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The effect of fecundity derivatives on the condition of evolutionary branching in spatial models

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Abstract

By investigating metapopulation fitness, we present analytical expressions for the selection gradient and conditions for convergence stability and evolutionary stability in Wright's island model in terms of fecundity function. Coefficients of each derivative of fecundity function appearing in these conditions have fixed signs. This illustrates which kind of interaction promotes or inhibits evolutionary branching in spatial models. We observe that Taylor's cancellation result holds for any fecundity function: Not only singular strategies but also their convergence stability is identical to that in the corresponding well-mixed model. We show that evolutionary branching never occurs when the dispersal rate is close to zero. Furthermore, for a wide class of fecundity functions (including those determined by any pairwise game), evolutionary branching is impossible for any dispersal rate if branching does not occur in the corresponding well-mixed model. Spatial structure thus often inhibits evolutionary branching, although we can construct a fecundity function for which evolutionary branching only occurs for intermediate dispersal rates.

Keywords: Adaptive dynamics; cooperation; evolutionary branching; natural selection

Highlights:

- We study trait evolution in Wright’s island model through metapopulation fitness.
- First- and second-order conditions are derived in terms of fecundity derivatives.
- In most cases, an introduction of spatial structure hinders evolutionary branching.
- Space never favors branching when the fecundity function is based on pairwise games.
- Though rare, we can construct an example where space promotes evolutionary branching.

1. Introduction

2 Evolutionary branching is a process in which the trait of an evolving
 3 monomorphic population first approaches a so-called singular trait, but then
 4 disruptive selection causes the population to become dimorphic, i.e., to con-
 5 tain two different resident traits, and these two traits evolve away from each
 6 other (Metz et al., 1992, 1996; Geritz et al., 1997, 1998). When mutations
 7 are so frequent that there is no clear separation between ecological and evo-
 8 lutionary time-scales, evolutionary branching means that a unimodal trait
 9 distribution first concentrates around the singular strategy, and then the
 10 distribution becomes bimodal.

Invasion fitness (Metz et al., 1992) is the long-term exponential growth
 12 rate of a rare mutant in an environment set by the resident. At singular
 13 strategies the first-order derivative of the invasion fitness vanishes. The con-
 14 dition for evolutionary branching is usually given by calculating the second-
 15 order derivatives of invasion fitness at a singular strategy. There is, however,
 16 another approach to study the branching condition. Instead of considering
 17 a mutant–resident system, we can study the dynamics of a continuous trait
 18 distribution and identify evolutionary branching as the increase of the vari-
 19 ance of the distribution (Sasaki and Dieckmann, 2011; Wakano and Iwasa,
 20 2012). In a case of a well-mixed population, the branching condition derived
 21 by calculating invasion fitness and that by calculating variance dynamics
 22 have been shown to be identical when the trait distribution is approximated

by the Gaussian distribution. In case of a spatially structured population,
24 comparing these approaches requires more detailed calculations.

The metapopulation reproduction ratio (metapopulation fitness) is a fit-
26 ness proxy that measures the growth of a mutant population between dis-
persal generations in an environment set by resident. (Metz and Gyllenberg,
28 2001; Ajar, 2003; Parvinen and Metz, 2008). By investigating the metapopu-
lation fitness, the branching conditions have been studied for several different
30 metapopulation models (Parvinen, 2002, 2006; Nurmi and Parvinen, 2008,
2011). On the other hand, the trait distribution approach can also be ex-
32 tended to spatially structured populations and an analytic expression for the
branching condition has been derived by Wakano and Lehmann (2014) for
34 a specific model. In structured populations, the trait distribution cannot be
described by a single Gaussian distribution (as in a well-mixed case) because
36 different demes (local patches) can have different trait distributions and be-
cause individuals in the same deme tend to have similar trait values. In other
38 words, the individual trait value is no longer an independent random vari-
able sampled from the same distribution and we need to take into account
40 the positive correlation of trait values within a deme. This correlation can
be expressed in terms of relatedness and as a result the branching condition
42 is given by a combination of fitness derivatives and relatedness coefficients.
The analytically derived condition by Wakano and Lehmann (2014) agreed
44 with their simulations.

In this article we investigate Wright's island model, which is a discrete-
46 time metapopulation model in which the number of adults in each deme
is fixed through generations. The relative fecundity of each adult depends
48 on its own inheritable trait and the traits of other adults in the same deme.
The individuals to become adults in the next generation are randomly chosen
50 among philopatric and dispersed offspring.

Assuming locally a fixed number of adults is not very realistic, and also
52 not strictly speaking even necessary, because evolution in metapopulation
models with more realistic local population dynamics has been successfully
54 analysed using the metapopulation fitness (see references above). However,
this simplifying assumption allows one to obtain general analytic expressions
56 for the selection gradient and conditions for convergence stability and evo-
lutionary stability. Ajar (2003) obtained such expressions by calculating the
58 metapopulation fitness, while Wakano and Lehmann (2014) used the trait
distribution approach. Both studies express their main results in such terms
60 of relatedness coefficients, which might discourage researchers to apply these

62 results to practical questions if they are not very familiar with inclusive fitness theory.

The first goal of this study is to explicitly show the selection gradient and conditions for convergence stability and evolutionary stability in terms of derivatives of the fecundity function and original spatial parameters (deme size, dispersal rate and the probability to survive dispersal). The use of our expressions is straightforward, and they are valid for any fecundity function. In this form it will be clearly observed that singular strategies in the spatial model are the same as in the well-mixed case (Taylor, 1992a; Taylor and Irwin, 2000), also called a cancellation result. Also the condition for convergence stability remains unchanged, whereas the condition for evolutionary stability is affected by the spatial structure.

The second goal is to study whether spatial structure promotes or inhibits evolutionary branching. For the direction of evolution in spatial models (e.g., evolution of cooperation), tremendous amount of papers have been published. Compared to them, the effect of spatial structure on evolutionary branching has been far less studied. Wakano and Lehmann (2014) have shown that when fecundity is determined by repeated snowdrift games (Doebeli et al., 2004) between individuals within the deme, a smaller dispersal rate inhibits branching. This was confirmed by their individual-based simulations but their analysis is only a numerical calculation of the general formula of the condition for evolutionary stability. Thus, it is not clear whether spatial structure always inhibits branching for any kind of local interactions or there exist some kind of interactions that trigger branching only when spatial structure is introduced. We aim to answer this question by investigating the explicit expression determining evolutionary stability.

This paper is organized as follows. In section 2 we describe the model and formulate the metapopulation reproduction number. The general explicit expression for the selection gradient and the second order derivatives are presented in section 3. Especially, in the condition of evolutionary stability the coefficients of each fecundity derivative (= derivative of the fecundity function) have fixed signs. In section 4 we prove general results suggesting that the spatial structure of Wright's island model often, but not always, inhibits evolutionary branching. As a counterexample we present an artificial fecundity function for which branching occurs only for intermediate values of the dispersal rate. In section 5 we apply our results to situations in which fecundity is determined by any pairwise game (not just the snowdrift game), or by a public-goods game.

2. Model description and metapopulation fitness

100 2.1. Island model and fecundity function

102 We consider an extended version of Wright's island model (Wright, 1931).
 104 We assume that there are infinitely many habitat patches (demes). In the
 106 beginning of the season each patch contains $n(\geq 2)$ adult individuals. These
 108 adults may differ in their strategies s , which affect their fecundity γF that
 represents the number of juveniles that they produce. Throughout the manuscript,
 γ is considered to be very large (actually $\gamma \rightarrow \infty$). More precisely, the relative
 fecundity for an adult with strategy s_1 , when the strategies of the other
 individuals are $\mathbf{s}_{n-1} = (s_2, \dots, s_n)$ is

$$F(s_1; \mathbf{s}_{n-1}) = F(s_1; (s_2, \dots, s_n)) \quad (2.1)$$

Naturally, the order of strategies in the vector \mathbf{s}_{n-1} does not affect fecundity,
 110 which we assume from now on. A proportion $0 < m \leq 1$ of the juveniles
 will disperse. The proportion $0 < p \leq 1$ will survive dispersal and land in
 112 a random patch, but the rest die out during dispersal. The present adults
 are assumed not to survive until the next season. The local adult population
 114 size is assumed to be fixed, so that the n individuals to become adults in
 the next season are randomly chosen among the juveniles in each patch after
 116 immigration. Throughout the paper, we assume that m and p are constant
 parameters in the model; they are independent of the strategy s .

118 In the following we investigate the invasion potential of a mutant with
 strategy s_{mut} in an environment set by a resident with strategy s_{res} . For this
 120 purpose, we denote the relative fecundity of a mutant and that of a resident
 by F_{mut} and F_{res} , respectively. More specifically, the relative fecundity of a
 122 resident, when there are i mutants and $n - i$ residents (including the focal
 resident) in its patch is denoted by

$$F_{\text{res}}^i = F_{\text{res}}^i(s_{\text{res}}, s_{\text{mut}}) = F(s_{\text{res}}; \underbrace{(s_{\text{mut}}, \dots, s_{\text{mut}})}_{\# = i}, \underbrace{(s_{\text{res}}, \dots, s_{\text{res}})}_{\# = n - i - 1}). \quad (2.2)$$

124 Similarly, the relative fecundity of a mutant, when there are i mutants (in-
 cluding the focal mutant) and $n - i$ residents in its patch is denoted by

$$F_{\text{mut}}^i = F_{\text{mut}}^i(s_{\text{res}}, s_{\text{mut}}) = F(s_{\text{mut}}; \underbrace{(s_{\text{mut}}, \dots, s_{\text{mut}})}_{\# = i - 1}, \underbrace{(s_{\text{res}}, \dots, s_{\text{res}})}_{\# = n - i}). \quad (2.3)$$

126 In particular, the relative fecundity of a resident, when all individuals in
 the same patch are residents is denoted by

$$F_{\text{res}}^0 = F(s_{\text{res}}, (s_{\text{res}}, \dots, s_{\text{res}})). \quad (2.4)$$

128 *2.2. The metapopulation fitness R_m*

Suppose that all residents have the same strategy s_{res} . Consider a dispersing mutant juvenile with strategy s_{mut} . With some probability it survives dispersal and settles in a patch and becomes an adult there. In that case it will next produce juveniles, and a part of those juveniles remain in the focal patch, and may be chosen to be adults in the next generation. These mutant adults again produce juveniles. The initial mutant and its descendants in the focal patch form a mutant colony. The metapopulation reproduction number (metapopulation fitness) R_m is the expected number of mutant juveniles that are sent from this mutant colony during its lifetime (taking the initial survival and settlement probability into account) (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). Obviously it is a function of s_{res} and s_{mut} . Given the fecundity function F , an expression of R_m is derived in Appendix A.

Invasion fitness is the long-term exponential growth rate of a mutant in an environment set by the resident (Metz et al., 1992). A mutant may invade the resident, if it has positive invasion fitness. However, positive invasion fitness does not guarantee invasion success, because the initial stage of a potential invasion involves demographic stochasticity. For many metapopulation models, the metapopulation fitness is easier to calculate than the invasion fitness. In general, invasion fitness is positive if and only if $R_m > 1$, and therefore metapopulation fitness can be used as a fitness proxy and it plays a central role in metapopulation theory. In Appendix B we provide a formal proof about their relation in this particular model. Intuitively speaking, metapopulation fitness being greater than one means that a single mutant colony produces more than one descendant mutant colonies.

The basic reproduction number (ratio) is a widely used concept in the field of epidemics, in which it is used to describe the expected number of infections caused by a single infected individual. The same concept can also be used to describe population growth, in which context it is the expected number of offspring that an individual will get during its lifetime. It thus measures population growth between real generations in an analogous way that the metapopulation reproduction number measures growth between dispersal generations. In contrast, the invasion fitness measures population growth in real time. The invasion criterion can also be formulated using the basic reproduction ratio, and therefore it acts as another fitness proxy. For a further discussion about fitness (proxies) and variants of the basic reproduction number see Lehmann et al. (2016)

When the effect of mutation is small enough (i.e. s_{mut} is close to s_{res}), we
 166 can use the Taylor expansion with respect to s_{mut} around s_{res} to study the
 potential for invasion. Because the metapopulation fitness is equal to one
 168 when $s_{\text{mut}} = s_{\text{res}}$, we have

$$R_m \approx 1 + (s_{\text{mut}} - s_{\text{res}})D_1(s_{\text{res}}) + \frac{1}{2}(s_{\text{mut}} - s_{\text{res}})^2 D_2(s_{\text{res}}), \quad (2.5)$$

where $D_1(s_{\text{res}})$ and $D_2(s_{\text{res}})$ are the first- and second- order derivatives of R_m ,
 170 calculated as

$$\begin{aligned} D_1(s_{\text{res}}) &= \left. \frac{\partial}{\partial s_{\text{mut}}} R_m \right|_{s_{\text{mut}}=s_{\text{res}}}, \\ D_2(s_{\text{res}}) &= \left. \frac{\partial^2}{\partial s_{\text{mut}}^2} R_m \right|_{s_{\text{mut}}=s_{\text{res}}}. \end{aligned} \quad (2.6)$$

In particular, the first-order derivative, $D_1(s_{\text{res}})$, is usually called *selection*
 172 *gradient* or *fitness gradient*.

2.3. Ajar's (2003) general formulae

Ajar (2003) gave a general formula of the first-order derivative, $D_1(s_{\text{res}})$,
 174 (i.e. equation (5) in Ajar (2003)) in terms of relatedness coefficients via a
 176 metapopulation fitness calculation. To use Ajar's result, we need to inves-
 tigate the expected number of surviving offspring of a mutant in a patch
 178 where there are j mutants (including the focal mutant). Let us use the same
 symbol as Ajar (2003) and denote it by w_j . It is given as

$$\begin{aligned} w_j &= w_j^{\text{P}} + w_j^{\text{A}} \\ &= \underbrace{\frac{n(1-m)F_{\text{mut}}^j}{(1-m)\{jF_{\text{mut}}^j + (n-j)F_{\text{res}}^j\} + pmnF_{\text{res}}^0}}_{w_j^{\text{P}}} + \underbrace{\frac{pmF_{\text{mut}}^j}{(1-m+pm)F_{\text{res}}^0}}_{w_j^{\text{A}}}, \end{aligned} \quad (2.7)$$

180 where w_j^{P} and w_j^{A} respectively represent the philopatric and allopatric com-
 ponents of surviving offspring; namely, the expected number of offspring that
 182 settle down in the local patch and the expected number of offspring that settle
 down in other patches. Since the mutant is (at least initially) rare, the de-
 184 nominator of the allopatric component does not contain mutant immigrants.

Ajar (2003) also gave a formula of the second-order derivative, $D_2(s_{\text{res}})$, (i.e. equation (9) in Ajar (2003)) in terms of relatedness coefficients that is valid at the strategy s_{res} where $D_1(s_{\text{res}})$ vanishes. To use the formula, we need to further derive the quantity called π_j in Ajar (2003), but it is equivalent to our $(j/n)w_j^P$ in equation (2.7).

In the next section we present explicit expressions of the selection gradient and conditions for convergence stability and evolutionary stability in terms of derivatives of the fecundity function (2.1) and original spatial parameters (deme size n , dispersal probability m and the probability to survive dispersal p). We believe that the benefit of deriving these results are twofold. First, Ajar's results are expressed in terms of w , but not in terms of fecundity, F . In practical application, it is useful to understand the effect of functional forms of fecundity on evolutionary consequences. Second, Ajar's formulae are very general but therefore somewhat tedious to use. In contrast, the numbering of other strategies s_2, \dots, s_n in our fecundity function $F(s_1; (s_2, \dots, s_n))$ is arbitrary, and therefore by using this symmetry we are able to obtain much simpler expressions of the first and second order derivatives, which give us insightful intuitions. A large part of the results in the next section can be derived by applying Ajar (2003) formulae to the expression w_j (2.7), although we present the derivation of the expressions starting from the metapopulation fitness (in the Appendix).

3. Evolution of strategy s

3.1. First-order results

Because of the symmetry property of $F(s_1; (s_2, \dots, s_n))$, there are essentially only two different first-order derivatives of F . One is the first-order derivative with respect to the strategy of self, which is defined as

$$F_S = \left. \frac{\partial}{\partial s_1} F(s_1; (s_2, \dots, s_n)) \right|_{s_1 = \dots = s_n = s_{\text{res}}} . \quad (3.1)$$

The other is the first-order derivative with respect to the strategy of anybody else in the patch, defined as

$$F_D = \left. \frac{\partial}{\partial s_k} F(s_1; (s_2, \dots, s_n)) \right|_{s_1 = \dots = s_n = s_{\text{res}}} , \text{ where } k \in \{2, \dots, n\}, \quad (3.2)$$

because the right-hand side of that equality is independent of the choice of
 214 k . Note that the subscripts “S” and “D” respectively represent “Self” and
 “Different”.

216 Especially, by differentiating (2.2) and (2.3) we obtain

$$\begin{aligned} \frac{\partial}{\partial s_{\text{mut}}} F_{\text{res}}^i(s_{\text{res}}, s_{\text{mut}}) \Big|_{s_{\text{mut}}=s_{\text{res}}} &= iF_{\text{D}} \\ \frac{\partial}{\partial s_{\text{mut}}} F_{\text{mut}}^i(s_{\text{res}}, s_{\text{mut}}) \Big|_{s_{\text{mut}}=s_{\text{res}}} &= F_{\text{S}} + (i-1)F_{\text{D}}. \end{aligned} \quad (3.3)$$

Theorem 1. *By using (3.3), the first-order derivative of the metapopulation
 218 fitness (the selection gradient) can be written as*

$$D_1(s_{\text{res}}) = \frac{n(2-d)}{n - (n-1)(1-d)^2} \cdot \left(\frac{F_{\text{S}}}{F_{\text{res}}^0} \right) \quad (3.4)$$

where

$$d = \frac{pm}{(1-m) + pm} \quad (3.5)$$

220 *is the backward migration probability, i.e., the proportion of adults that are*
immigrant in a monomorphic population (everybody has the same strategy),
 222 $0 < d \leq 1$.

Proof. The result is obtained by applying the implicit function theorem on
 224 the expression of metapopulation fitness. See the Appendix C. \square

We note that such first order effects have been derived for a wider class of
 226 models by Ajar (2003) (by using metapopulation fitness, in terms of fitness
 derivatives; see eq. (5) therein), by Wakano and Lehmann (2014) (by using
 228 trait distribution approach, in terms of fitness derivatives; see their eq. (12),
 also see Appendix F of this paper), and by Mullan et al. (2016) (by using
 230 lineage fitness; their eq. (12) is written in terms of fitness derivatives, and
 their eq. (18) is written in terms of “payoff” derivatives). In particular, our
 232 Theorem 1 is a direct consequence of eq. (18) in Mullan et al. (2016) when
 we calculate the κ -parameter there according to our Wright-Fisher life-cycle
 234 assumption.

A strategy s^* is called a *singular strategy* (Geritz et al., 1997, 1998) if the
 236 selection gradient vanishes when that strategy is resident, $D_1(s^*) = 0$.

Corollary 2. *Because the factor in front of $(F_{\text{S}}/F_{\text{res}}^0)$ in (3.4) is always
 238 positive, the sign of the selection gradient is determined by F_{S} alone, and
 singular strategies are such strategies for which $F_{\text{S}} = 0$.*

240 A good reference point for understanding (3.4) is when everybody dis-
 242 perses (i.e. $m = 1$ and hence $d = 1$). In this case, the population is es-
 Equation (3.4) states that the (sign of the) selection gradient is preserved
 244 even when the island structure is introduced. From (3.3) we could naively
 expect that the other derivative, F_D , should also be relevant in the selection
 246 gradient, but (3.4) says that it is not the case.

To facilitate our understanding, imagine social interaction in a patch
 248 of n individuals. Each individual can independently choose the amount of
 cooperation s . Cooperation is costly to the individual performing the act, but
 250 beneficial to the others: The benefit of cooperation will be equally distributed
 to the other $n - 1$ individuals excluding self. The described situation is one
 252 instance of public-goods games, and a natural choice of fecundity function of
 this game model would be

$$F(s_1; (s_2, \dots, s_n)) = F_{\text{baseline}} - cs_1 + b \frac{s_2 + \dots + s_n}{n - 1}, \quad (3.6)$$

254 where $b > 0$, $c > 0$ and $F_{\text{baseline}} > 0$ is a baseline fecundity. We have $F_S = -c$
 and $F_D = b/(n - 1)$ in this example. Equation (3.4) therefore suggests that
 256 a smaller amount of cooperation is favored as long as $c > 0$ and that the
 value of b does not affect the sign of the selection gradient *at all*. Indeed,
 258 Taylor (1992a) studied the evolution of cooperation in Wright's island model,
 and showed that cooperation can evolve if the act of cooperation provides a
 260 net benefit to the actor herself (his equation 5). In other words, altruism,
 which is defined as an act that does not provide a net benefit to the actor
 262 but does yield benefit to others, never evolves in the island model. In viscous
 populations, altruists tend to cluster in locality, which favors its evolution.
 264 At the same time, however, limited dispersal causes competition among kin,
 which disfavors altruism. Here these two opposing effects precisely cancel
 266 each other. This result is called Taylor's cancellation result, and has been
 shown shown to hold when one adopts the same life-cycle assumptions (non-
 268 overlapping generations and so on) as ours (Taylor, 1992a,b; Queller, 1992;
 Wilson et al., 1992; Rousset, 2004; Gardner and West, 2006; Lehmann et al.,
 270 2007; Lehmann and Rousset, 2010; Taylor et al., 2011; Ohtsuki, 2012). In
 this sense, our result (Corollary 2) confirms the results of Taylor (1992a) and
 272 Taylor et al. (2011). Under different life-cycle assumptions, spatial structure
 has been shown to affect the evolution of cooperation (e.g., Taylor and Ir-
 274 win, 2000; Lehmann and Rousset, 2010; Parvinen, 2010, 2011; Seppänen and

Parvinen, 2014).

276 *3.2. Second-order results*

Similarly to before, by using the property of the fecundity function,
278 $F(s_1; (s_2, \dots, s_n))$, that the order of the other strategies than s_1 can be freely
permutated, we see that there are only four kinds of second-order derivatives
280 of F :

$$\begin{aligned}
 F_{SS} &= \frac{\partial^2}{\partial s_1^2} F(s_1; (s_2, \dots, s_n)) \Big|_{s_1=\dots=s_n=s_{\text{res}}} \\
 F_{DD} &= \frac{\partial^2}{\partial s_k^2} F(s_1; (s_2, \dots, s_n)) \Big|_{s_1=\dots=s_n=s_{\text{res}}}, \text{ where } k \in \{2, \dots, n\} \\
 F_{SD} &= \frac{\partial^2}{\partial s_1 \partial s_k} F(s_1; (s_2, \dots, s_n)) \Big|_{s_1=\dots=s_n=s_{\text{res}}}, \text{ where } k \in \{2, \dots, n\} \\
 F_{DD'} &= \frac{\partial^2}{\partial s_j \partial s_k} F(s_1; (s_2, \dots, s_n)) \Big|_{s_1=\dots=s_n=s_{\text{res}}}, \text{ where } j, k \in \{2, \dots, n\}, j \neq k.
 \end{aligned} \tag{3.7}$$

Especially, by differentiating (2.2) and (2.3) we obtain

$$\begin{aligned}
 \frac{\partial^2}{\partial s_{\text{mut}}^2} F_{\text{res}}^i(s_{\text{res}}, s_{\text{mut}}) \Big|_{s_{\text{mut}}=s_{\text{res}}} &= iF_{DD} + i(i-1)F_{DD'}, \\
 \frac{\partial^2}{\partial s_{\text{mut}}^2} F_{\text{mut}}^i(s_{\text{res}}, s_{\text{mut}}) \Big|_{s_{\text{mut}}=s_{\text{res}}} &= F_{SS} + (i-1)F_{DD} + 2(i-1)F_{SD} \\
 &\quad + (i-1)(i-2)F_{DD'}.
 \end{aligned} \tag{3.8}$$

282 *3.2.1. Convergence stability*

A (singular) strategy s^* is an evolutionary attractor (convergence stable)
284 if the repeated invasion of nearby mutant strategies into resident strategies
will lead to the convergence of resident strategies towards s^* (Christiansen,
286 1991). For one-dimensional strategies this occurs when the sign of the deriva-
tive of $D_1(s_{\text{res}})$ with respect to s_{res} is negative.

288 **Theorem 3.** *The condition $D'_1(s) < 0$ for a singular strategy s to be an
evolutionary attractor (convergence stable) is expressed in terms of F as*

$$F_{SS} + (n-1)F_{SD} < 0. \tag{3.9}$$

290 *Proof.* At a singular strategy we have $F_S(s) = 0$. Therefore the derivative of $D_1(s)$ is, up to some positive constant, equal to

$$\frac{d}{ds} \left(\frac{F_S(s)}{F_{\text{res}}^0(s)} \right) = \frac{F'_S(s)F_{\text{res}}^0(s) - F_S(s)(F_{\text{res}}^0)'(s)}{(F_{\text{res}}^0(s))^2} = \frac{F'_S(s)}{F_{\text{res}}^0(s)}.$$

292 We also know that

$$F'_S(s) = \frac{d}{ds} F_S(s; (s, \dots, s)) = F_{SS} + (n-1)F_{SD}.$$

Hence the result holds. Note that the condition of convergence stability is
294 the same as that in the well-mixed model (Wakano and Lehmann, 2014). \square

3.2.2. Evolutionary stability

296 The second-order derivative of metapopulation fitness is given by the following formula.

298 **Theorem 4.** *Using the properties (3.3) and (3.8) the second-order derivative of metapopulation fitness can be written as*

$$D_2(s_{\text{res}}) = C \left[\phi_{SS} \left(\frac{F_{SS}}{F_{\text{res}}^0} \right) + \phi_{SD} \left(\frac{F_{SD}}{F_{\text{res}}^0} \right) + \phi_{DD'} \left(\frac{F_{DD'}}{F_{\text{res}}^0} \right) + \psi_{S \times S} \left(\frac{F_S}{F_{\text{res}}^0} \right)^2 + \psi_{S \times D} \left(\frac{F_S}{F_{\text{res}}^0} \right) \left(\frac{F_D}{F_{\text{res}}^0} \right) + \psi_{D \times D} \left(\frac{F_D}{F_{\text{res}}^0} \right)^2 \right], \quad (3.10)$$

300 where

$$\begin{aligned} \phi_{SS} &= (2-d) \{n - (n-1)(1-d)^2\} \{n^2 - (n-1)(n-2)(1-d)^3\} > 0, \\ \phi_{SD} &= 2(n-1)(1-d)^2 \{n - (n-1)(1-d)^2\} \{n + n(1-d) + (n-2)(1-d)^2\} \geq q0, \\ \phi_{DD'} &= (n-1)(n-2)d(1-d)^3 \{n - (n-1)(1-d)^2\} \geq q0, \\ \psi_{S \times S} &= 2(1-d) \left\{ n^3 + 2n^2(n-1)(1-d) + n(n-1)^2(1-d)^2 - n^2(n-1)(1-d)^3 \right. \\ &\quad \left. - (2n^3 - 6n^2 + 5n - 1)(1-d)^4 - (n-1)^3(1-d)^5 \right\} \geq q0, \\ \psi_{S \times D} &= -2(n-1)(1-d)^4 \{n + 2(n-1)(1-d)^2\} \leq q0, \\ \psi_{D \times D} &= -2(n-1)^2 d(1-d)^3 \{n - (n-1)(1-d)^2\} \leq q0, \\ C &= \frac{n}{\{n - (n-1)(1-d)^2\}^2 \{n^2 - (n-1)(n-2)(1-d)^3\}} > 0. \end{aligned}$$

Proof. The result is again obtained by applying the implicit function theorem
 302 on the expression of metapopulation fitness. See the Appendix D. \square

Note that such second-order results (not necessarily at singular points)
 304 have been obtained by Mullon et al. (2016) for a wider class of models (by
 using lineage fitness; their eq. (13) is written in terms of fitness derivatives,
 306 and their eq. (19) is written in terms of “payoff” derivatives under the as-
 sumption that traits have no effect on pairwise relatedness). Also note that
 308 this result is not derived from Ajar (2003), because Ajar (2003) provided a
 formula of the second-order derivative only at a singular strategy.

310 Comparison with the result of Mullon et al. (2016) elucidates that the
 first three terms in the square brackets of (3.10) correspond to the effect
 312 of joint deviation of two players’ strategies on one’s fitness, whereas the last
 three terms correspond to the effect of deviation of strategies on demography
 314 (relatedness). For more intuition, we cite Mullon et al. (2016).

Setting $F_S = 0$ reproduces the following result.

316 **Corollary 5.** *At a singular strategy, the second derivative $D_2(s_{\text{res}})$ has the
 same sign as*

$$\tilde{D}_2(s_{\text{res}}) = \tilde{\phi}_{\text{SS}} \left(\frac{F_{\text{SS}}}{F_{\text{res}}^0} \right) + \tilde{\phi}_{\text{SD}} \left(\frac{F_{\text{SD}}}{F_{\text{res}}^0} \right) + \tilde{\phi}_{\text{DD}'} \left(\frac{F_{\text{DD}'}}{F_{\text{res}}^0} \right) + \tilde{\psi}_{\text{D} \times \text{D}} \left(\frac{F_{\text{D}}}{F_{\text{res}}^0} \right)^2, \quad (3.11)$$

318 where

$$\begin{aligned} \tilde{\phi}_{\text{SS}} &= (2-d) \{n^2 - (n-1)(n-2)(1-d)^3\} > 0, \\ \tilde{\phi}_{\text{SD}} &= 2(n-1)(1-d)^2 \{n + n(1-d) + (n-2)(1-d)^2\} \geq q0, \\ \tilde{\phi}_{\text{DD}'} &= (n-1)(n-2)d(1-d)^3 \geq q0, \\ \tilde{\psi}_{\text{D} \times \text{D}} &= -2(n-1)^2d(1-d)^3 \leq q0. \end{aligned} \quad (3.12)$$

If $\tilde{D}_2(s_{\text{res}})$ is negative, the singular strategy is evolutionarily stable (ES). If
 320 positive, on the other hand, it is not evolutionarily stable. The expression
 $\tilde{D}_2(s_{\text{res}})$ can also be written as

$$\tilde{D}_2(s_{\text{res}}) = \tilde{\xi}_{\text{SS}} \left(\frac{F_{\text{SS}}}{F_{\text{res}}^0} \right) + \frac{\tilde{\phi}_{\text{SD}}}{n-1} \left(\frac{F_{\text{SS}} + (n-1)F_{\text{SD}}}{F_{\text{res}}^0} \right) + \tilde{\phi}_{\text{DD}'} \left(\frac{F_{\text{DD}'}}{F_{\text{res}}^0} \right) + \tilde{\psi}_{\text{D} \times \text{D}} \left(\frac{F_{\text{D}}}{F_{\text{res}}^0} \right)^2, \quad (3.13)$$

322 *where*

$$\begin{aligned}\tilde{\xi}_{\text{SS}} &= \tilde{\phi}_{\text{SS}} - \frac{\tilde{\phi}_{\text{SD}}}{n-1} \\ &= d \left[n^2 + 2(1-d)n^2 + 2(1-d)^2n(n-1) + (1-d)^3(n-2)(n+1) \right] \geq 0.\end{aligned}\tag{3.14}$$

The form (3.13) is especially helpful, because $F_{\text{SS}} + (n-1)F_{\text{SD}} < 0$ holds
324 for a convergence stable singular strategy. Especially, for low d the term with
 $\tilde{\phi}_{\text{SD}}$ dominates, and for d close to 1 the term with $\tilde{\xi}_{\text{SS}}$ dominates (See Fig. 1
326 for illustration). We will use these properties in the next section.

Note that such second-order results at singular points as our (3.11) have
328 been derived by Ajar (2003) (by using metapopulation fitness, in terms of
fitness derivatives; see eq. (9) therein) and by Wakano and Lehmann (2014)
330 (by using trait distribution approach, in terms of fitness derivatives; see their
eqs. (26–28), also see Appendix F of this paper).

332 It is notable that one of the four second-order derivatives of fecundity
function, F_{DD} , does not appear in $D_2(s_{\text{res}})$ or $\tilde{D}_2(s_{\text{res}})$. It can be deemed as
334 another “cancellation result” that holds under the present assumptions about
the life cycle. This was observed also by Wakano and Lehmann (2014) in case
336 of pairwise games: in their equation (37) their parameter $\kappa = 0$ for Wright-
Fisher update rule. Theorem 4, from which Corollary 5 follows, was obtained
338 by applying the implicit function theorem on the expression of metapopula-
tion fitness. Note also that exactly the same result as in Corollary 5 can be
340 derived by the trait distribution approach (see Appendix F).

4. Does spatial structure inhibit branching?

342 4.1. *Spatial structure inhibits branching in a wide class of fecundity functions*

Using a continuous snowdrift game (Doebeli et al., 2004) as an example,
344 Wakano and Lehmann (2014) have shown that a branching point (evolution-
arily attracting singular strategy, which is not uninvadable) in a well-mixed
346 model changes to be evolutionarily stable (uninvadable) as the migration rate
decreases below a threshold value. We can generalize this result in the form
348 of the following theorem.

Theorem 6. *Evolutionary branching is not possible for a sufficiently small*
350 *value of d (that is, small m or small p).*

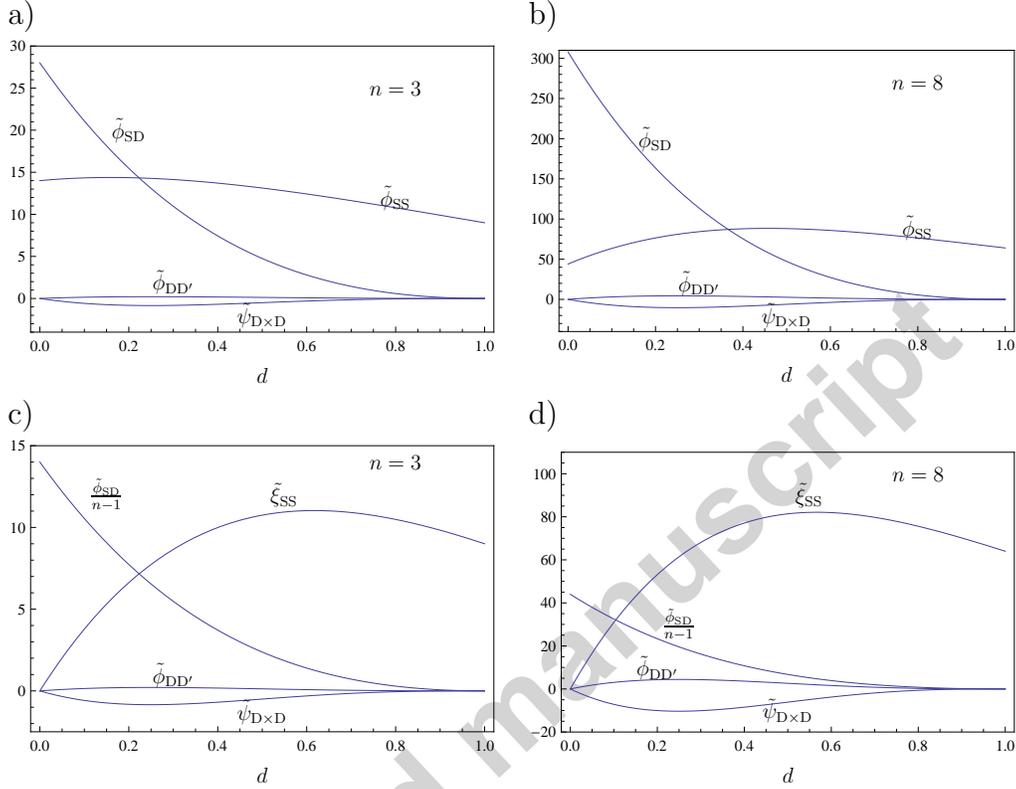


Figure 1: Effect of the fecundity derivatives on evolutionary stability. Coefficients of $\tilde{D}_2(s_{\text{res}})$ given (a,b) by equation (3.12) and (c,d) by equation (3.13) as a function of d when (a,c) $n = 3$ and (b,d) $n = 8$.

Proof. In the limit of $d \rightarrow 0$ ($m \rightarrow 0$ or $p \rightarrow 0$), we have $\tilde{\xi}_{SS} = \tilde{\phi}_{DD'} = \tilde{\psi}_{D \times D} = 0$ (See Fig. 1c,d), and $\tilde{D}_2(s_{\text{res}})$ (equation 3.13) becomes

$$\tilde{D}_2(s_{\text{res}})\Big|_{d=0} = 2(3n - 2) \frac{F_{SS} + (n - 1)F_{SD}}{F_{\text{res}}^0}. \quad (4.1)$$

According to Theorem 3 (Equation 3.9), if a singular strategy s is convergence stable we have $F_{SS} + (n - 1)F_{SD} < 0$, which means that (4.1) is negative. This means that any convergence stable singular strategy is (locally) uninvadable (evolutionary stable). Based on continuity arguments, evolutionary branching is not possible when d is close to 0. \square

Theorem 6 shows that a branching point never exists for a sufficiently small d . However, there is still a possibility that a singular strategy which is

360 evolutionarily stable and convergence stable in a well-mixed model becomes
 362 a branching point in structured models with intermediate d values. The
 following theorem shows that this will not happen for a wide class of fecundity
 functions.

364 **Theorem 7.** *Suppose a singular strategy s is evolutionarily stable and con-*
vergence stable in a well-mixed model, that is

$$F_S = 0, F_{SS} + (n - 1)F_{SD} < 0, \text{ and } F_{SS} < 0. \quad (4.2)$$

366 *If*

$$F_{DD'} \leq 0 \quad (4.3)$$

or

$$F_{DD'} \leq F_{SD} \quad (4.4)$$

368 *then s is also evolutionarily stable and convergence stable in the corresponding*
structured models, that is

$$\tilde{D}_2(s) < 0 \quad (4.5)$$

370 *holds for $0 < d < 1$.*

Proof. According to (3.13)

$$\begin{aligned} \tilde{D}_2(s_{\text{res}}) = & \underbrace{\tilde{\xi}_{SS}}_{\geq 0} \underbrace{\left(\frac{F_{SS}}{F_{\text{res}}^0}\right)}_{< 0} + \underbrace{\frac{\tilde{\phi}_{SD}}{n-1}}_{\geq 0} \underbrace{\left(\frac{F_{SS} + (n-1)F_{SD}}{F_{\text{res}}^0}\right)}_{< 0} \\ & + \underbrace{\tilde{\phi}_{DD'}}_{\geq 0} \underbrace{\left(\frac{F_{DD'}}{F_{\text{res}}^0}\right)}_{\leq 0} + \underbrace{\tilde{\psi}_{D \times D}}_{\leq 0} \underbrace{\left(\frac{F_D}{F_{\text{res}}^0}\right)^2}_{\geq 0} < 0 \end{aligned} \quad (4.6)$$

372 where the inequalities follow from the assumptions (4.2) and (4.3) together
 with properties $\tilde{\xi}_{SS} \geq 0$, $\tilde{\phi}_{SD} \geq 0$, $\tilde{\phi}_{DD'} \geq 0$ and $\tilde{\psi}_{D \times D} \leq 0$, which proves
 374 the first part of the theorem. Using the assumptions (4.2) and (4.4) and the

properties $\tilde{\phi}_{SD} \geq 0$, $\tilde{\phi}_{DD'} \geq 0$ and $\tilde{\psi}_{D \times D} \leq 0$, we have

$$\begin{aligned}
\tilde{D}_2(s) &\leq \tilde{\phi}_{SS} \left(\frac{F_{SS}}{F_{res}^0} \right) + \tilde{\phi}_{SD} \left(\frac{F_{SD}}{F_{res}^0} \right) + \tilde{\phi}_{DD'} \left(\frac{F_{DD'}}{F_{res}^0} \right) \\
&= \tilde{\phi}_{SS} \left(\frac{F_{SS}}{F_{res}^0} \right) + (\tilde{\phi}_{SD} + \tilde{\phi}_{DD'}) \left(\frac{F_{SD}}{F_{res}^0} \right) + \tilde{\phi}_{DD'} \left(\frac{F_{DD'} - F_{SD}}{F_{res}^0} \right) \\
&\leq \tilde{\phi}_{SS} \left(\frac{F_{SS}}{F_{res}^0} \right) + (\tilde{\phi}_{SD} + \tilde{\phi}_{DD'}) \left(\frac{F_{SD}}{F_{res}^0} \right) \\
&= \left(\tilde{\phi}_{SS} - \frac{\tilde{\phi}_{SD} + \tilde{\phi}_{DD'}}{n-1} \right) \left(\frac{F_{SS}}{F_{res}^0} \right) + (\tilde{\phi}_{SD} + \tilde{\phi}_{DD'}) \left(\frac{F_{SS} + (n-1)F_{SD}}{(n-1)F_{res}^0} \right) \quad (4.7) \\
&\leq \left(\tilde{\phi}_{SS} - \frac{\tilde{\phi}_{SD} + \tilde{\phi}_{DD'}}{n-1} \right) \left(\frac{F_{SS}}{F_{res}^0} \right) \\
&= d(2-d)n\{(1-d)^2(n-2) + (2-d)n\} \left(\frac{F_{SS}}{F_{res}^0} \right) \\
&< 0.
\end{aligned}$$

376

□

4.2. Spatial structure can promote evolutionary branching with some fecundity functions

The convergence stability of a singular strategy is determined by the sign of $F_{SS} + (n-1)F_{SD}$, and evolutionary stability by the sign of equation (3.11) involving the derivatives F_{SS} , F_{SD} , $F_{DD'}$ and F_D . The two latter derivatives thus only affect evolutionary stability, and not convergence stability. The corresponding coefficients of $\tilde{D}_2(s_{res})$, $\tilde{\phi}_{DD'} \geq 0$ and $\tilde{\psi}_{D \times D} \leq 0$ (3.12) are zero for $d = 0$ and $d = 1$, so they affect evolutionary stability for intermediate values of d . Therefore, when $\frac{F_{DD'}}{F_{res}^0}$ is positive and large compared to $\left(\frac{F_D}{F_{res}^0}\right)^2$, $\tilde{D}_2(s)$ can be positive for intermediate values of d , even though branching does not occur for $d = 1$, $F_{SS} < 0$.

Now consider the following fecundity function, for which strategies $s \in [0, 2]$.

$$F(s_1; (s_2, s_3, \dots, s_n)) = 1 - (s_1 - 1)^2 + b \left(\frac{s_2 + s_3 + \dots + s_n}{n-1} - 1 \right)^2, \quad b > 0. \quad (4.8)$$

This fecundity function is to some extent artificial. It can be thought to describe some kind of public-goods situation in which deviation from $s = 1$ is costly to the actor, and benefits are obtained according to how much others on average deviate from $s = 1$. Although (4.8) is of form (5.9), results presented in Section 5.2 do not apply here, because functions $f(s) = 1 + b(s-1)^2$ and

$g(s) = (s - 1)^2$ (notation of equation 5.9) are not increasing for all $s \in [0, 2]$.
 396 For this model $F_S = -2(s - 1)$ and $F_{SS} + (n - 1)F_{SD} = -2$, which means that
 $s = 1$ is a singular strategy, and convergence stable for all d . Furthermore,
 398 $F_{SS} = -2$, so that the singular strategy is evolutionarily stable in the well-
 mixed model. Since for $s = 1$ we have $F_D = 0$ and $\frac{F_{DD'}}{F_{res}^0} = \frac{2b}{(n-1)^2}$ is positive,
 400 the conditions listed in the previous paragraph hold when b is large enough.
 Figure 2 indeed shows, that when b is large, the strategy $s = 1$ is a branching
 402 point for intermediate values of d . The threshold value for b , above which
 branching is possible, is, however, unrealistically large, and increases with n .
 404 Finding such cases in reality would be unlikely. Nevertheless, this example
 shows that spatial structure can promote branching with some fecundity
 406 functions, and thus it is not possible to prove that spatial structure would
 always inhibit evolutionary branching.

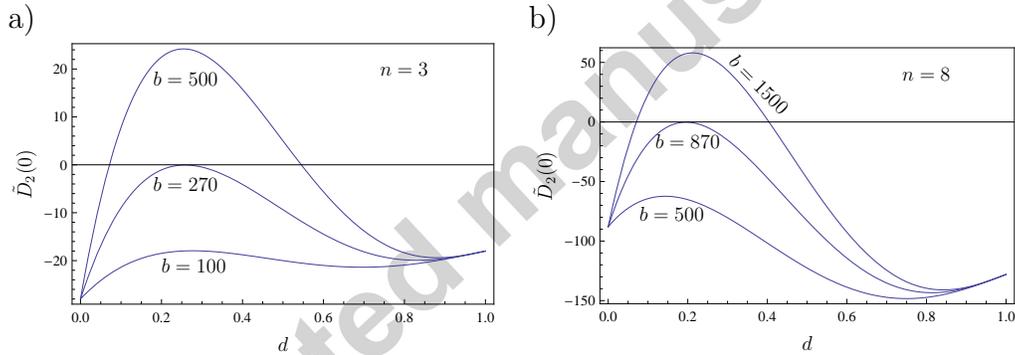


Figure 2: Spatial structure can promote evolutionary branching with some fecundity functions. The expression $\tilde{D}_2(s_{res})$ determining evolutionary stability given by equation (3.11) of the singular strategy $s_{res} = 1$ as a function of d for the fecundity function (4.8) with a) $n = 3$ and b) $n = 8$ for different values of the parameter b .

408 5. Examples

5.1. Pairwise games

410 Assume that individuals in the deme play pairwise games among each
 other and that the total payoff from these games determines the fecundity
 412 of each individual. We can either assume that a certain number of games is
 played, and the game participants are randomly chosen, or that all possible
 414 combinations of games take place. In some games the role of individuals

416 matters. In such a situation, let $G_i(s_{\text{self}}, s_{\text{opponent}})$ denote the payoff of the
 418 individual using strategy s_{self} in role i matched with the player using strategy
 s_{opponent} . Assume that the player has a list of strategies, represented by a
 420 vector $\mathbf{s} = (s^{(1)}, s^{(2)})$ for playing strategy $s^{(1)}$ in role 1 and playing $s^{(2)}$ in
 422 role 2. When player 1 with the list $\mathbf{s}_1 = (s_1^{(1)}, s_1^{(2)})$ is matched with player 2
 424 with the list $\mathbf{s}_2 = (s_2^{(1)}, s_2^{(2)})$ and if their roles are determined randomly, the
 426 expected payoff of player 1 will be $G(\mathbf{s}_1, \mathbf{s}_2) = G_1(s_1^{(1)}, s_2^{(2)}) + G_2(s_1^{(2)}, s_2^{(1)})$ up
 to a factor of $1/2$. Some games are symmetric, so that roles do not matter,
 in which case it is rather easy to write the function $G(s_1, s_2)$ directly as
 the payoff of an individual playing s_1 playing against an s_2 opponent. An
 example of a symmetric game is the nonlinear snowdrift game studied by
 Doebeli et al. (2004).

$$G(s_1, s_2) = 1 + \underbrace{b_1(s_1 + s_2) + b_2(s_1 + s_2)^2}_{\text{common benefit}} - \underbrace{c_2(s_1)^2 - c_1 s_1}_{\text{individual cost}}, \quad (5.1)$$

428 where s denotes the cooperation strategy of individuals. The common benefit
 of the game is a function of the sum of the two investments, but the cost
 of investment is paid by the investor only. For example, when $b_1 = 6, b_2 =$
 430 $-1.4, c_1 = 4.56, c_2 = -1.6$, evolutionary branching occurs in the well-mixed
 situation (Figure 1A by Doebeli et al. (2004)).

432 In general, we assume that the fecundity of a focal individual in the deme
 is given by

$$F(s_1; (s_2, \dots, s_n)) = F_{\text{baseline}} + \sum_{j=2}^n G(s_1, s_j) \quad (5.2)$$

434 Here, F_{baseline} represents the baseline fecundity that is common to all individ-
 uals, and G is a payoff function of an ‘elementary’ pairwise (i.e. two-player)
 436 game played in the population.

438 We are interested in how the introduction of spatial structure affects con-
 ditions of evolutionary branching. The first-order and second-order deriva-
 tives of F are written in terms of G as follows;

$$\begin{aligned} F_S &= (n-1)G_1, & F_{SD} &= G_{12}, \\ F_D &= (n-1)G_2, & F_{DD} &= G_{22}, \\ F_{SS} &= (n-1)G_{11}, & F_{DD'} &= 0, \end{aligned} \quad (5.3)$$

440 where

$$G_1 = \frac{\partial}{\partial s_1} G(s_1, s_2) \Big|_{s_1=s_2=s_{\text{res}}}, \quad G_2 = \frac{\partial}{\partial s_2} G(s_1, s_2) \Big|_{s_1=s_2=s_{\text{res}}}, \quad (5.4)$$

$$\begin{aligned} G_{11} &= \frac{\partial^2}{\partial (s_1)^2} G(s_1, s_2) \Big|_{s_1=s_2=s_{\text{res}}}, \quad G_{12} = \frac{\partial^2}{\partial s_1 \partial s_2} G(s_1, s_2) \Big|_{s_1=s_2=s_{\text{res}}}, \\ G_{22} &= \frac{\partial^2}{\partial (s_2)^2} G(s_1, s_2) \Big|_{s_1=s_2=s_{\text{res}}}. \end{aligned} \quad (5.5)$$

442 A notable feature of pairwise games is that evolutionary branching is never
 443 favored by spatial structure. This is because $F_{\text{DD}'} = 0$ and Theorem 7 ap-
 444 plies. Intuitively speaking, a non-zero $F_{\text{DD}'}$ suggests that there is a synergetic
 445 interaction between two others' strategies. However, the fecundity function
 446 of the form (5.2) does not allow such synergy because a focal individual plays
 447 the pairwise game separately with every other. In contrast, the result in the
 448 previous section implies that we can construct a certain 'elementary' three-
 449 person game $G(s_1, s_2, s_3)$ that generates a fecundity function with which
 450 spatial structure promotes evolutionary branching. In other words, we need
 451 an elementary game that involves at least three players simultaneously to
 452 find a positive effect of spatiality of evolutionary branching.

5.2. Public-goods game

454 Another important class of games other than pairwise game is multi-
 455 person public goods games. Suppose that all n players in the same patch are
 456 engaged in a single n -person public-goods game with non-linear benefit and
 457 cost functions. In this game, one's strategy is often an amount of investment
 458 to a public-good (and hence non-negative). In most cases cost is given as a
 459 function of the investment level by self. However, there are two major ways
 460 of formulating the benefit function (Sigmund, 2010). One way is to assume
 461 that one's benefit is a function of the average investment level of all n players
 462 in the same patch including self. In this case, the fecundity function is given
 by

$$F(s_1; (s_2, \dots, s_n)) = f\left(\frac{s_1 + s_2 + \dots + s_n}{n}\right) - g(s_1), \quad (5.6)$$

464 where f and g are benefit and cost functions, respectively. Both are assumed
 to be increasing functions. The first order derivatives are given by

$$F_S = \frac{f'(s_{\text{res}})}{n} - g'(s_{\text{res}}), \quad F_D = \frac{f'(s_{\text{res}})}{n}. \quad (5.7)$$

466 The boundary strategy $s = 0$ is evolutionarily repelling, if $F_S = \frac{f'(0)}{n} - g'(0) >$
 468 0 , in which case positive investment levels can evolve in an initially non-
 investing population. Singular strategies s are positive strategies for which
 $F_S = 0$. The second order derivatives are given by

$$\begin{aligned} F_{SS} &= \frac{f''(s_{\text{res}})}{n^2} - g''(s_{\text{res}}), \\ F_{SD} &= F_{DD} = F_{DD'} = \frac{f''(s_{\text{res}})}{n^2}. \end{aligned} \quad (5.8)$$

470 Because $F_{SD} = F_{DD}$ holds, from Theorem 7 we conclude that spatial structure
 in our model never favors evolutionary branching in this type of public goods
 472 game.

Another common way to think about benefit in a public-goods game is
 474 that one's benefit is a function of the average investment level of all the other
 $n - 1$ players in the same patch excluding self, in which case eq. (5.6) receives
 476 a minor change as

$$F(s_1; (s_2, \dots, s_n)) = f\left(\frac{s_2 + \dots + s_n}{n - 1}\right) - g(s_1). \quad (5.9)$$

The first order derivatives are given by

$$F_S = -g'(s_{\text{res}}), \quad F_D = \frac{f'(s_{\text{res}})}{n - 1}, \quad (5.10)$$

478 but given usual monotonicity of the cost function g , $g'(s) > 0$, the investment
 level s will evolve to zero both in a well-mixed population and in Wright's
 480 island model studied here.

6. Discussion

482 We have studied evolution by natural selection in Wright's island model
 in which there is an infinite number of patches (demes) of constant, finite
 484 size. In each season adults produce offspring, and the fecundity of each adult
 depends on its own strategy as well as the strategies of other individuals in
 486 the focal patch. A proportion of juveniles disperses to other patches. Since
 adults do not survive until the next season, the fixed number offspring to be-
 488 come adults are randomly chosen among the offspring present in each patch
 after dispersal. We have derived explicit conditions for evolutionary singu-
 490 larity, evolutionary stability, and convergence stability in terms of various

derivatives of the fecundity function. A notable difference from the previous work by Ajar (2003) is that his expressions are formulated in terms of a series expansion of the fitness component (w_j) of individuals, which is the expected number of surviving offspring of a mutant in a patch where there are j mutants (including the focal mutant), our equation (2.7). This expression includes successful offspring both in the focal patch, and those who dispersed to other patches. Such difference might seem trivial but it is actually profound. In evolutionary game theory with genetic inheritance, a payoff through game interactions is sometimes directly translated into one's fecundity. In contrast, one's fitness involves not only the contribution from one's fecundity (called primary effect (West and Gardner, 2010)) but that of fecundity others (called secondary effect) who are in reproductive competition with the focal individual. Therefore, fitness is a complex aggregate of information including structure of the game itself, structure of interaction partners, and structure of offspring dispersal. In contrast, fecundity has a very simple interpretation; a result of games. We hence think it worthwhile to derive several conditions in terms of derivatives of the fecundity function in order to obtain a more intuitive understanding of evolutionary branching. We have used the metapopulation fitness to obtain the branching condition, but note that it can also be derived using the trait-distribution approach (for details, see Appendix F).

We have firstly confirmed in Theorem 1 that an evolutionary singular strategy in the corresponding well-mixed model is not affected by the presence of spatial structure (Taylor, 1992a). More technically, the sign of the selection gradient (3.4) is given by the sign of the derivative F_S , and the derivative F_D does not appear in the singularity condition. As for second-order results, we have also confirmed that the condition of convergence stability is not affected by the spatial structure, either. A technical observation is that one of the second order derivatives, F_{DD} does not at all appear in the condition of evolutionary stability (see Theorem 4).

Our paper has not only reproduced those previously known results but given several novel findings. We found that spatial structure inhibits branching for a wide class of fecundity functions. This statement is based on the following results: First, evolutionary branching never occurs when the effective migration rate d is close to zero (Theorem 6). Moreover we have also found two sufficient conditions (Theorem 7) under which evolutionary branching never occurs in spatial models when the corresponding well-mixed model does not allow branching. Roughly speaking, Theorem 7 holds un-

less the derivative $F_{DD'}$ is positive and large. However, spatial structure can
 530 occasionally promote evolutionary branching with some fecundity functions.
 In fact, in the example in Section 4.2, evolutionary branching can occur only
 532 for intermediate values of d . In other words, although evolutionary branch-
 ing is not possible in a well-mixed setting, it does occur in a spatial setting.
 534 The parameter values for which this scenario happens are, however, not very
 realistic.

Applications of our general theory have revealed that when the fecundity
 536 of individuals is determined only by pairwise interactions between individu-
 538 als (pairwise games), spatial structure never favors evolutionary branching.
 The same observation applies to a wide class of public goods games. It may
 540 suggest that in many biologically reasonable situations, evolutionary branch-
 ing is suppressed in spatial models compared to well-mixed models. Strictly
 542 speaking, our results are valid for Wright's island model with several specific
 life-history assumptions, such as non-overlapping generations, local regula-
 544 tion among adults after dispersal but before reproduction (in contrast with
 population regulation among juveniles after reproduction but before disper-
 546 sal), when a fecundity-affecting trait is under natural selection. Actually, it is
 known that already a slight modification to those life-cycle assumptions made
 548 here may change evolutionary outcomes (Taylor and Irwin, 2000; Lehmann
 and Rousset, 2010). It is better, therefore, to take our result as one reference
 550 point, not as one that applies to all life-history assumptions. For example,
 an iteroparous species with a survival-affecting trait under natural selection
 552 may respond differently to spatial structure.

Structured metapopulation models (Metz and Gyllenberg, 2001; Gyllen-
 554 berg and Metz, 2001) typically also have an island structure (global disper-
 sal), but incorporate more realistic local population dynamics than Wright's
 556 island model. In such models, Taylor's cancellation result typically does not
 hold, as spatial structure has been shown to affect the numerical value of
 558 singular strategies (e.g., Alizon and Taylor, 2008; Nurmi and Parvinen, 2008,
 2011; Parvinen, 2011; Seppänen and Parvinen, 2014). In some cases spatial
 560 structure still inhibits evolutionary branching. For example, see Figure 4 of
 Parvinen (2011), in which evolutionary branching of cooperation does not
 562 occur for low dispersal rates. For a counterexample in the context of re-
 source specialization, see Figure 8b of Nurmi and Parvinen (2008), according
 564 to which a branching point can become evolutionarily stable when the em-
 igration probability is increased. Note, however, that in that model not all
 566 patches are ecologically equal, as the resource distribution is different among

568 patches. Evolutionary branching under high environmental heterogeneity
and low emigration has been observed also by Heinz et al. (2009) and Payne
et al. (2011). Spatial structure might thus promote evolutionary branching
570 in Wright's island model with ecologically different patches.

In summary, by deriving conditions for convergence stability and evolutionary
572 stability (and thus also for evolutionary branching) in terms of
derivatives of the fecundity function, we have derived much simpler expressions
574 than before. We believe that those expressions provide accessible tools
for researchers interested in evolution in Wright's island model. Finally, these
576 expressions help us to understand when and how evolutionary branching is
favored or disfavored by the spatial structure of the population.

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682 **Appendix A. The metapopulation fitness, R_m**

The metapopulation reproduction number (metapopulation fitness) is the
 684 expected number of dispersing mutant juveniles that are produced by the mutant colony of one dispersing mutant juvenile (Gyllenberg and Metz, 2001;
 686 Metz and Gyllenberg, 2001). Consider a mutant juvenile that has just emigrated from a patch. It will survive dispersal with probability p . Next we
 688 need to calculate the probability that it settles in a patch and becomes an adult there. For this purpose, consider one dispersing mutant juvenile, who
 690 arrives in a random patch. Its proportion of the whole amount of juveniles in this patch is approximately

$$q = \frac{1}{n\gamma F_{\text{res}}(1-m) + n\gamma F_{\text{res}}pm + 1} \quad (\text{A.1})$$

692 The probability that the mutant will be among the n juveniles chosen to be adults in the patch is

$$P(\text{settlement}) = q + (1-q)q + \dots + (1-q)^{n-1}q = 1 - (1-q)^n \approx nq. \quad (\text{A.2})$$

694 The probability to survive dispersal and become an adult in a patch is thus $pP(\text{settlement})$. The initial mutant and its descendants in the focal patch form a mutant colony. Next we consider the dynamics of such a colony. Assume that there are currently i adult mutants in the patch, which also
 696 means that there are $n-i$ residents. The proportion of mutant juveniles competing in this patch in the next generation is

$$p_i = \frac{(1-m)i\gamma F_{\text{mut}}^i}{(1-m)i\gamma F_{\text{mut}}^i + (1-m)(n-i)\gamma F_{\text{res}}^i + mnp\gamma F_{\text{res}}^0} \quad (\text{A.3})$$

$$= \frac{(1-m)iF_{\text{mut}}^i}{(1-m)iF_{\text{mut}}^i + (1-m)(n-i)F_{\text{res}}^i + mnpF_{\text{res}}^0}.$$

700 The probability that there will be j adult mutants in this patch in the next generation is

$$t_{ji} = \binom{n}{j} p_i^j (1-p_i)^{n-j}. \quad (\text{A.4})$$

702 We collect these values into the transition matrix $\mathbf{T} = (t_{ji})$ where $i, j = 1, \dots, n$. We leave on purpose the absorbing state $i = 0$ away. The probability distribution at time t satisfies the recursion

$$\alpha(t) = \mathbf{T}^t \alpha_0, \text{ where } \alpha_0 = \{1, 0, \dots, 0\}^T \quad (\text{A.5})$$

The amount of juveniles that a mutant colony of size i will send is
 706 $im\gamma F_{\text{mut}}(i)$. We multiply these values with $pP(\text{settlement})$, which is the
 probability that the initial dispersing mutant juvenile survived dispersal and
 708 settled as an adult, and collect them into a column vector

$$\begin{aligned} E &= pP(\text{settlement})\{m\gamma F_{\text{mut}}(1), 2m\gamma F_{\text{mut}}(2), \dots, nm\gamma F_{\text{mut}}(n)\}^T \\ &= pm\gamma P(\text{settlement})\{F_{\text{mut}}(1), 2F_{\text{mut}}(2), \dots, nF_{\text{mut}}(n)\}^T \\ &= \frac{pm}{(1-m+pm)F_{\text{res}}}\{F_{\text{mut}}(1), 2F_{\text{mut}}(2), \dots, nF_{\text{mut}}(n)\}^T, \end{aligned} \quad (\text{A.6})$$

where the last equality holds because γ is large:

$$\begin{aligned} \lim_{\gamma \rightarrow \infty} \gamma P(\text{settlement}) &= \lim_{\gamma \rightarrow \infty} \gamma nq \\ &= \lim_{\gamma \rightarrow \infty} \frac{\gamma n}{n\gamma(1-m+pm)F_{\text{res}} + 1} = \frac{1}{(1-m+pm)F_{\text{res}}}. \end{aligned} \quad (\text{A.7})$$

710 Next we want to calculate the expected number of times that a mutant
 colony will have size i during its lifetime. It is obtained from

$$\omega = \sum_{t=0}^{\infty} \alpha(t) = \sum_{t=0}^{\infty} \mathbf{T}^t \alpha_0 = \alpha_0 + \mathbf{T} \sum_{t=0}^{\infty} \mathbf{T}^t \alpha_0 = \alpha_0 + \mathbf{T}\omega. \quad (\text{A.8})$$

712 From $\omega = \alpha_0 + \mathbf{T}\omega$ we obtain

$$(\mathbf{I} - \mathbf{T})\omega = \alpha_0 \Rightarrow \omega = (\mathbf{I} - \mathbf{T})^{-1} \alpha_0. \quad (\text{A.9})$$

It can be numerically calculated as the limit of the recurrence $\omega_{t+1} = \mathbf{T}\omega + \alpha_0$,
 714 for any initial condition. Finally, the metapopulation reproduction ratio
 (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001) is

$$R_{\text{m}} = E^T \omega. \quad (\text{A.10})$$

716 See also Ajar (2003).

Appendix B. Consistency between metapopulation fitness and in- 718 vasion fitness

The metapopulation reproduction ratio measures growth of the mutant
 720 population between dispersal generations. We can also consider dynamics

in real time. The transition matrix \mathbf{T} gives the transition probabilities for
 722 the focal patch. In addition, emigrants may be able to settle into resident-
 dominated patches. Such successful event results in a patch with one mutant
 724 only. Altogether we get the next generation matrix

$$\mathbf{\Gamma} = \mathbf{T} + \begin{pmatrix} E^T \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad (\text{B.1})$$

Invasion fitness, defined as the long-term exponential growth rate of a mutant
 726 in an environment set by the resident, is the logarithm of the dominant
 eigenvalue of the matrix $\mathbf{\Gamma}$:

$$r = \ln(\lambda_d(\mathbf{\Gamma})) \quad (\text{B.2})$$

Theorem 8. *The invasion fitness and the metapopulation reproduction ratio
 728 are consistent: $r = 0$ if $R_m = 1$*

Proof. From the definitions of $\mathbf{\Gamma}$ and R_m (equations B.1 and A.10) we have
 730

$$\mathbf{\Gamma}\omega = \mathbf{T}\omega + \begin{pmatrix} E^T\omega \\ 0 \\ \vdots \\ 0 \end{pmatrix} = \mathbf{T}\omega + \begin{pmatrix} R_m \\ 0 \\ \vdots \\ 0 \end{pmatrix} \quad (\text{B.3})$$

If $R_m = 1$, equation (B.3) becomes

$$\mathbf{\Gamma}\omega = \mathbf{T}\omega + \alpha_0 = \omega, \quad (\text{B.4})$$

732 where the last equality follows from (A.8). This means that ω is an eigen-
 vector of the matrix $\mathbf{\Gamma}$ corresponding to the eigenvalue 1, so that $r = 0$. \square

734 According to Caswell (2000), the derivative of an eigenvalue of a matrix
 can be written using the left and right eigenvectors of the matrix. Above we
 736 already observed that when $s_{\text{mut}} = s_{\text{res}}$, the vector ω_{res} is a right eigenvector
 of $\mathbf{\Gamma}$ corresponding to the eigenvalue 1. Based on (A.6) and (E.2) we have

$$L_1^T \mathbf{\Gamma}_{\text{res}} = L_1^T \mathbf{T}_{\text{res}} + E_{\text{res}}^T = (1-d)L_1^T + dL_1^T = L_1^T, \quad (\text{B.5})$$

738 so that the vector $L_1^T = \{1, 2, 3, \dots, n\}$ is a left eigenvector of $\mathbf{\Gamma}_{\text{res}}$ corre-
 740 sponding to the eigenvalue 1. Therefore, we obtain (with the help of (E.7)
 and (C.3))

$$\begin{aligned} \frac{\partial}{\partial s_{\text{mut}}} \lambda(\mathbf{\Gamma}) \Big|_{s_{\text{mut}}=s_{\text{res}}} &= \frac{L_1^T \left(\frac{\partial}{\partial s_{\text{mut}}} \mathbf{\Gamma} \right) \omega_{\text{res}}}{L_1^T \omega_{\text{res}}} = d \left(L_1^T \frac{\partial}{\partial s_{\text{mut}}} \mathbf{T} + E'^T \right) \omega_{\text{res}} \quad (\text{B.6}) \\ &= dD(s_{\text{res}}). \end{aligned}$$

The metapopulation fitness gradient $D(s_{\text{res}})$ is thus sign-equivalent with the
 742 fitness gradient calculated using the next-generation operator $\mathbf{\Gamma}$. For rela-
 tions between different fitness proxies, see also Lehmann et al. (2016).

744 Appendix C. Proof of the first-order results (Theorem 1)

In this part of the Appendix, our aim is to provide a proof for Theo-
 746 rem 1, which gives an explicit expression for the selection gradient in terms
 of derivatives of the fecundity function. This proof consists of two parts. As
 748 explained in Appendix A, the vector ω needed in the calculation of metapop-
 ulation fitness is obtained by solving a system of linear equations. Therefore,
 750 we first use the implicit function theorem to obtain an explicit expression for
 the first derivative of metapopulation fitness. Second, by taking advantage
 752 of symmetry properties of the fecundity function, we obtain the equation
 presented in Theorem 1. Throughout the appendix we will use the notations

$$L_1 = \{1, 2, 3, \dots, n\}^T, \text{ and in more general, } L_j = \{1^j, 2^j, 3^j, \dots, n^j\}^T. \quad (\text{C.1})$$

754 Equations involving vectors L_j , the vector ω , and the matrix \mathbf{T} needed in
 the proof are derived in Appendix E.

756 Since $R_{\text{m}} = E^T \omega$, the metapopulation fitness gradient is

$$D_{\text{m}}(s_{\text{res}}) = \frac{\partial}{\partial s_{\text{mut}}} R_{\text{m}} \Big|_{s_{\text{mut}}=s_{\text{res}}} = E_{\text{res}}^T \omega' + E'^T \omega_{\text{res}}. \quad (\text{C.2})$$

Vectors E and ω have an intuitive meaning. The elements E_i describe the
 758 expected number of successful emigrants from a deme with i mutants, and ω_i
 is the average time that a mutant colony spends in state with i mutants (the
 760 sojourn time). The metapopulation fitness (reproduction number) $R_{\text{m}} =$
 $E^T \omega$ is the average number of successful emigrants of a mutant colony. The

762 first component of the fitness gradient ($E_{\text{res}}^T \omega'$) describes how a (first-order)
 764 change in the sojourn time affects the total number of emigrants of the colony,
 provided that the emigrant production in each deme remains fixed. The
 766 second term ($E'^T \omega_{\text{res}}$) describes the effect of changed emigrant production
 (first-order) in each deme, provided that the sojourn times remain fixed.
 These two first-order components together form the fitness gradient.

768 **Proposition 9.** *The metapopulation fitness gradient can be written as*

$$D_m(s_{\text{res}}) = \left(\frac{\partial}{\partial s_{\text{mut}}} L_1^T \mathbf{T} \right) \omega_{\text{res}} + E'^T \omega_{\text{res}} \quad (\text{C.3})$$

Proof. According to equation (A.9), the sojourn times ω are implicitly de-
 770 fined by $(I - \mathbf{T})\omega = \alpha_0$. From the implicit function theorem we have

$$\begin{aligned} \omega' &= \left. \frac{\partial}{\partial s_{\text{mut}}} \omega \right|_{s_{\text{mut}}=s_{\text{res}}} = (I - \mathbf{T}_{\text{res}})^{-1} \left(-\frac{\partial}{\partial s_{\text{mut}}} (I - \mathbf{T}) \omega_{\text{res}} \right) \\ &= (I - \mathbf{T}_{\text{res}})^{-1} \left(\frac{\partial}{\partial s_{\text{mut}}} \mathbf{T} \right) \omega_{\text{res}} \end{aligned} \quad (\text{C.4})$$

According to (E.2) $L_1^T (I - \mathbf{T}_{\text{res}}) = dL_1^T = E_{\text{res}}^T$, so that

$$E_{\text{res}}^T (I - \mathbf{T}_{\text{res}})^{-1} = L_1^T. \quad (\text{C.5})$$

772 From (C.4) and (C.2) it follows that $E_{\text{res}}^T \omega' = L_1^T \left(\frac{\partial}{\partial s_{\text{mut}}} \mathbf{T} \right) \omega_{\text{res}} = \left(\frac{\partial}{\partial s_{\text{mut}}} L_1^T \mathbf{T} \right) \omega_{\text{res}}$,
 and thus (C.2) becomes (C.3). \square

774 Let us investigate the first term of (C.3). According to (E.1) we have
 $(L_1^T \mathbf{T})_i = np_i$. By differentiating p_i (Equation A.3) we obtain

$$\begin{aligned} \left. \frac{\partial}{\partial s_{\text{mut}}} np_i \right|_{s_{\text{mut}}=s_{\text{res}}} &= (1-m)i \frac{[n(1-m+pm) - (1-m)i]F'_{\text{mut}}(i) - (1-m)(n-i)F'_{\text{res}}(i)}{n(1-m+pm)^2 F_{\text{res}}(0)} \\ &= \frac{1}{F_{\text{res}}(0)} [iK_1 + i^2 K_2], \end{aligned} \quad (\text{C.6})$$

776 where the second equality follows from (3.3) and (3.5), where

$$\begin{aligned} K_1 &= (1-d)(F_S - F_D) \\ K_2 &= \frac{1-d}{n} [dnF_D - (1-d)(F_S - F_D)]. \end{aligned} \quad (\text{C.7})$$

Therefore

$$\frac{\partial}{\partial s_{\text{mut}}} L_1^T \mathbf{T} = \frac{1}{F_{\text{res}}(0)} [K_1 L_1 + K_2 L_2]. \quad (\text{C.8})$$

778 Then consider the second term of (C.3). By differentiating (A.6) we obtain $E'_i = \frac{mp}{(1-m+pm)F_{\text{res}}(0)} i F'_{\text{mut}}(i)$. By using (3.3) and (3.5) we obtain

$$E' = \frac{d}{F_{\text{res}}(0)} [(F_S - F_D)L_1 + F_D L_2] \quad (\text{C.9})$$

780 By applying expressions (E.7) for $L_1^T \omega_{\text{res}}$ and (E.9) for $L_2^T \omega_{\text{res}}$, we obtain (3.4).

782 Appendix D. Proof of second-order results (Theorem 4)

In this part of the appendix, we prove Theorem 4, which gives an explicit
784 expression for the second derivative of the metapopulation fitness (with respect to the strategy of the mutant) in terms of derivatives of the fecundity function. Analogously to Appendix C, we first use the implicit function
786 theorem, and then use symmetry properties of the fecundity function.

788 Differentiating $R_m = E^T \omega$ (Equation A.10) two times we obtain

$$\frac{\partial^2}{\partial s_{\text{mut}}^2} R_m \Big|_{s_{\text{mut}}=s_{\text{res}}} = E^T \omega'' + 2E'^T \omega' + E''^T \omega, \quad (\text{D.1})$$

where $E'' = \frac{\partial^2}{\partial s_{\text{mut}}^2} E \Big|_{s_{\text{mut}}=s_{\text{res}}}$. The second-order effects of a mutation on
790 metapopulation fitness thus contain second order effects on sojourn time ω , provided that emigrant production E remains fixed (first term), and second-order effects on emigrant production, provided that the sojourn time remains
792 fixed (third term), and finally first-order effects on both (second term).

794 **Proposition 10.** *The second derivative (D.1) can be written as*

$$\frac{\partial^2}{\partial s_{\text{mut}}^2} R_m \Big|_{s_{\text{mut}}=s_{\text{res}}} = \frac{\partial^2}{\partial s_{\text{mut}}^2} (L_1^T \mathbf{T}) \omega_{\text{res}} + 2 \left[\frac{\partial}{\partial s_{\text{mut}}} (L_1^T \mathbf{T}) + E'^T \right] \omega' + E''^T \omega \quad (\text{D.2})$$

796 *Proof.* Consider the terms of (D.1). We can use the implicit function theorem to obtain

$$\begin{aligned}\omega'' &= \frac{\partial^2}{\partial s_{\text{mut}}^2} \omega \Big|_{s_{\text{mut}}=s_{\text{res}}} = (I - \mathbf{T}_{\text{res}})^{-1} \left[- \left(\frac{\partial^2}{\partial s_{\text{mut}}^2} (I - \mathbf{T}) \omega_{\text{res}} + 2 \frac{\partial}{\partial s_{\text{mut}}} (I - \mathbf{T}) \omega' \right) \right] \\ &= (I - \mathbf{T}_{\text{res}})^{-1} \left(\frac{\partial^2}{\partial s_{\text{mut}}^2} \mathbf{T} \omega_{\text{res}} + 2 \frac{\partial}{\partial s_{\text{mut}}} \mathbf{T} \omega' \right)\end{aligned}\quad (\text{D.3})$$

Based on (D.3) and (C.5) we have

$$E_{\text{res}}^T \omega'' = L_1^T \left(\frac{\partial^2}{\partial s_{\text{mut}}^2} \mathbf{T} \omega_{\text{res}} + 2 \frac{\partial}{\partial s_{\text{mut}}} \mathbf{T} \omega' \right). \quad (\text{D.4})$$

798

□

800 We investigate the three terms of the expression (D.2) for the second derivative in turns. First look at the component $\frac{\partial^2}{\partial s_{\text{mut}}^2} (L_1^T \mathbf{T})$. According to (E.1) we have $(L_1^T \mathbf{T})_i = np_i$. By differentiating p_i (Equation A.3) and using 802 (3.8) we obtain

$$\frac{\partial^2}{\partial s_{\text{mut}}^2} np_i \Big|_{s_{\text{mut}}=s_{\text{res}}} = A_1 i + A_2 i^2 + A_3 i^3, \quad (\text{D.5})$$

where

$$A_1 = \frac{(1-d)(-F_{\text{DD}} + 2F_{\text{DD}'} - 2F_{\text{SD}} + F_{\text{SS}})}{F_{\text{res}}(0)}. \quad (\text{D.6})$$

804 Also the expressions for A_2 and A_3 depend on d and the derivatives of the fecundity function, but they are quite lengthy. For details, see the electronic 806 supplement. We obtain $\frac{\partial^2}{\partial s_{\text{mut}}^2} (L_1^T \mathbf{T}) \omega_{\text{res}} = (A_1 L_1^T + A_2 L_2^T + A_3 L_3^T) \omega_{\text{res}}$, and by using (E.7), (E.9) and (E.10) we get the first part ready. It is not shown 808 separately, since we only need the sum in (D.2).

Concerning the second term, $\frac{\partial}{\partial s_{\text{mut}}} (L_1^T \mathbf{T})$ is given by (C.8) and E'^T is 810 given by (C.9). We need to calculate their product with ω' , obtained from (C.4). For this purpose we first need expressions (E.11) and (E.12) for $L_j(I - \mathbf{T}_{\text{res}})^{-1}$, thereafter (C.8) and (E.13) for $\frac{\partial}{\partial s_{\text{mut}}} (L_j \mathbf{T})$, and finally (E.7), (E.9) 812 and (E.10) for $L_i^T \omega_{\text{res}}$ to obtain an explicit expression (not shown separately).

814 The third term is obtained by differentiating E :

$$E''\omega_{\text{res}} = \frac{d}{F_{\text{res}}(0)} (C_1 L_1 + C_2 L_2 + C_3 L_3) \omega_{\text{res}}, \quad (\text{D.7})$$

where $C_1 = -F_{\text{DD}} + 2F_{\text{DD}'} - 2F_{\text{SD}} + F_{\text{SS}}$, $C_2 = F_{\text{DD}} - 3F_{\text{DD}'} + 2F_{\text{SD}}$ and
816 $C_3 = F_{\text{DD}'}$. By applying (E.7), (E.9) and (E.10) for $L_i^T \omega_{\text{res}}$ we obtain an explicit expression for $E''\omega_{\text{res}}$ (not shown separately).

818 The final result (Equation 3.10 of Theorem 4) is obtained by adding together the three expressions mentioned above.

820 Appendix E. Vectors L_1 , L_2 and L_3

Appendix E.1. The vectors $L_i^T \mathbf{T}$

822 According to the definition of (A.4), we have

$$(L_1^T \mathbf{T})_i = \sum_{j=1}^n j t_{ji} = \sum_{j=1}^n j \binom{n}{j} p_i^j (1-p_i)^{n-j} = \mathbb{E}(\mathbf{X}_i) = n p_i, \quad (\text{E.1})$$

where \mathbf{X}_i is a binomially distributed random variable with parameters n and
824 p_i . According to (A.3) and (3.5), $p_i = \frac{(1-m)i}{n(1-m+mp)} = \frac{(1-d)i}{n}$ for the resident, and thus

$$L_1^T \mathbf{T}_{\text{res}} = (1-d)L_1^T. \quad (\text{E.2})$$

826 Analogously, we have

$$\begin{aligned} (L_2^T \mathbf{T})_i &= \sum_{j=1}^n j^2 t_{ji} = \sum_{j=1}^n j^2 \binom{n}{j} p_i^j (1-p_i)^{n-j} = \mathbb{E}(\mathbf{X}_i^2) \\ &= n p_i + n(n-1)p_i^2. \end{aligned} \quad (\text{E.3})$$

Again, by using (A.3) and (3.5) we obtain

$$(L_2^T \mathbf{T}_{\text{res}})_i = (1-d)i + \frac{(n-1)(1-d)^2}{n} i^2. \quad (\text{E.4})$$

828 In a similar way, we have

$$\begin{aligned} (L_3^T \mathbf{T})_i &= \sum_{j=1}^n j^3 t_{ji} = \sum_{j=1}^n j^3 \binom{n}{j} p_i^j (1-p_i)^{n-j} = \mathbb{E}(\mathbf{X}_i^3) \\ &= n p_i + 3n(n-1)p_i^2 + n(n-1)(n-2)p_i^3 \\ &= (1-d)i + 3 \frac{(n-1)(1-d)^2}{n} i^2 + \frac{(n-1)(n-2)(1-d)^3}{n^2} i^3. \end{aligned} \quad (\text{E.5})$$

Appendix E.2. The scalars $L_i^T \omega_{\text{res}}$

830 When the mutant and resident have the same strategy, by definition (A.6) we have $E_{\text{res}} = \frac{mp}{1-m+mp} L_1 = dL_1$, and thus

$$1 = R_m = E^T \omega_{\text{res}} = dL_1^T \omega_{\text{res}}, \quad (\text{E.6})$$

832 from which we get

$$L_1^T \omega_{\text{res}} = \frac{1}{d}. \quad (\text{E.7})$$

According to (A.8) we have $\mathbf{T}\omega = \omega - \alpha_0$, so that

$$L_i^T \mathbf{T}\omega = L_i^T (\omega - \alpha_0) = L_i^T \omega - 1. \quad (\text{E.8})$$

834 By using (E.4) and (E.7), the equation (E.8) with $i = 2$ gets a form from which $L_2^T \omega_{\text{res}}$ can be solved:

$$L_2^T \omega_{\text{res}} = \frac{n}{d(1 + (n-1)d(2-d))}. \quad (\text{E.9})$$

836 In a similar way, by using (E.5) and (E.8) with $i = 3$ together with results above, we can solve

$$L_3^T \omega_{\text{res}} = \frac{(n + 2(n-1)(1-d)^2) n^2}{d(1 + (n-1)d(2-d)) (n^2 - (n-1)(n-2)(1-d)^3)}. \quad (\text{E.10})$$

838 *Appendix E.3. Vectors $L_i^T (I - \mathbf{T}_{\text{res}})^{-1}$*

From (E.2) we get $L_1^T (I - \mathbf{T}_{\text{res}}) = dL_1^T$ so that

$$L_1^T (I - \mathbf{T}_{\text{res}})^{-1} = \frac{1}{d} L_1^T. \quad (\text{E.11})$$

840 Furthermore, from (E.4) we have $L_2^T (I - \mathbf{T}_{\text{res}}) = (d-1)L_1^T + \left(1 - \frac{(1-d)^2(n-1)}{n}\right) L_2^T$.

842 By multiplying with $(I - \mathbf{T}_{\text{res}})^{-1}$ from the right we get an expression from which we can solve

$$L_2^T (I - \mathbf{T}_{\text{res}})^{-1} = \frac{n}{n - (n-1)(1-d)^2} \left(\frac{1-d}{d} L_1^T + L_2^T \right). \quad (\text{E.12})$$

Appendix E.4. Vectors $L_i^T \mathbf{T}'$

844 The expression for $L_1^T \mathbf{T}'$ was already obtained in (C.8). By differentiating (E.3) and using (A.3) and (3.5) we obtain

$$\begin{aligned} L_2^T \mathbf{T}' = & \frac{1}{F_{\text{res}}(0)} \left((1-d)(F_S - F_D) L_1^T \right. \\ & + \frac{(1-d)}{n} \left((1-d)(2n-3)F_S + (3(1-d) + n(3d-2))F_D \right) L_2^T \\ & \left. + 2 \frac{(1-d)^2(n-1)}{n^2} \left((1+d(n-1))F_D - (1-d)F_S \right) L_3^T \right). \end{aligned} \quad (\text{E.13})$$

846 **Appendix F. Connection to results based on trait distribution approach**

848 *Appendix F.1. Previous result*

Wakano and Lehmann (2014) obtained the following results in terms of fitness derivatives, where fitness w was defined as the expected number of successful offspring of a focal individual in the next generation. Note that w only measures direct individual reproductive success, and is not the same concept as invasion fitness or metapopulation fitness. Under the Gaussian approximation and under Wright's island model spatial structure, they have shown that the dynamics of the mean trait \bar{s} is given by

$$\Delta \bar{s} = V(w_S + R_2 w_D) \quad (\text{F.1})$$

856 and the dynamics of the variance V is given by

$$\Delta V = Q_{\text{ES}} V^2 \quad (\text{F.2})$$

where

$$Q_{\text{ES}} = \Delta w + \Delta r \quad (\text{F.3})$$

858

$$\Delta w = w_{\text{SS}} + (2w_{\text{SD}} + w_{\text{DD}})R_2 + w_{\text{DD}'}R_3 \quad (\text{F.4})$$

$$\Delta r = 4R_2 \frac{(2R_2 + (n-2)R_3)w_D^p + (1 + (n-1)R_2)w_S^p}{1-m} w_D \quad (\text{F.5})$$

where R_2 and R_3 are the solutions of

$$R_2 = (1 - m)^2 \left(\frac{1}{n} + \frac{n-1}{n} R_2 \right). \quad (\text{F.6})$$

860

$$R_3 = (1 - m)^3 \left\{ \frac{1}{n^2} + 3 \frac{n-1}{n^2} R_2 + \left(\frac{n-1}{n} \right) \left(\frac{n-2}{n} \right) R_3 \right\} \quad (\text{F.7})$$

The definitions of $w_S, w_D, w_{SS}, w_{SD}, w_{DD}, w_{DD'}, w_S^P, w_D^P$ are explained shortly. Note that eq. (28) in Wakano and Lehmann (2014) contains a typo and it should be replaced by eq. (F.5) shown above.

864 *Appendix F.2. Rewriting in terms of fecundity derivatives*

First, the previous results are derived for a case without dispersal mortality, i.e., they assumed $p = 1$. If we closely follow their derivations, we can confirm that their calculations are all correct when we replace their m by our d . Second, they are written in terms of (individual) fitness derivatives. To show the connection to our results, we need to rewrite them by derivatives of the fecundity function. Below we show how we obtain our results based on trait distribution approach by following Wakano and Lehmann (2014). In their notation, fitness w is a function of trait values of all individuals $w_{ki} = w_{ki}(s_{11}, s_{12}, \dots, s_{1n}, s_{21}, \dots)$ where s_{ki} is the trait value of individual i in deme k . Fitness w_{ki} is given by the sum of the expected number of successful offspring in a focal deme and those in other demes

$$w_{ki} = w_{ki}^P + w_{ki}^A \quad (\text{F.8})$$

876 They are called philopatric and allopatric components of fitness, respectively. They are explicitly given by

$$w_{ki}^P = \frac{(1-d)F_{ki}}{d\bar{F} + (1-d)F_k} \quad (\text{F.9})$$

878

$$w_{ki}^A = \frac{dF_{ki}}{\bar{F}} \quad (\text{F.10})$$

where \bar{F} is the average fecundity of the total population and F_k is the average fecundity of n individuals in the focal deme k . Subscripts S and D have similar meanings as ours, but the effects of individuals in the same class are collected. For example,

$$w_D = (n-1) \left. \frac{\partial w_{ki}}{\partial s_{kj}} \right|_{s_{11}=s_{12}=\dots=\bar{s}}, \quad (i \neq j) \quad (\text{F.11})$$

884 represents the fitness effect when all the $n - 1$ deme-mates change the trait value by the same amount. Similarly, they defined

$$w_S = \left. \frac{\partial w_{ki}}{\partial s_{ki}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} \quad (\text{F.12})$$

$$w_{SS} = \left. \frac{\partial^2 w_{ki}}{\partial s_{ki}^2} \right|_{s_{11}=s_{12}=\dots=\bar{s}} \quad (\text{F.13})$$

886 $w_{SD} = (n - 1) \left. \frac{\partial^2 w_{ki}}{\partial s_{ki} \partial s_{kj}} \right|_{s_{11}=s_{12}=\dots=\bar{s}}, \quad (i \neq j) \quad (\text{F.14})$

$$w_{DD} = (n - 1) \left. \frac{\partial^2 w_{ki}}{\partial s_{kj}^2} \right|_{s_{11}=s_{12}=\dots=\bar{s}}, \quad (i \neq j) \quad (\text{F.15})$$

888 $w_{DD'} = (n - 1)(n - 2) \left. \frac{\partial^2 w_{ki}}{\partial s_{kj} \partial s_{kl}} \right|_{s_{11}=s_{12}=\dots=\bar{s}}, \quad (i \neq j, j \neq l, l \neq i) \quad (\text{F.16})$

$$w_S^P = \left. \frac{\partial w_{ki}^P}{\partial s_{ki}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} \quad (\text{F.17})$$

890 $w_D^P = (n - 1) \left. \frac{\partial w_{ki}^P}{\partial s_{kj}} \right|_{s_{11}=s_{12}=\dots=\bar{s}}, \quad (i \neq j) \quad (\text{F.18})$

They do not define mutant nor resident, but the average trait value at a given snapshot \bar{s} plays a similar role as s_{res} . To rewrite w_S and w_D appearing in Eq. (F.1) as functions of F_S and F_D , we differentiate Eqs. (F.8) with respect to s_{ki} for w_S and with respect to s_{kj} for w_D and use the following rules

$$\left. \frac{\partial F_{ki}}{\partial s_{ki}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} = F_S \quad (\text{F.19})$$

896 $\left. \frac{\partial F_{ki}}{\partial s_{kj}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} = F_D, \quad (i \neq j) \quad (\text{F.20})$

$$\bar{F} = F_{\text{res}}^0 \quad (\text{F.21})$$

898 $\left. \frac{\partial \bar{F}}{\partial s_{ki}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} = 0 \quad (\text{F.22})$

$$\left. \frac{\partial F_k}{\partial s_{ki}} \right|_{s_{11}=s_{12}=\dots=\bar{s}} = \frac{F_S + (n - 1)F_D}{n} \quad (\text{F.23})$$

Then a straightforward calculation shows the selection gradient satisfies

$$\frac{w_S + R_2 w_D}{d} = D_1(s_{\text{res}}) \quad (\text{F.24})$$

900 where the explicit form of $D_1(s_{\text{res}})$ is identical to ours shown in Theorem 1.

To rewrite Q_{ES} , fitness derivatives w_{SS} , w_{SD} , w_{DD} , $w_{\text{DD}'}$, w_{S}^P , and w_{D}^P appearing in Δw and Δr should be rewritten in terms of F_{S} , F_{D} , F_{SS} , F_{SD} , F_{DD} , and $F_{\text{DD}'}$. Using the singular condition $F_{\text{S}} = 0$ and using the similar rules as above, we obtain these six functions. Note that $w_{\text{DD}'} \neq 0$ even if $F_{\text{DD}'} = 0$. Then a very lengthy but straightforward calculation shows

$$\frac{Q_{\text{ES}}}{d} = D_2(s_{\text{res}}) \quad (\text{F.25})$$

906 where the explicit form of $D_2(s_{\text{res}})$ is identical to ours shown in Theorem 4 when $F_{\text{S}} = 0$. Wakano and Lehmann (2014)'s Appendix D only provided how
908 to obtain $D_2(s_{\text{res}})$ in case of pairwise games and they wrote "The result is not shown here since it is very lengthy." We did further calculations to confirm
910 that it is identical to our Theorem 4 when $F_{\text{S}} = 0$. On the other hand, when game payoff only slightly changes fecundity, $Q_{\text{ES}} \simeq \Delta w$ holds and a simple
912 expression in terms of derivatives of the fecundity function and relatedness coefficients that approximately holds for a broader class of updating rules
914 can be derived (their eq.37-39).

Conceptually speaking, the trait distribution approach considers the mean and variance of a distribution ($s_{11}, s_{12}, \dots, s_{1n}, s_{21}, \dots$) in the next generation, while the metapopulation fitness approach calculates the accumulated allopatric components of fitness w^A until mutants get extinct in a focal deme. Calculations leading to the the final result look very different, but both approaches produce exactly the same conditions which are given by very complicated equations. This fact strongly suggest that both approaches are correct.