the recursion

$$\begin{aligned} r_2^{(1)}(s') &= \frac{1}{q^{(0)}(s')} \sum_{s \in \mathcal{S}} \left[ \frac{\partial w_{2,s'|s}^I}{\partial z_1} + (n_s - 1) \frac{\partial w_{2,s'|s}^I}{\partial z_2} r_2^{(0)}(s) \right. \\ &\quad \left. + 2(n_s - 1) \frac{\partial w_{2,s'|s}^{II}}{\partial z_1} r_2^{(0)}(s) + (n_s - 1)(n_s - 2) \frac{\partial w_{2,s'|s}^{II}}{\partial z_3} r_3^{(0)}(s) \right] q^{(0)}(s) \\ &\quad + \frac{1}{q^{(0)}(s')} \sum_{s \in \mathcal{S}} \left[ (n_s - 1) w_{2,s'|s}^{II} r_2^{(1)}(s) \right] q^{(0)}(s) \\ &\quad + \frac{1}{q^{(0)}(s')} \sum_{s \in \mathcal{S}} \left[ w_{2,s'|s}^I + (n_s - 1) w_{2,s'|s}^{II} r_2^{(0)}(s) \right] q^{(1)}(s) \\ &\quad - r_2^{(0)}(s') \frac{q^{(1)}(s')}{q^{(0)}(s')}. \end{aligned} \quad (37)$$

Equation (35) shows that  $q^{(1)}(s)$  depends on the state-specific inclusive fitness effect (compare the first summand in eq.(35) to the term in brackets in eq.(32)). Thus, the probability that a mutant is in a certain state  $s$  increases with its state-specific inclusive fitness effect. Equation (36) for the three-way relatedness coefficient depends on  $w_{3,s'|s}^I$ ,  $w_{3,s'|s}^{II}$  and  $w_{3,s'|s}^{III}$  and it is a generalization of the pairwise relatedness coefficient given by eq.(33). Finally, eq.(37) shows that  $r_2^{(1)}(s)$  depends on direct and indirect effects on  $w_{2,s'|s}^I$  and  $w_{2,s'|s}^{II}$ . Note, that eq.(37) together with eqs.(15a), (15b), (33), (35), and (36) form a linear system of equations with a dimension equal to six times the number of states  $N$ . Its solution allows us to determine the disruptive selection coefficient  $\rho^{(2)}$ . This system of equations in turn is fully

501 determined once the the  $k$ -fitnesses for  $k = 1, 2, 3$  are specified for a resident population, namely,  $w_{1,s'|s}$ ,  
 502  $w_{2,s'|s}^I$ ,  $w_{2,s'|s}^{II}$ ,  $w_{3,s'|s}^I$ ,  $w_{3,s'|s}^{II}$ , and  $w_{3,s'|s}^{III}$ .

503 In general, if the state space  $\mathcal{S}$  is large, solving this system of equations (and those needed for  $\rho^{(1)}$ )  
 504 may be complicated. Similarly, the 2- and 3-fitnesses may be complicated. We here give two directions  
 505 for approximating  $\rho^{(1)}$  and  $\rho^{(2)}$ . First, individual fitness generally depends on vital rates like fecundity  
 506 and survival (see eqs.(45)–(46) for a concrete example) and variation of these vital rates may have small  
 507 effects on fitness, which induces weak selection regardless of the magnitude of the phenotypic deviation  
 508  $\delta$  (called “ $\omega$ -weak selection” by Wild and Traulsen, 2007, and “weak payoff” by Van Cleve, 2015). For  
 509 “weak payoffs” (or  $\omega$ -weak selection),  $\rho^{(2)} \approx \rho^{(2w)}$  because one can neglect  $\rho^{(2q)}$  and  $\rho^{(2r)}$ . Indeed,  
 510 both these terms involve products of marginal changes in fitness, which implies that these products  
 511 are of second-order effect under weak payoffs and first-order effects will thus dominate. Since  $\rho^{(2w)}$   
 512 only involves first-order effects it dominates the disruptive selection coefficient. See Van Cleve (2015)  
 513 for an applications of this approximation to  $\rho^{(1)}$  and Wakano and Lehmann (2014) and Mullon et al.  
 514 (2016) to  $\rho^{(2)}$ . Second, variation of vital rates and fitness across states may be small under certain  
 515 biological scenarios in which case one may apply a so-called small noise approximation (e.g., Tuljapurkar,  
 516 1990; Caswell, 2001) to  $\rho^{(1)}$  and  $\rho^{(2)}$ , whereby the magnitude of variation are taken to be small. This  
 517 simplification has been used to approximate  $\rho^{(1)}$  in a multi-species meta-population model that is covered  
 518 by our general model (Mullon and Lehmann, 2018), but has not yet been applied to  $\rho^{(2)}$ , which would  
 519 be interesting in future work.

520 Finally, for some specific life-cycles the 2- and 3-fitness functions can be expressed in terms of com-  
 521 ponents of the 1-fitness functions. This greatly simplifies the calculations because all recursions can then  
 522 be solved explicitly. We will now provide an application of our model along this latter line, which still  
 523 covers a large class of models.

## 524 4 Application to a lottery model with spatial heterogeneity

525 We now study a lottery model with overlapping generations and spatial heterogeneity. Such a model  
 526 can be formulated for a variety of life-cycles and we here take a hierarchical approach in which we make  
 527 increasingly more specific assumptions. Accordingly, this section is divided in three parts. Section 4.1  
 528 provides general results about the components of the selection coefficients based on the assumption of  
 529 fixed group states  $s$ . In Section 4.2 we introduce two forms of population regulation resulting in hard  
 530 and soft selection, respectively. Finally, in Section 4.3 we specify an explicit fitness function which allows  
 531 us to present a fully worked example for the effect of group size and spatial heterogeneity on disruptive  
 532 selection.

### 533 4.1 Spatial lottery model

#### 534 4.1.1 Decomposition into philatric and dispersal components

535 We start by making the following three assumptions. (i) Group states  $s$  describe environmental variables  
 536 that do not change in time. Thus, group states are fixed and we here refer to them as habitats. By  $\pi_s$   
 537 we denote the relative proportion of groups in habitat  $s$ , hence  $\sum_{s \in \mathcal{S}} \pi_s = 1$ . (ii) Individuals survive

538 independently of each other with probability  $\gamma_s < 1$  to the next time step in a group in habitat  $s$ . Note  
 539 that  $\gamma_s = 0$  corresponds to the Wright-Fisher update where all adults die simultaneously, and that  $\gamma_s \sim 1$   
 540 corresponds to the Moran update where at most one individual dies in a group. (iii) Dispersal occurs  
 541 individually and independently to a random destination (no propagule dispersal). (iv) The evolving trait  
 542 does not affect survival. With these assumptions we can decompose the 1-fitness of a focal individual  
 543 into a philopatric and dispersal component as

$$w_{1,s'|s}(z_1, \mathbf{z}_{-\{1\}}, z) = \begin{cases} \underbrace{w_{1,s|s}^p(z_1, \mathbf{z}_{-\{1\}}, z)}_{\text{philopatric}} + \underbrace{w_{1,s|s}^d(z_1, \mathbf{z}_{-\{1\}}, z)}_{\text{dispersal}} & (s' = s) \\ \underbrace{w_{1,s'|s}^d(z_1, \mathbf{z}_{-\{1\}}, z)}_{\text{dispersal}} & (s' \neq s). \end{cases} \quad (38a)$$

544 Offspring that have left from their natal group and successfully settled elsewhere are counted in the dis-  
 545 persal component  $w_{1,s'|s}^d(z_1, \mathbf{z}_{-\{1\}}, z)$ . The philopatric component  $w_{1,s|s}^p(z_1, \mathbf{z}_{-\{1\}}, z)$  counts the number  
 546 of non-dispersing offspring, possibly including self through survival. Thus, we further decompose the  
 547 philopatric part into a survival part and a reproduction part as

$$w_{1,s|s}^p(z_1, \mathbf{z}_{-\{1\}}, z) = \underbrace{\gamma_s}_{\text{philopatric survival}} + \underbrace{(1 - \gamma_s)w_{1,s|s}^{\text{pr}}(z_1, \mathbf{z}_{-\{1\}}, z)}_{\text{philopatric reproduction}}. \quad (38b)$$

548 Similarly, for the dispersal part we write

$$w_{1,s'|s}^d(z_1, \mathbf{z}_{-\{1\}}, z) = \underbrace{(1 - \gamma_{s'})w_{1,s'|s}^{\text{dr}}(z_1, \mathbf{z}_{-\{1\}}, z)}_{\text{dispersal reproduction}}. \quad (38c)$$

#### 549 4.1.2 General results for spatial lottery model

550 For this model, we explicitly compute the components of the selection gradient and disruptive selection  
 551 coefficient in sections ?? and ?? of the Supplementary Material. In particular, we show that the prob-  
 552 ability that a random lineage member is sampled from a group in state  $s$  under neutrality equals the  
 553 weighted frequency

$$q^{(0)}(s) = \frac{\pi_s n_s}{\sum_{s' \in \mathcal{S}} \pi_{s'} n_{s'}}, \quad (39)$$

554 where the weights are the number of individuals in the group state.

555 For the reproductive value, it is instructive to provide a formula for  $v^{(0)}(s')q^{(0)}(s)$ , because the  
 556 reproductive value always appears as a product with  $q^{(0)}(s)$  in  $\rho^{(1)}$  (eq.(32)) and  $\rho^{(2)}$  (eq.(34)) (the only  
 557 exception is eq.(34b), but see the discussion below eq.(43)). This product is given by

$$v^{(0)}(s')q^{(0)}(s) = \frac{w_{1,s|s'}^{\text{dr}}}{(1 - \gamma_{s'})(1 - w_{1,s'|s'}^{\text{pr}})(1 - w_{1,s|s}^{\text{pr}})} \bigg/ \left( \sum_{s'' \in \mathcal{S}} \frac{w_{1,s''|s''}^{\text{dr}}}{(1 - \gamma_{s''})(1 - w_{1,s''|s''}^{\text{pr}})^2} \right) \quad (40)$$

558 (section ?? in the Supplementary Material). Furthermore, the neutral pairwise relatedness coefficient  
 559 equals

$$r_2^{(0)}(s) = \frac{2\gamma_s w_{1,s|s}^{\text{pr}} + (1 - \gamma_s) \left( w_{1,s|s}^{\text{pr}} \right)^2}{n_s(1 + \gamma_s) - 2(n_s - 1)\gamma_s w_{1,s|s}^{\text{pr}} - (n_s - 1)(1 - \gamma_s) \left( w_{1,s|s}^{\text{pr}} \right)^2} \quad (41)$$

(section ?? in the Supplementary Material). The general solution for  $r_3^{(0)}(s)$  remains complicated (see eq.(??) for the full expression), but for special cases it is

$$r_3^{(0)}(s) = \begin{cases} \frac{\left(w_{1,s|s}^{\text{pr}}\right)^3 \left[n_s + 2(n_s - 1) \left(w_{1,s|s}^{\text{pr}}\right)^2\right]}{\left[n_s - (n_s - 1) \left(w_{1,s|s}^{\text{pr}}\right)^2\right] \left[n_s^2 - (n_s - 1)(n_s - 2) \left(w_{1,s|s}^{\text{pr}}\right)^3\right]} & \text{(Wright-Fisher process, } \gamma_s = 0), \\ \frac{2 \left(w_{1,s|s}^{\text{pr}}\right)^2}{\left[n_s - (n_s - 1)w_{1,s|s}^{\text{pr}}\right] \left[n_s - (n_s - 2)w_{1,s|s}^{\text{pr}}\right]} & \text{(Moran process, } \gamma_s \sim 1). \end{cases} \quad (42)$$

If the resident trait value is equal to the singular strategy where  $\rho^{(1)} = 0$ , then the first-order perturbation of the stationary mutant distribution is

$$q^{(1)}(s) = \left\{ \frac{1}{1 - w_{1,s|s}^{\text{pr}}} \left[ \frac{\partial w_{1,s|s}^{\text{pr}}}{\partial z_1} + (n_s - 1) \frac{\partial w_{1,s|s}^{\text{pr}}}{\partial z_2} r_2^{(0)}(s) \right] - \sum_{s' \in \mathcal{S}} \frac{1}{1 - w_{1,s'|s'}^{\text{pr}}} \left[ \frac{\partial w_{1,s'|s'}^{\text{pr}}}{\partial z_1} + (n_{s'} - 1) \frac{\partial w_{1,s'|s'}^{\text{pr}}}{\partial z_2} r_2^{(0)}(s') \right] q^{(0)}(s') \right\} q^{(0)}(s) \quad (43)$$

(section ?? in the Supplementary Material). Note that we can obtain the fraction  $q^{(1)}(s)/q^{(0)}(s)$  by dividing both sides of eq.(43) by  $q^{(0)}(s)$ , which, when combined with eq.(40), allows to directly obtain the product  $v^{(0)}(s')q^{(1)}(s)$ . This quantity is required to compute eq.(34b). Finally, for  $\rho^{(1)} = 0$  we have

$$r_2^{(1)}(s) = 2r_2^{(0)}(s) \frac{\gamma_s + (1 - \gamma_s)w_{1,s|s}^{\text{pr}}}{2\gamma_s w_{1,s|s}^{\text{pr}} + (1 - \gamma_s) \left(w_{1,s|s}^{\text{pr}}\right)^2} \times \left\{ \left[ 1 + (n_s - 1)r_2^{(0)}(s) \right] \frac{\partial w_{1,s|s}^{\text{pr}}}{\partial z_1} + (n_s - 1) \left[ 2r_2^{(0)}(s) + (n_s - 2)r_3^{(0)}(s) \right] \frac{\partial w_{1,s|s}^{\text{pr}}}{\partial z_2} \right\} \quad (44)$$

(see Section ?? in the Supplementary Material where we also make the connection to previous work).

With eqs.(40) and (41) we can compute the first-order perturbation of invasion fitness, eq.(32), explicitly given specific life-cycle assumptions (since all recursions have been solved). Similarly, under the assumption that  $\rho^{(1)} = 0$ , and with eqs.(39)–(44) in hand, we can explicitly compute the second-order perturbation of invasion fitness, eq.(34).

## 4.2 Fecundity selection under two different forms of density regulation

We further refine our assumptions in order to arrive at two life-cycles with concrete expressions for  $w_{1,s|s}^{\text{pr}}$  and  $w_{1,s'|s'}^{\text{dr}}$ . The first one is as follows. (1) Each adult individual in a group in habitat  $s$  produces on average a very large number  $f_s$  of offspring, and then either survives with probability  $\gamma_s$  or dies with the complementary probability. (2) Offspring disperse independently of each other to a uniformly randomly chosen non-natal group with the non-zero probability  $m_s$ . An offspring survives dispersal with probability  $p_s$  when dispersing from a group in habitat  $s$ . (3) All offspring aspiring to settle in a group in habitat  $s$  compete for the average number  $(1 - \gamma_s)n_s$  of breeding sites vacated by the death of adults and are recruited until all  $n_s$  breeding sites are occupied. (4) The evolving trait does not affect dispersal.

In this life cycle, density-dependent population regulation occurs after dispersal when offspring aspire to settle and we refer to this regime as *hard selection*. We also consider a *soft-selection* variant in which



583 density regulation occurs in two steps (as in Fig. 1 of Svoldal et al., 2015). First, a local trait-dependent  
 584 stage of density-dependent regulation occurs immediately after reproduction (after stage (1) in the above  
 585 life cycle) in which the offspring pool in each group is brought back to a size proportional to the local  
 586 group size  $n_s$ , say size  $Kn_s$ , where  $K$  is a large number. From here on dispersal and recruitment (second  
 587 regulation step) proceed as in the hard-selection life cycle.

For these two life cycles, the philopatric and dispersal fitness components can be written as

$$w_{1,s|s}^{\text{pr}}(z_1, \mathbf{z}_{-\{1\}}, z) = \begin{cases} n_s \frac{(1 - m_s) f_s(z_1, \mathbf{z}_{-\{1\}}, z)}{(1 - m_s) \sum_{i=1}^{n_s} f_s(z_i, \mathbf{z}_{-\{i\}}, z) + I_{\text{hard}}(z)} & \text{(hard selection)} \quad (45a) \\ \underbrace{n_s \frac{(1 - m_s)}{(1 - m_s)n_s + I_{\text{soft}}}}_{\text{trait independent recruitment}} \times \underbrace{n_s \frac{f_s(z_1, \mathbf{z}_{-\{1\}}, z)}{\sum_{i=1}^{n_s} f_s(z_i, \mathbf{z}_{-\{i\}}, z)}}_{\text{trait dependent regulation}} & \text{(soft selection),} \quad (45b) \end{cases}$$

589 and

$$w_{1,s'|s}^{\text{dr}}(z_1, \mathbf{z}_{-\{1\}}, z) = \begin{cases} \pi_{s'} n_{s'} \frac{p_s m_s f_s(z_1, \mathbf{z}_{-\{1\}}, z)}{(1 - m_{s'}) \sum_{i=1}^{n_{s'}} f_{s'}(z, \mathbf{z}, z) + I_{\text{hard}}(z)} & \text{(hard selection)} \quad (46a) \\ \pi_{s'} n_{s'} \frac{p_s m_s}{(1 - m_{s'})n_{s'} + I_{\text{soft}}} \times \underbrace{n_s \frac{f_s(z_1, \mathbf{z}_{-\{1\}}, z)}{\sum_{i=1}^{n_s} f_s(z_i, \mathbf{z}_{-\{i\}}, z)}}_{\text{trait dependent regulation}} & \text{(soft selection),} \quad (46b) \end{cases}$$

590 respectively, where  $f_s(z_i, \mathbf{z}_{-\{i\}}, z)$  is the fecundity of individual  $i$  in a group in habitat  $s$  and

$$I_{\text{hard}}(z) \equiv \sum_{s \in \mathcal{S}} \pi_s n_s p_s m_s f_s(z, \mathbf{z}, z) \quad (47a)$$

$$I_{\text{soft}} \equiv \sum_{s \in \mathcal{S}} \pi_s n_s p_s m_s \quad (47b)$$

591 are the trait-dependent immigration terms for the hard-selection model and trait-independent immigra-  
 592 tion term for the soft selection model, respectively.

593 Equations (45b) and (46b) can be understood as follows. During the stage of trait-dependent reg-  
 594 ulation the local offspring pool in a group in habitat  $s$  is brought back to a size proportional to  $n_s$ ,  
 595 namely  $Kn_s$ , whereby the proportion of individuals among the surviving offspring descending from a  
 596 focal individual is  $f_s(z_1, \mathbf{z}_{-\{1\}}, z) / \sum_{i=1}^{n_s} f_s(z_i, \mathbf{z}_{-\{i\}}, z)$ . Each of these offspring either disperses or stays  
 597 local and then competes to be recruited. With probability  $1 - m_s$  an offspring is philopatric, and  
 598 this philopatric offspring gets recruited with probability  $1 / [K((1 - m_s)n_s + I_{\text{soft}})]$  per open spot. Here  
 599  $K((1 - m_s)n_s + I_{\text{soft}})$  is the expected number of local competitors, where the number of migrant off-  
 600 spring competing in a given group for recruitment and coming from a group in habitat  $s$  is proportional  
 601 to  $\pi_s n_s p_s m_s$ . Offspring dispersing to a group in habitat  $s'$  experience on average  $K((1 - m_{s'})n_{s'} + I_{\text{soft}})$   
 602 competitors and the probability to compete in such a group is  $\pi_{s'}$ . The likelihood to be recruited (either  
 603 after dispersing or without dispersing) is then multiplied by the expected number of open breeding sites,  
 604 which equals  $n_s(1 - \gamma_s)$  in the natal group and  $n_{s'}(1 - \gamma_{s'})$  in non-natal groups in habitat  $s'$ , but the  
 605 factors  $(1 - \gamma_s)$  and  $(1 - \gamma_{s'})$  are already accounted for in eqs.(38b) and (38c). Note that the constant  
 606  $K$  does not appear in eqs.(45b) and (46b) because it appears both in the numerator and denominator  
 607 of these equations and thus cancels out.

608 Using eq.(45) and eq.(46) along with eqs.(39)–(44) allows to compute  $\rho^{(1)}$  and  $\rho^{(2)}$  for a large class  
 609 of models. In sections ??, ?? and ?? in the Supplementary Material, we show that we recover a number

of previously published results belonging to this class of models, some of which were derived with quite different calculations (Pen, 2000; Ohtsuki, 2010; Lehmann and Rousset, 2010; Rodrigues and Gardner, 2012; Wakano and Lehmann, 2014; Svardal et al., 2015; Mullon et al., 2016; Parvinen et al., 2018). This indirectly confirms the validity of our calculations. For simplicity of notation we assumed that the evolving trait does neither affect survival nor dispersal (it only affects fecundity), extensions to include effects on survival and dispersal are in principle straightforward.

### 4.3 Selection analysis

In this section, we finally present explicit expressions for the selection gradient  $\rho^{(1)}$  and the coefficient of disruptive selection  $\rho^{(2)}$  for both the model of hard and soft selection. We then introduce an explicit fecundity function, which, under some additional symmetry assumptions, allows us to have a completely worked example.

#### 4.3.1 Hard selection

Inserting eqs.(45a) and (46a) into eqs.(38b) and (38c), respectively, we show in section ?? in the Supplementary Material that the selection gradient for the hard selection lottery model is

$$\rho^{(1)} \propto \sum_{s \in \mathcal{S}} \frac{\pi_s n_s p_s m_s f_s}{d_{s,\text{hard}}} \left\{ \frac{\partial f_s}{\partial z_1} + r_2^{(0)}(s)(n_s - 1) \frac{\partial f_s}{\partial z_2} - (1 - d_{s,\text{hard}})^2 r_{2,\text{R}}^{(0)}(s) \left( \frac{\partial f_s}{\partial z_1} + (n_s - 1) \frac{\partial f_s}{\partial z_2} \right) \right\}, \quad (48)$$

where the proportionality constant is positive (and given by the inverse of eq.(??)) and  $d_{s,\text{hard}}$  is the backward migration rate from groups in state  $s$  under neutrality defined as

$$d_{s,\text{hard}} \equiv \frac{I_{\text{hard}}}{(1 - m_s)n_s f_s + I_{\text{hard}}}. \quad (49)$$

This rate depends on  $y$  because  $I_{\text{hard}}$  and  $f_s$  are evaluated at  $(y, \dots, y)$ . Equation (48) further depends on

$$r_{2,\text{R}}^{(0)}(s) \equiv \frac{1}{n_s} + \frac{n_s - 1}{n_s} r_2^{(0)}(s), \quad (50)$$

which is the relatedness between two individuals sampled with replacement in a group in state  $s$  and where

$$r_2^{(0)}(s) = \frac{2\gamma_s(1 - d_{s,\text{hard}}) + (1 - \gamma_s)(1 - d_{s,\text{hard}})^2}{n_s(1 + \gamma_s) - 2(n_s - 1)\gamma_s(1 - d_{s,\text{hard}}) - (n_s - 1)(1 - \gamma_s)(1 - d_{s,\text{hard}})^2}. \quad (51)$$

Equation (48) can be understood as follows. The first term in the curly brackets is the marginal fecundity effect by a focal individual on itself, while the second term is the marginal fecundity effect conferred by all group members to the focal individual weighted by the coefficient of pairwise relatedness. Finally, the third term reflects competition for the finite number of breeding spots in a group. A change in the trait value of a focal individual that increases its fecundity or that of its neighbors increases the strength of local competition. This reduces the fitness of the focal individual if the additional offspring remain philopatric and compete with own offspring. Equation (48) is a generalization of previous results obtained for the island model (see section ?? in the Supplementary Material for the detail of these connections).

639 Similarly, inserting eqs.(45a) and (46a) into eqs.(38b) and (38c), respectively, and using these in  
 640 eq.(34), we obtain a general expression for the disruptive selection coefficient  $\rho^{(2)}$  under hard selection.  
 641 The resulting expression, while useful for numerical calculations, is too lengthy to be presented here  
 642 and we refer to section ?? in the Supplementary Material for details. Therein, we show that under a  
 643 Wright-Fisher process ( $\gamma_s = 0$ ) the results of Parvinen et al. (2018) are recovered, who obtained an  
 644 expression of  $\rho^{(2)}$  expressed in terms of first- and second-order derivatives of  $f_s$ .

645 To complement these results and to approach a fully worked example, we assume a Moran pro-  
 646 cess (*i.e.*,  $\gamma_s \sim 1$ ) and that fecundity of an adult individual depends only on its own phenotype (*i.e.*,  
 647  $f_s(z_1, \mathbf{z}_{-\{1\}}, z) = f_s(z_1)$ ). Under these assumptions, we show in section ?? in the Supplementary Ma-  
 648 terial that the selection gradient is a weighted sum of  $df_s/dz_1$  over different states  $s$  (see eq.(??)), and  
 649 that the disruptive selection coefficient is

$$\rho^{(2)} \propto \sum_{s \in S} \frac{\pi_s n_s p_s m_s f_s}{d_{s,\text{hard}}} \left\{ X_{1,s,\text{hard}} \frac{d^2 f_s}{dz_1^2} + X_{2,s,\text{hard}} \left( \frac{df_s}{dz_1} \right)^2 \right\}, \quad (52a)$$

650 where the positive proportionality constant is the same as in eq.(48), and

$$X_{1,s,\text{hard}} = \frac{1}{2} \frac{d_{s,\text{hard}}(1 - d_{s,\text{hard}} + n_s)}{1 + d_{s,\text{hard}}(n_s - 1)} \quad (\geq 0) \quad (52b)$$

$$X_{2,s,\text{hard}} = \frac{d_{s,\text{hard}}(1 - d_{s,\text{hard}})(1 - d_{s,\text{hard}} + n_s)n_s}{\{2 + d_{s,\text{hard}}(n_s - 2)\}\{1 + d_{s,\text{hard}}(n_s - 1)\}} \quad (\geq 0) \quad (52c)$$

651 For complete dispersal (*i.e.*,  $d_{s,\text{hard}} = 1$ )<sup>3</sup> we obtain that  $X_{1,s,\text{hard}} = 1/2$  and  $X_{2,s,\text{hard}} = 0$ . As the  
 652 dispersal rate  $d_{s,\text{hard}}$  decreases, the ratio  $X_{2,s,\text{hard}}/X_{1,s,\text{hard}}$  increases monotonically. Hence, as dispersal  
 653 becomes more limited, relatively more weight is put on the squared first-order derivative  $(df_s/dz_1)^2$   
 654 compared to the second-order derivative  $d^2 f_s/dz_1^2$ , indicating that limited dispersal facilitates disruptive  
 655 selection (and, if the singular strategy  $y^*$  is convergence stable and remains so when varying disper-  
 656 sal, then evolutionary branching is facilitated). On the other hand, for a fixed  $d_{s,\text{hard}} < 1$ , the ratio  
 657  $X_{2,s,\text{hard}}/X_{1,s,\text{hard}}$  monotonically decreases as group size decreases. Hence, with decreasing group size  
 658 less weight is put on the squared first-order derivative  $(df_s/dz_1)^2$ , which acts to limit disruptive selection.  
 659 We finally note that the functional form of eq.(52a) holds beyond the Moran process, provided all other  
 660 assumptions are the same. While the weights will depend on the specifics of the reproductive process,  
 661 we conjecture that the weights will feature the same qualitative dependence on dispersal and group size.

662 We now make two further assumptions. First, we follow Svardal et al. (2015) and assume that  
 663 fecundity is under Gaussian stabilising selection with habitat specific optimum  $y_{\text{op},s}$ . Thus,

$$f_s(z_1) = f_{\text{max}} \exp \left[ -\frac{(z_1 - y_{\text{op},s})^2}{2\sigma_{\text{st}}^2} \right], \quad (53)$$

664 where  $f_{\text{max}}$  is the maximal fecundity of an individual and  $\sigma_{\text{st}}^2$  is inversely proportional to the strength  
 665 of stabilising selection. Second, we assume that group size, migration and juvenile survival are identical  
 666 for all habitats, *i.e.*,  $n_s = n$ ,  $m_s = m$ , and  $p_s = p$  for all  $s$ . Hence, habitats only differ in the trait value  
 667  $y_{\text{op},s}$  that maximizes fecundity.

<sup>3</sup>For a homogeneous population with a single habitat  $s$ , a singular point is characterized by  $df_s/dz_1 = 0$ , and therefore eq.(52) predicts that the sign of the disruptive selection coefficient is solely determined by the sign of  $d^2 f_s/dz_1^2$  no matter whether dispersal is complete or locally limited. A similar result has been shown in Parvinen et al. (2017) by assuming a Wright-Fisher process.

668 Under these assumptions, the singular strategy  $y^*$  is implicitly given by

$$y^* = \sum_{s \in \mathcal{S}} \psi_s(y^*) y_{\text{op},s}, \quad (54)$$

669 which is a weighted average of the habitat specific trait optima with the weights  $\psi_s$  being complicated  
670 functions of the model parameters (see section ?? in the Supplementary Material). The condition for  
671 the disruptive selection coefficient at the singular point  $y^*$  (eq.(52a)) being positive can be expressed as

$$\sum_{s \in \mathcal{S}} \Psi_s(y^*) (y_{\text{op},s} - y^*)^2 > \sigma_{\text{st}}^2, \quad (55)$$

672 where the  $\Psi_s$ 's are again complicated weights (section ?? in the Supplementary Material).

673 These expressions greatly simplify when we consider only two habitats with equal proportions, *i.e.*  
674  $\mathcal{S} = \{1, 2\}$  with  $\pi_1 = \pi_2 = 1/2$ , no mortality in dispersal,  $p = 1$ , and symmetric optima in the sense  
675 that  $y_{\text{op},2} = -y_{\text{op},1}$ . Due to this symmetry,  $y^* = 0$  is a solution of eq.(53) and therefore a singular strat-  
676 egy. Furthermore, in section ?? in the Supplementary Material, we find that under the aforementioned  
677 assumptions

$$\Psi_s(y^*) = \frac{1}{2} \left( \frac{2-m}{m} - \frac{4(1-m)^2}{m(2+m(n-2))} \right). \quad (56)$$

678 Then, by using the variance of the habitat optima defined by

$$\sigma_{\text{op}}^2 = \sum_{s \in \mathcal{S}} \pi_s (y_{\text{op},s} - y^*)^2 \quad (57)$$

679 (in the current case, with  $\pi_1 = \pi_2 = 1/2$ ), condition (55) can be written as

$$\left( \frac{2-m}{m} - \underbrace{\frac{4(1-m)^2}{m(2+m(n-2))}}_{\rightarrow 0 \text{ when } n \rightarrow \infty} \right) \sigma_{\text{op}}^2 > \sigma_{\text{st}}^2. \quad (58)$$

680 The first term in the parenthesis is the effect of limited dispersal on disruptive selection in the absence  
681 of kin selection (that is, under infinite group size). This term increases with decreasing dispersal, which  
682 facilitates disruptive selection. Indeed, low dispersal increases the probability that lineage members  
683 experience the same group-specific state favoring local adaptation. The second term in the parenthesis  
684 captures the effect of kin selection. The absolute value of this negative term increases with both decreasing  
685 dispersal and decreasing group size, which inhibits disruptive selection. This effect can be understood  
686 as follows. All philopatric offspring within a group compete with each other for the limited number of  
687 spots to settle within a group. Relatedness among individuals within a group increases with decreasing  
688 group size. Thus, in smaller groups competing individuals are more likely to be related with each other  
689 and this diminishes the benefit of mutations increasing adaptation to the group-specific state. This effect  
690 becomes more pronounced with decreasing dispersal since this increases relatedness within groups even  
691 more. We therefore expect that the singular point  $y^*$  is more likely to be uninvadable for small groups  
692 and this is indeed what we observe in Figure 3, especially evident in panel (f). It can be shown that the  
693 effect of decreasing dispersal on the first term on the left-hand side of (58) dominates the effect on the  
694 second term. Thus, decreasing  $m$  indeed facilitates disruptive selection as illustrated in Figure 3(b-f).

695 In the limit of  $m = 0$  and  $m = 1$  the condition for the disruptive selection coefficient being positive  
696 (58) becomes

$$\begin{cases} (1+n)\sigma_{\text{op}}^2 > \sigma_{\text{st}}^2 & \text{when } m \rightarrow 0 \\ \sigma_{\text{op}}^2 > \sigma_{\text{st}}^2 & \text{when } m = 1. \end{cases} \quad (59)$$

697 Thus, at very low dispersal the singular point changes from being uninvadable to invadable when group  
698 size exceeds  $n = (\sigma_{\text{st}}^2 - \sigma_{\text{op}}^2)/\sigma_{\text{op}}^2$  (as can be seen in Figure 3(f) where the boundary between CSS and  
699 branching point for very low  $m$  occurs at  $n = 4$ ). At complete dispersal, the singular point is uninvadable  
700 for  $\sigma_{\text{op}}^2 < \sigma_{\text{st}}^2$  and invadable otherwise. Finally, the singular strategy is more likely to be under stabilizing  
701 selection the larger the ratio  $\sigma_{\text{st}}^2/\sigma_{\text{op}}^2$ , as is clearly illustrated in Figure 3(a-f).

702 A singular point at which selection is disruptive is an evolutionary branching point if it is also  
703 convergence stable. Substituting eq.(48) under all mentioned assumptions into eq.(19) we obtain after  
704 rearrangements that  $y^* = 0$  is convergence stable if

$$\left( 2 - m - \underbrace{\frac{(1-m)^2(1-m+(1+m)n)}{(1+m(n-1))(1-m+n)}}_{\rightarrow 0 \text{ when } n \rightarrow \infty} \right) \sigma_{\text{op}}^2 < \sigma_{\text{st}}^2 \quad (60)$$

705 and repelling otherwise. From inspecting the left-hand side of this condition, the coefficient of  $\sigma_{\text{op}}^2$  is a  
706 unimodal function of  $m$  and takes the minimum value 1 at  $m = 0, 1$  and the maximum at

$$m = \frac{\sqrt{1+n}}{n + \sqrt{1+n}} \quad (61)$$

707 for any fixed  $n$ . Therefore, it is clear that  $\sigma_{\text{op}}^2 < \sigma_{\text{st}}^2$  is a necessary but not sufficient condition for  
708 convergence stability. More generally, increasing  $\sigma_{\text{st}}^2$  relative to  $\sigma_{\text{op}}^2$  increases the space in the  $(m, n)$ -plane  
709 for which the singular point is convergence stable (*cf.* Figure 3(a-f)). In section ?? in the Supplementary  
710 Material we show that  $2\sigma_{\text{op}}^2 < \sigma_{\text{st}}^2$  is a sufficient condition for convergence stability (*cf.* Figure 3(e-f)).  
711 Interestingly, from the unimodality above, the singular point can be repelling for intermediate values of  
712  $m$  as can be seen in Figure 3(b-d). For large group size, condition (60) becomes  $(2-m)\sigma_{\text{op}}^2 < \sigma_{\text{st}}^2$  and  
713 therefore convergence stability changes at  $m = 2 - (\sigma_{\text{st}}^2/\sigma_{\text{op}}^2)$ , which coincides very well with where the  
714 singular point turns from convergence stable to repelling at group size  $n = 100$  in Figure 3(b-d). For the  
715 effect of group size  $n$  on convergence stability, the coefficient of  $\sigma_{\text{op}}^2$  in condition (60) is, for any fixed  
716  $0 < m < 1$ , an increasing function of  $n$ . Thus, smaller group sizes are more favorable for convergence  
717 stability of the singular point  $y^* = 0$ .

718 An immediate conclusion from these observations is that for  $m = 1$  evolutionary branching does not  
719 occur under hard selection (with fecundity given by eq.(53)). This is so because for  $m = 1$  competition  
720 is global and does not occur between individuals within a group. This removes any frequency-dependent  
721 selection effect. Indeed, under our assumptions setting  $m = 1$  (and  $p = 1$ ) in eq.(45a) and eq.(46a) results  
722 in  $w_{1,s|s}^{\text{DR}}(z_1, \mathbf{z}_{-\{1\}}, z) = 0$  and  $w_{1,s'|s}^{\text{DR}}(z_1, \mathbf{z}_{-\{1\}}, z) = \pi_{s'} n_{s'} f_s(z_1)/I_{\text{hard}}(z)$  for all  $s'$  and  $s$ . Thus, there  
723 is no longer any state specific frequency-dependence, since  $I_{\text{hard}}(z)$  is common to all fitness functions.  
724 In this case, the singular point is both convergence stable and uninvadable if  $\sigma_{\text{op}}^2 < \sigma_{\text{st}}^2$  and both  
725 repelling and invadable if  $\sigma_{\text{op}}^2 > \sigma_{\text{st}}^2$ . This is in agreement with the well-known finding that under hard  
726 selection and complete dispersal selection is frequency-independent and adaptive polymorphism cannot

727 be maintained by spatial heterogeneity alone (Dempster, 1955; Ravigné, 2004; Ravigné et al., 2009;  
728 Débarre and Gandon, 2011).

### 729 4.3.2 Soft selection

730 Inserting eqs.(45b) and (46b) into eqs.(38b) and (38c), respectively, we show in section ?? in the Sup-  
731 plementary Material that the selection gradient for the soft selection lottery model is

$$\rho^{(1)} \propto \sum_{s \in \mathcal{S}} \frac{\pi_s n_s p_s m_s}{d_{s,\text{soft}}} \left\{ \frac{\partial f_s}{\partial z_1} + r_2^{(0)}(s)(n_s - 1) \frac{\partial f_s}{\partial z_2} - r_{2,R}^{(0)}(s) \left( \frac{\partial f_s}{\partial z_1} + (n_s - 1) \frac{\partial f_s}{\partial z_2} \right) \right\}, \quad (62)$$

732 where the positive proportionality constant is positive (and given by the inverse of eq.(??)) and

$$d_{s,\text{soft}} \equiv \frac{I_{\text{soft}}}{(1 - m_s)n_s + I_{\text{soft}}} \quad (63)$$

733 is the backward migration rate from groups in habitat  $s$  under neutrality. In contrast to the case of hard  
734 selection, eq.(63) is independent of  $y$ . Pairwise relatedness under neutrality  $r_2^{(0)}(s)$  takes the same form  
735 as in eq.(51) where all  $d_{s,\text{hard}}$  have to be replaced with  $d_{s,\text{soft}}$ . The key difference between eq.(48) and  
736 eq.(62) is that under soft selection the competition term is larger than under hard selection because the  
737 weighting by the backward dispersal probability has disappeared in the latter case. This reflects the fact  
738 that under soft selection density regulation occurs before dispersal. Again, eq.(62) is a generalization of  
739 previous results as detailed in section ?? in the Supplementary Material.

740 Similarly, inserting eqs.(45b) and (46b) into eqs.(38b) and (38c), respectively, and using these in  
741 eq.(34), we obtain a general expression for the disruptive selection coefficient  $\rho^{(2)}$  under soft selection.  
742 As was the case for hard selection, the resulting expression can be useful for numerical calculations, but  
743 is too lengthy to be presented here and we refer to section ?? in the Supplementary Material for details.

744 Paralleling the analysis under hard selection, we assume a Moran process (*i.e.*,  $\gamma_s \sim 1$ ) and that the  
745 fecundity of adult individuals depends only on their own phenotype ( $f_s(z_1, \mathbf{z}_{-\{1\}}, z) = f_s(z_1)$ ). Under  
746 these assumptions we show in section ?? in the Supplementary Material that

$$\rho^{(2)} \propto \sum_{s \in \mathcal{S}} \frac{\pi_s n_s p_s m_s}{d_{s,\text{soft}}} \left\{ X_{1,s,\text{soft}} \frac{d^2 f_s}{dz_1^2} + X_{2,s,\text{soft}} \left( \frac{df_s}{f_s} \right)^2 \right\}, \quad (64a)$$

747 where the positive proportionality constant is the same as in eq.(62), and

$$X_{1,s,\text{soft}} = \frac{1}{2} \frac{d_{s,\text{soft}}(n_s - 1)}{1 + d_{s,\text{soft}}(n_s - 1)} \quad (\geq 0) \quad (64b)$$

$$X_{2,s,\text{soft}} = \frac{d_{s,\text{soft}}(n_s - 1) \{d_{s,\text{soft}}(1 - d_{s,\text{soft}})(n_s - 1)(n_s - 2) - 2d_{s,\text{soft}}(n_s - 1) + (n_s - 2)\}}{\{2 + d_{s,\text{soft}}(n_s - 2)\} \{1 + d_{s,\text{soft}}(n_s - 1)\}^2}. \quad (64c)$$

748 The ratio of these weights,  $X_{2,s,\text{soft}}/X_{1,s,\text{soft}}$ , shows qualitatively the same behavior as the corresponding  
749 expressions under hard selection (eqs.(52b) and (52c)) with respect to changes in  $d_{s,\text{soft}}$  and  $n_s$ . However,  
750 a notable difference from the hard selection case is that  $X_{2,s,\text{soft}}$  (and hence the ratio,  $X_{2,s,\text{soft}}/X_{1,s,\text{soft}}$ )  
751 can be negative for small  $n_s$  and large  $d_s$ . We finally note that, as was the case for eq.(52a), the functional  
752 form of eq.(64a) holds beyond the Moran process, provided all other assumptions are the same.

753 Under the assumption of Gaussian fecundity selection (eq.(53)) and  $n_s = n$ ,  $m_s = m$ ,  $p_s = p = 1$   
754 for all states  $s$ , which entails  $d_{\text{soft}} = m$ , we again obtain a fully worked example. The value  $y^*$  for the

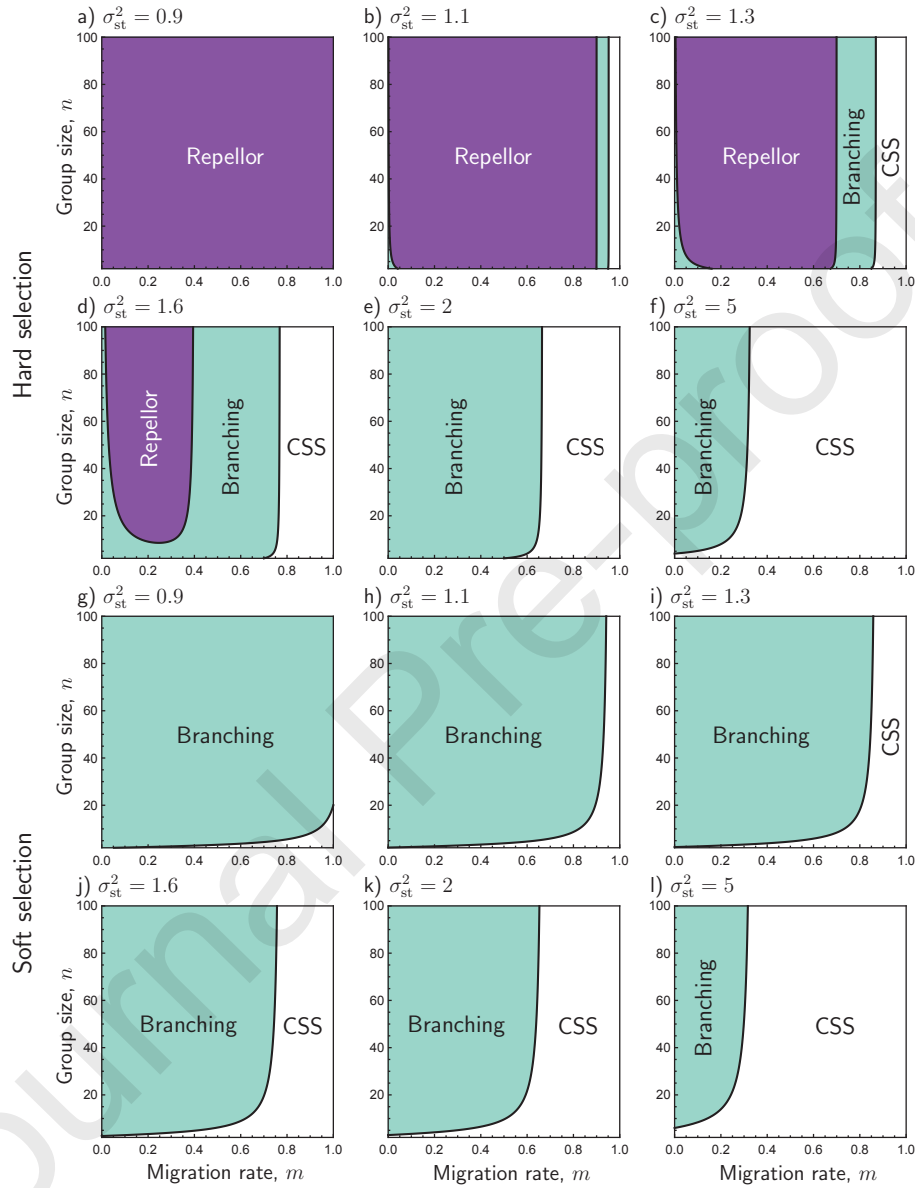


Figure 3: Bifurcation diagrams for the singular point  $y^* = 0$  as a function of the migration rate  $m$  (x-axis) and group size  $n$  (y-axis) for six different values of the within group selection parameter  $\sigma_{st}^2$  (see eq.(53)). (a-f) Hard selection, (g-l) soft selection. Purple: evolutionary repellor, blue: evolutionary branching point, white: uninvadable and convergence stable singular point, *i.e.*, continuously stable strategy (CSS). Other parameter values:  $y_{op,1} = 1 = -y_{op,2}$  (implying  $\sigma_{op}^2 = 1$ ).



755 singular strategy is given by the average habitat optimum,

$$y^* = \sum_{s \in S} \pi_s y_{op,s} \quad (65)$$

756 (section ?? in the Supplementary Material). Furthermore, the coefficient of disruptive selection is positive  
757 if and only if

$$\left( \frac{2-m}{m} - \underbrace{\frac{4+2m(2-m)(n-2)}{m(2+m(n-2))(1+m(n-1))}}_{\rightarrow 0 \text{ when } n \rightarrow \infty} \right) \sigma_{op}^2 > \sigma_{st}^2, \quad (66)$$

758 where  $\sigma_{op}^2$  is the variance in the habitat optima defined by eq.(57). Note that condition (66) is valid only  
759 for  $n \geq 2$  (because otherwise eqs.(64b) and (64c) evaluate to zero). The two terms in parenthesis on the  
760 left-hand side of condition (66) have the same interpretation as the corresponding terms in condition (58)  
761 for the case of hard selection and they respond in the same direction with respect to changes in dispersal  
762  $m$  and group size  $n$ . In the limit of infinitely large group size ( $n \rightarrow \infty$ ) the second term vanishes and we  
763 recover eq.(C.15) of Svardal et al. (2015).

764 In section ?? in the Supplementary Material, we show that  $y^*$  as given by eq.(65) is convergence stable  
765 for any value of  $\sigma_{st}^2$  and  $\sigma_{op}^2$  and independent of group size  $n$  and dispersal probability  $m$ . Thus, the  
766 singular point is an evolutionary branching point when it is invadable and an endpoint of the evolutionary  
767 dynamics (continuously stable strategy, CSS) when uninvadable. For the special case of only two habitats  
768 with  $y_{op,1} = 1 = -y_{op,2}$ , Figure 3 shows how  $n$ ,  $m$  and  $\sigma_{st}^2$  determine whether  $y^* = 0$  is a branching  
769 point or a CSS. In summary, stronger selection (smaller values of  $\sigma_{st}^2$ ), lower migration and larger groups  
770 favor adaptive diversification at an evolutionary branching point.

## 771 5 Discussion

772 The main result of this paper is an expression for the disruptive selection coefficient  $\rho^{(2)}$  in heterogeneous  
773 group-structured populations (eq.(34)). We show that  $\rho^{(2)}$  depends on three types of differentials: (a) the  
774 first- and second-order perturbations of the expected number of offspring in different states produced by  
775 an individual in a given state, (b) the first-order perturbation of the probability that an individual is in the  
776 different states, and (c) the first-order perturbation of the probability that a randomly sampled neighbor  
777 of an individual carries alleles identical by descent (perturbation of relatedness). These differentials  
778 depend on and are weighted by three quantities evaluated under neutrality: (i) the reproductive values  
779  $v^{(0)}(s)$  of individuals in state  $s$ , (ii) the pairwise and three-way relatedness coefficients  $r_2^{(0)}(s)$  and  $r_3^{(0)}(s)$   
780 in state  $s$ , and (iii) the probability  $q^{(0)}(s)$  that a randomly sampled individual resides in a group in state  
781  $s$ .

782 At a conceptual level, our results about the components of  $\rho^{(2)}$  can be thought of as a direct extension  
783 of the result that the three types of neutral weights – reproductive values, relatednesses, and probabilities  
784 of occurrence in state  $s$  – are needed to evaluate the selection gradient  $\rho^{(1)}$  for quantitative traits in group-  
785 structured populations (Taylor and Frank, 1996; Frank, 1998; Rousset, 2004). All the above mentioned  
786 differentials and their weights can be obtained by solving systems of linear equations that are at most  
787 of dimension  $N$ , *i.e.*, the number of states groups can be in. This represents a significant reduction

788 compared to the dimension of the state space of the original evolutionary process, which is equal to the  
 789 dimension of the mutant transition matrix  $\mathbf{A}$ .

790 A distinctive and novel feature of our analysis is the introduction of the concept of individual  $k$ -  
 791 fitness,  $w_k(s'|s, i)$ , which describes the expected number of descendants of a mutant in an  $(s, i)$  group  
 792 (possibly including self through survival) that settle in state- $s'$  groups and have  $k - 1$  randomly sampled  
 793 neighbors that are also mutants (*i.e.*, that descend from the same common ancestor). In the context of  
 794 our perturbation analysis, we show that  $w_k(s'|s, i)$  can be themselves expressed in terms of individual  
 795  $k$ -fitness functions for  $k = 1, 2, 3$  where individuals are labelled as focal, group neighbor and population  
 796 member, and which are sufficient to evaluate all aforementioned quantities and thus  $\rho^{(1)}$  and  $\rho^{(2)}$  (see  
 797 sections 3.2.1-3.3). These latter individual  $k$ -fitness functions do not depend on the mutant type and  
 798 provide for  $k = 2, 3$  the generalizations of the fitness functions for  $k = 1$  already in use in the direct  
 799 fitness method (Taylor and Frank, 1996; Frank, 1998; Rousset, 2004). They are thus sufficient biological  
 800 ingredients to determine whether or not disruptive selection occurs. In a well-mixed populations in which  
 801 individuals do not interact with relatives only individual 1-fitness functions are required to evaluate  $\rho^{(1)}$   
 802 and  $\rho^{(2)}$ . Individual 2- and 3-fitnesses describe the possibility that under limited dispersal the offspring  
 803 of a given parent can have neighbors (here one or two) that belong to the same lineage and are thus  
 804 more likely to have the same trait value than randomly sampled individuals from the population. This  
 805 causes non-random mutant-mutant interactions, which is well known to critically affect the nature of  
 806 selection on traits affecting own and others' reproduction and survival (Hamilton, 1964; Michod, 1982;  
 807 Frank, 1998; Rousset, 2004). Because the individual  $k$ -fitnesses describe group configurations in which  
 808 offspring have neighbors that belong to the same lineage, the ancestral lineages of the  $k$  interacting  
 809 individuals must coalesce in a common ancestor, and this can occur only if there is a non-zero probability  
 810 that at least two individuals descend from the same parent over a generation (see section ?? in the  
 811 Supplementary Material for the connection to coalescence theory). Neutral relatedness in evolutionary  
 812 models is indeed usually computed by using coalescence arguments and thus use a “backward” perspective  
 813 on allele transmission (*e.g.* Taylor and Frank, 1996; Frank, 1998; Rousset, 2004). This may somewhat  
 814 disconnect relatedness from the “forward” perspective of allele transmission induced by reproduction.  
 815 Using individual 2-fitnesses to evaluate relatedness (see eq.(33)) brings upfront the connection between  
 816 relatedness and reproduction (note that the “backward” approach may nevertheless be more useful for  
 817 concrete calculations of relatedness).

818 As an application of our results, we analyze a lottery model with overlapping generations in hetero-  
 819 geneous habitats that allows for both hard and soft selection regimes. For this scenario, we show that  
 820  $\rho^{(1)}$  and  $\rho^{(2)}$  can in principle be solved explicitly (all systems of equation can be solved explicitly) but  
 821 that generic expressions remain complicated functions, since they apply to any kind of social interactions  
 822 (*i.e.*, any “game”) and different ecologies. In doing these calculations, we recover a number of previous  
 823 results concerning relatedness, selection gradients and disruptive selection coefficients for lottery models  
 824 (in particular those of Pen, 2000; Rousset and Ronce, 2004; Ohtsuki, 2010; Lehmann and Rousset, 2010;  
 825 Rodrigues and Gardner, 2012; Wakano and Lehmann, 2014; Svardal et al., 2015; Mullon et al., 2016;  
 826 Parvinen et al., 2018, see sections ??, ?? and ?? in the Supplementary Material for details), which

827 confirms the validity of our approach. Finally, as a fully worked example, we investigate the evolution  
828 of adaptive polymorphism due to local adaption by extending the soft selection model of Svardal et al.  
829 (2015) to finite group size and hard selection. We confirm that adaptive polymorphism is generally  
830 favored by limited migration under soft selection and that small group size does not change this result  
831 qualitatively but tends to inhibit disruptive selection. For hard selection, however, the situation is more  
832 complicated as limited dispersal and finite group size favors not only disruptive selection but also re-  
833 pelling generalist strategies so that it becomes less likely that polymorphism can emerge from gradual  
834 evolution (Figure 3). With respect to limited migration this finding is also described by Débarre and  
835 Gandon (2011).

836 While our model allows for many different types of interactions between individuals within groups, it  
837 also has several limitations. At the individual level, we consider only scalar traits, but multidimensional  
838 (or functional-valued) traits can be taken into account by replacing derivatives by directional derivatives,  
839 which will not change the structure of our perturbation analysis. At the group level, we do not consider  
840 heterogeneity within groups, but in natural populations individuals within groups are likely to differ in  
841 their physiological state such as age, size and sex. To incorporate physiological heterogeneity requires  
842 an extension of the state space  $\mathcal{S}$  and to take into account the distribution of mutants within sub-groups  
843 of individuals belonging to the same physiological state in a group. The structure of our perturbation  
844 analysis, however, will remain unchanged by adding within-group heterogeneity, and only additional  
845 reproductive values and relatednesses will be needed. Likewise, in order to take isolation-by-distance into  
846 account, one again needs to extend the state space  $\mathcal{S}$ , while to include diploidy one needs to extend the  
847 number of genetic states and this should only impact the relatedness coefficients. While such extensions  
848 remain to be done (and have all been done for the selection gradient  $\rho^{(1)}$  (*e.g.* Rousset, 2004)), they are  
849 unlikely to change the required components of the disruptive selection coefficient  $\rho^{(2)}$  and how they are  
850 connected algebraically. We thus conjecture that the representation of  $\rho^{(2)}$  holds generally.

851 In conclusion, for a large class of models we describe the consequences of limited dispersal and finite  
852 group size on evolutionary stability and diversification in heterogeneous populations, which we hope will  
853 help to formulate and analyze concrete biological models.

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## References

- 859
- 860 Ajar, E. 2003. Analysis of disruptive selection in subdivided populations. *BMC Evolutionary Biology*  
861 3:22.
- 862 Bulmer, M. G. 1986. Sex ratio theory in geographically structured populations. *Heredity* 56:69–73.
- 863 Caswell, H. 2001. *Matrix Population Models*. 2nd ed. Sinauer.
- 864 Chesson, P. L. 1981. Models for spatially distributed populations: the effect of within-patch variability.  
865 *Theoretical Population Biology* 19:288–325.
- 866 Day, T. 2001. Population structure inhibits evolutionary diversification under competition for resources.  
867 *Genetica* 112-113:71–86.
- 868 Débarre, F., and S. Gandon. 2011. Evolution in heterogeneous environments: Between soft and hard  
869 selection. *The American Naturalist* 177:E84–E97.
- 870 Dempster, E. 1955. Maintenance of genetic heterogeneity. *Cold Spring Harbor Symposia on Quantitative*  
871 *Biology* 20:25–32.
- 872 Eshel, I. 1972. On the neighbor effect and the evolution of altruistic traits. *Theoretical Population*  
873 *Biology* 11:258–277.
- 874 Frank, S. A. 1998. *Foundations of Social Evolution*. Princeton University Press, Princeton, NJ.
- 875 Geritz, S. A. H., É. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and  
876 the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology* 12:35–57.
- 877 Grafen, A. 1985. A geometric view of relatedness. *Oxford surveys in evolutionary biology* 2:28–89.
- 878 ———. 1991. Modeling in behavioural ecology. Pages 5–31 *in* J. R. Krebs and N. Davies, eds. *Behavioural*  
879 *Ecology*. Blackwell Scientific Publications, Oxford.
- 880 Grey, D., V. Hutson, and E. Szathmáry. 1995. A re-examination of the stochastic corrector model.  
881 *Proceedings of the Royal Society London B* 262:29–35.
- 882 Hamilton, W. D. 1964. The evolution of social behavior. *Journal of Theoretical Biology* 7:1–16.
- 883 Harris, T. E. 1963. *The Theory of Branching Processes*. Springer-Verlag Berlin Heidelberg.
- 884 Karlin, S., and H. M. Taylor. 1975. *A First Course in Stochastic Processes*. Academic Press, San Diego.
- 885 Kisdi, E. 2016. Dispersal polymorphism in stable habitats. *Journal of Theoretical Biology* 392:69–82.
- 886 Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. *Evolution*  
887 37:1210–1226.
- 888 Lehmann, L., C. Mullon, E. Akçay, and J. Van Cleve. 2016. Invasion fitness, inclusive fitness, and  
889 reproductive numbers in heterogeneous populations. *Evolution* 70:1689–1702.

- 890 Lehmann, L., and F. Rousset. 2010. How life-history and demography promote or inhibit the evolution  
891 of helping behaviors. *Philosophical Transactions of the Royal Society B* 365:2599–2617.
- 892 Massol, F., and F. Débarre. 2015. Evolution of dispersal in spatially and temporally variable environ-  
893 nments: The importance of life cycles. *Evolution* 69:1925–1937.
- 894 Massol, F., A. Duputiè, P. David, and P. Jarne. 2011. Asymmetric patch size distribution leads to  
895 disruptive selection on dispersal. *Evolution* 65:490–500.
- 896 Metz, J. A. J., S. A. H. Geritz, G. Meszéna, F. J. A. Jacobs, and J. S. Van Heerwaarden. 1996. Adaptive  
897 dynamics: A geometrical study of the consequences of nearly faithful reproduction. Pages 183–231  
898 in S. van Strien and S. Verduyn Lunel, eds. *Stochastic and spatial structures of dynamical systems*,  
899 *Proceedings of the Royal Dutch Academy of Science*. North Holland, Dordrecht, Netherlands; available  
900 at <http://pure.iiasa.ac.at/id/eprint/4497/>.
- 901 Metz, J. A. J., and M. Gyllenberg. 2001. How should we define fitness in structured metapopulation mod-  
902 els? including an application to the calculation of evolutionary stable dispersal strategies. *Proceedings*  
903 *of the Royal Society of London, B* 268:499–508.
- 904 Michod, R. E. 1982. The theory of kin selection. *Annual Review of Ecology and Systematics* 13:23–55.
- 905 Mullon, C., L. Keller, and L. Lehmann. 2016. Evolutionary stability of jointly evolving traits in subdivi-  
906 ded populations. *The American Naturalist* 188:175–195.
- 907 Mullon, C., and L. Lehmann. 2018. Eco-evolutionary dynamics in metacommunities: ecological inheri-  
908 tance, helping within species, and harming between species. *American Naturalist* 192:664–685.
- 909 Ohtsuki, H. 2010. Evolutionary games in Wright’s island model: kin selection meets evolutionary game  
910 theory. *Evolution* 64:3344–53.
- 911 Parker, G. A., and J. Maynard Smith. 1990. Optimality theory in evolutionary biology. *Nature* 348:27–33.
- 912 Parvinen, K., H. Ohtsuki, and J. Y. Wakano. 2017. The effect of fecundity derivatives on the condition  
913 of evolutionary branching in spatial models. *Journal of Theoretical Biology* 416:129–143.
- 914 ———. 2018. Spatial heterogeneity and evolution of fecundity-affecting traits. *Journal of Theoretical*  
915 *Biology* 454:190–204.
- 916 ———. 2020. Evolution of dispersal in a spatially heterogeneous population with finite patch sizes.  
917 *Proceedings of the National Academy of Sciences USA* 117:7290–7295.
- 918 Pen, I. 2000. Reproductive effort in viscous populations. *Evolution* 54:293–297.
- 919 Phillips, P. A., and S. J. Arnold. 1989. Visualizing multivariate selection. *Evolution* 43:1209–1222.
- 920 Ravigné. 2004. Implications of habitat choice for protected polymorphisms. *Evolutionary Ecology Re-*  
921 *search* 6:125–145.

- 922 Ravigné, V., U. Dieckmann, and I. Olivieri. 2009. Live where you thrive: Joint evolution of habitat  
923 choice and local adaptation facilitates specialization and promotes diversity. *The American Naturalist*  
924 174:E141–E169.
- 925 Rodrigues, A. M. M., and A. Gardner. 2012. Evolution of helping and harming in heterogeneous popu-  
926 lations. *Evolution* 66:2065–2079.
- 927 Ronce, O., and D. Promislow. 2010. Kin competition, natal dispersal and the moulding of senescence by  
928 natural selection. *Proceedings of the Royal Society B-Biological Sciences* 277:3659–67.
- 929 Rousset, F. 2004. Genetic Structure and Selection in Subdivided Populations, vol. 40 of *Monographs in*  
930 *Population Biology*. Princeton University Press, Princeton, N.J.
- 931 Rousset, F., and O. Ronce. 2004. Inclusive fitness for traits affecting metapopulation demography. *The-*  
932 *oretical Population Biology* 65:127–141.
- 933 Rueffler, C., J. A. J. Metz, and T. J. M. Van Dooren. 2013. What life cycle graphs can tell about the  
934 evolution of life histories. *Journal of Mathematical Biology* 66:225–279.
- 935 Rueffler, C., T. J. M. Van Dooren, O. Leimar, and P. A. Abrams. 2006. Disruptive selection and then  
936 what? *Trends in Ecology and Evolution* 21:238–245.
- 937 Svoldal, H., C. Rueffler, and J. Hermisson. 2015. A general condition for adaptive genetic polymorphism  
938 in temporally and spatially heterogeneous environments. *Theoretical Population Biology* 99:76–97.
- 939 Szathmary, E., and L. Demeter. 1987. Group selection of early replicators and the origin of life. *Journal*  
940 *of Theoretical Biology* 128:463–486.
- 941 Taylor, P. D. 1989. Evolutionary stability of one-parameter models under weak selection. *Theoretical*  
942 *Population Biology* 36:125–143.
- 943 ———. 1990. Allele-frequency change in a class structured population. *The American Naturalist* 135:95–  
944 106.
- 945 Taylor, P. D., and S. A. Frank. 1996. How to make a kin selection model. *Journal of Theoretical Biology*  
946 180:27–37.
- 947 Tuljapurkar, S. 1990. Population Dynamics in variable environments, vol. 85 of *Lecture Notes in Biomath-*  
948 *ematics*. Springer Verlag, Berlin, Germany.
- 949 Van Cleve, J. 2015. Social evolution and genetic interactions in the short and long term. *Theoretical*  
950 *Population Biology* 103:2–26.
- 951 Wakano, J. Y., and L. Lehmann. 2014. Evolutionary branching in deme-structured populations. *Journal*  
952 *of Theoretical Biology* 351:83–95.
- 953 Wild, G. 2011. Inclusive fitness from multitype branching processes. *Bulletin of Mathematical Biology*  
954 73:1028–1051.

- 955 Wild, G., A. Gardner, and S. A. West. 2009. Adaptation and the evolution of parasite virulence in a  
956 connected world. *Nature* 459:983–986.
- 957 Wild, G., and A. Traulsen. 2007. The different limits of weak selection and the evolutionary dynamics  
958 of finite populations. *Journal of Theoretical Biology* 247:382–390.
- 959 Wright, S. 1943. Isolation by distance. *Genetics* 28:114–138.

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