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.

Key words: 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

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

Invasion fitness (Metz et al., 1992) is the long-term exponential growth rate of a rare mutant in an environment set by the resident. At singular strategies the first-order derivative of the invasion fitness vanishes. The condition for evolutionary branching is usually given by calculating the second-order derivatives of invasion fitness at a singular strategy. There is, however, another approach to study the branching condition. Instead of considering a mutant–resident system, we can study the dynamics of a continuous trait distribution and identify evolutionary branching as the increase of the variance of the distribution (Sasaki and Dieckmann, 2011; Wakano and Iwasa, 2012). In a case of a well-mixed population, the branching condition derived by calculating invasion fitness and that by calculating variance dynamics have been shown to be identical when the trait distribution is approximated by the Gaussian distribution. In case of a spatially structured population, comparing these approaches requires more detailed calculations.

The metapopulation reproduction ratio (metapopulation fitness) is a fitness proxy that measures the growth of a mutant population between dispersal generations in an environment set by resident. (Metz and Gyllenberg, 2001; Ajar, 2003; Parvinen and Metz, 2008). By investigating the metapopulation fitness, the branching conditions have been studied for several different metapopulation models (Parvinen, 2002, 2006; Nurmi and Parvinen, 2008, 2011). On the other hand, the trait distribution approach can also be extended to spatially structured populations and an analytic expression for the branching condition has been derived by Wakano and Lehmann (2014) for a specific model. In structured populations, the trait distribution cannot be described by a single Gaussian distribution (as in a well-mixed case) because different demes (local patches) can have different trait distributions and because individuals in the same deme tend to have similar trait values. In other words, the individual trait value is no longer an independent random variable sampled from the same distribution and we need to take into account 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 is given by a combination of fitness derivatives and relatedness coefficients. The analytically derived condition by Wakano and Lehmann (2014) agreed with their simulations.

In this article we investigate Wright's island model, which is a discrete-time metapopulation model in which the number of adults in each deme is fixed through generations. The relative fecundity of each adult depends 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 among philopatric and dispersed offspring.

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

2.1 Island model and fecundity function

We consider an extended version of Wright's island model (Wright, 1931). We assume that there are infinitely many habitat patches (demes). In the beginning of the season each patch contains $n(\geqslant 2)$ adult individuals. These 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 $\gamma \to \infty$). More precisely, the relative fecundity for an adult with strategy s_1, when the strategies of the other individuals are $\boldsymbol{s}_{n-1} = (s_2, \ldots, s_n)$ is

$$F(s_1; \boldsymbol{s}_{n-1}) = F(s_1; (s_2, \ldots, s_n)) \tag{2.1}$$

Naturally, the order of strategies in the vector $\boldsymbol{s}_{n-1}$ does not affect fecundity, which we assume from now on. A proportion $0 < m \leqslant 1$ of the juveniles will disperse. The proportion $0 < p \leqslant 1$ will survive dispersal and land in 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 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 immigration. Throughout the paper, we assume that m and p are constant parameters in the model; they are independent of the strategy s.

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 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 resident, when there are i mutants and $n - i$ residents (including the focal resident) in its patch is denoted by

$$F^i_{\mathrm{res}} = F^i_{\mathrm{res}}(s_{\mathrm{res}}, s_{\mathrm{mut}}) = F(s_{\mathrm{res}}; (\underbrace{s_{\mathrm{mut}}, \ldots, s_{\mathrm{mut}}}_{\#=i}, \underbrace{s_{\mathrm{res}}, \ldots, s_{\mathrm{res}}}_{\#=n-i-1})). \tag{2.2}$$

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

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

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

$$F^0_{\text{res}} = F(s_{\text{res}}, (s_{\text{res}}, \ldots, s_{\text{res}})). \tag{2.4}$$

2.2 The metapopulation fitness $R_{\mathbf{m}}$

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 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 $R_{\text{m}} > 1$, and therefore metapopulation fitness can be used as a fitness proxy and it plays a central role in metapopulation theory. In 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 disperser produces more than one descendant mutant dispersers.

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 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 when $s_{\mathrm{mut}} = s_{\mathrm{res}}$, we have

$$R_{\mathrm{m}} \approx 1 + (s_{\mathrm{mut}} - s_{\mathrm{res}})D_1(s_{\mathrm{res}}) + \frac{1}{2}(s_{\mathrm{mut}} - s_{\mathrm{res}})^2 D_2(s_{\mathrm{res}}), \tag{2.5}$$

where $D_1(s_{\mathrm{res}})$ and $D_2(s_{\mathrm{res}})$ are the first- and second- order derivatives of R_{m}, calculated as

$$\begin{aligned} D_1(s_{\mathrm{res}}) &= \frac{\partial}{\partial s_{\mathrm{mut}}} R_{\mathrm{m}} \bigg|_{s_{\mathrm{mut}}=s_{\mathrm{res}}}, \\ D_2(s_{\mathrm{res}}) &= \frac{\partial^2}{\partial s_{\mathrm{mut}}^2} R_{\mathrm{m}} \bigg|_{s_{\mathrm{mut}}=s_{\mathrm{res}}}. \end{aligned} \tag{2.6}$$

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

2.3 Ajar's (2003) general formulae

Ajar (2003) gave a general formula of the first-order derivative, $D_1(s_{\mathrm{res}})$, (i.e. equation (5) in Ajar (2003)) in terms of relatedness coefficients via a metapopulation fitness calculation. To use Ajar's result, we need to investigate the expected number of surviving offspring of a mutant in a patch 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

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

where w_j^{P} and w_j^{A} respectively represent the philopatric and allopatric components of surviving offspring; namely, the expected number of offspring that 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 denominator of the allopatric component does not contain mutant immigrants. Ajar (2003) also gave a formula of the second-order derivative, $D_2(s_{\mathrm{res}})$, (i.e. equation (9) in Ajar (2003)) in terms of relatedness coefficients that is valid at the strategy s_{res} where $D_1(s_{\mathrm{res}})$ vanishes. To use the formula, we need to further derive the quantity called π_j in Ajar (2003), but it is equivalent to our $(j/n)w_j^{\mathrm{P}}$ 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 $s_2, \ldots, s_n$ in our fecundity function $F(s_1; (s_2, \ldots, s_n))$ 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 $F(s_1; (s_2, \ldots, s_n))$, 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

$$F_{\mathrm{S}} = \frac{\partial}{\partial s_1} F(s_1; (s_2, \ldots, s_n))\bigg|_{s_1 = \cdots = s_n = s_{\mathrm{res}}} . \tag{3.1}$$

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

$$F_{\mathrm{D}} = \frac{\partial}{\partial s_k} F(s_1; (s_2, \ldots, s_n))\bigg|_{s_1 = \cdots = s_n = s_{\mathrm{res}}} , \quad \text{where } k \in \{2, \ldots, n\}, \tag{3.2}$$

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

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

$$\begin{aligned} \frac{\partial}{\partial s_{\mathrm{mut}}} F^i_{\mathrm{res}}(s_{\mathrm{res}}, s_{\mathrm{mut}})\big|_{s_{\mathrm{mut}}=s_{\mathrm{res}}} &= iF_{\mathrm{D}} \\ \frac{\partial}{\partial s_{\mathrm{mut}}} F^i_{\mathrm{mut}}(s_{\mathrm{res}}, s_{\mathrm{mut}})\big|_{s_{\mathrm{mut}}=s_{\mathrm{res}}} &= F_{\mathrm{S}} + (i-1)F_{\mathrm{D}}. \end{aligned} \tag{3.3}$$

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

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

where

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

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

Proof. The result is obtained by applying the implicit function theorem on the expression of metapopulation fitness. See the C. ☐

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

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

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

A good reference point for understanding (3.4) is when everybody disperses (i.e. $m = 1$ and hence $d = 1$). In this case, the population is essentially well-mixed and the selection gradient is simply given by $(F_{\text{S}}/F_{\text{res}})$. Equation (3.4) states that the (sign of the) selection gradient is preserved 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 gradient, but (3.4) says that it is not the case.

To facilitate our understanding, imagine social interaction in a patch of n individuals. Each individual can independently choose the amount of cooperation s. Cooperation is costly to the individual performing the act, but 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 instance of public-goods games, and a natural choice of fecundity function of this game model would be

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

where $b > 0$, $c > 0$ and $F_{\text{baseline}} > 0$ is a baseline fecundity. We have $F_{\text{S}} = -c$ and $F_{\text{D}} = b/(n-1)$ in this example. Equation (3.4) therefore suggests that 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, 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 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 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. At the same time, however, limited dispersal causes competition among kin, which disfavors altruism. Here these two opposing effects precisely cancel 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-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., 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 Taylor et al. (2011). Under different life-cycle assumptions, spatial structure has been shown to affect the evolution of cooperation (e.g., Taylor and Irwin, 2000; Lehmann and Rousset, 2010; Parvinen, 2010, 2011; Seppänen and Parvinen, 2014).

3.2 Second-order results

Similarly to before, by using the property of the fecundity function, $F(s_1; (s_2, \ldots, s_n))$, 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 of F:

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

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

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

3.2.1 Convergence stability

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

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*

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

Proof. At a singular strategy we have $F_{\mathrm{S}}(s) = 0$. Therefore the derivative of $D_1(s)$ is, up to some positive constant, equal to

$$\frac{\mathrm{d}}{\mathrm{ds}}\left(\frac{F_{\mathrm{S}}(s)}{F_{\mathrm{res}}^0(s)}\right) = \frac{F_{\mathrm{S}}'(s)F_{\mathrm{res}}^0(s) - F_{\mathrm{S}}(s)(F_{\mathrm{res}}^0)'(s)}{(F_{\mathrm{res}}^0(s))^2} = \frac{F_{\mathrm{S}}'(s)}{F_{\mathrm{res}}^0(s)}.$$

We also know that

$$F_{\mathrm{S}}'(s) = \frac{\mathrm{d}}{\mathrm{d}s} F_{\mathrm{S}}(s; (s, \ldots, s)) = F_{\mathrm{SS}} + (n-1) F_{\mathrm{SD}}.$$

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

3.2.2 Evolutionary stability

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

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

$$\begin{aligned} D_2(s_{\mathrm{res}}) = C \Bigg[& \phi_{\mathrm{SS}} \left(\frac{F_{\mathrm{SS}}}{F^0_{\mathrm{res}}} \right) + \phi_{\mathrm{SD}} \left(\frac{F_{\mathrm{SD}}}{F^0_{\mathrm{res}}} \right) + \phi_{\mathrm{DD'}} \left(\frac{F_{\mathrm{DD'}}}{F^0_{\mathrm{res}}} \right) \\ & + \psi_{\mathrm{S\times S}} \left(\frac{F_{\mathrm{S}}}{F^0_{\mathrm{res}}} \right)^2 + \psi_{\mathrm{S\times D}} \left(\frac{F_{\mathrm{S}}}{F^0_{\mathrm{res}}} \right) \left(\frac{F_{\mathrm{D}}}{F^0_{\mathrm{res}}} \right) + \psi_{\mathrm{D\times D}} \left(\frac{F_{\mathrm{D}}}{F^0_{\mathrm{res}}} \right)^2 \Bigg], \end{aligned} \tag{3.10}$$

where

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

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

Note that such second-order results (not necessarily at singular points) 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, and their eq. (19) is written in terms of "payoff" derivatives under the assumption that traits have no effect on pairwise relatedness). Also note that this result is not derived from Ajar (2003), because Ajar (2003) provided a formula of the second-order derivative only at a singular strategy.

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 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 (relatedness). For more intuition, we cite Mullon et al. (2016).

Setting $F_{\mathrm{S}} = 0$ reproduces the following result.

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

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

where

$$\begin{aligned}
\tilde{\phi}_{\mathrm{SS}} &= (2-d)\left\{n^2 - (n-1)(n-2)(1-d)^3\right\} > 0,\\
\tilde{\phi}_{\mathrm{SD}} &= 2(n-1)(1-d)^2\left\{n + n(1-d) + (n-2)(1-d)^2\right\} \geqslant q0,\\
\tilde{\phi}_{\mathrm{DD'}} &= (n-1)(n-2)d(1-d)^3 \geqslant q0,\\
\tilde{\psi}_{\mathrm{D\times D}} &= -2(n-1)^2 d(1-d)^3 \leqslant q0.
\end{aligned} \tag{3.12}$$

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

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

where

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

The form (3.13) is especially helpful, because $F_{\mathrm{SS}} + (n-1)F_{\mathrm{SD}} < 0$ holds for a convergence stable singular strategy. Especially, for low d the term with $\tilde{\phi}_{\mathrm{SD}}$ dominates, and for d close to 1 the term with $\tilde{\xi}_{\mathrm{SS}}$ dominates (See Fig. 1 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 been derived by Ajar (2003) (by using metapopulation fitness, in terms of fitness derivatives; see eq. (9) therein) and by Wakano and Lehmann (2014) (by using trait distribution approach, in terms of fitness derivatives; see their eqs. (26–28), also see Appendix F of this paper).

It is notable that one of the four second-order derivatives of fecundity function, $F_{\rm DD}$, does not appear in $D_2(s_{\rm res})$ or $\tilde{D}_2(s_{\rm res})$. It can be deemed as another "cancellation result" that holds under the present assumptions about the life cycle. This was observed also by Wakano and Lehmann (2014) in case 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 by applying the implicit function theorem on the expression of metapopulation fitness. Note also that exactly the same result as in Corollary 5 can be derived by the trait distribution approach (see F).

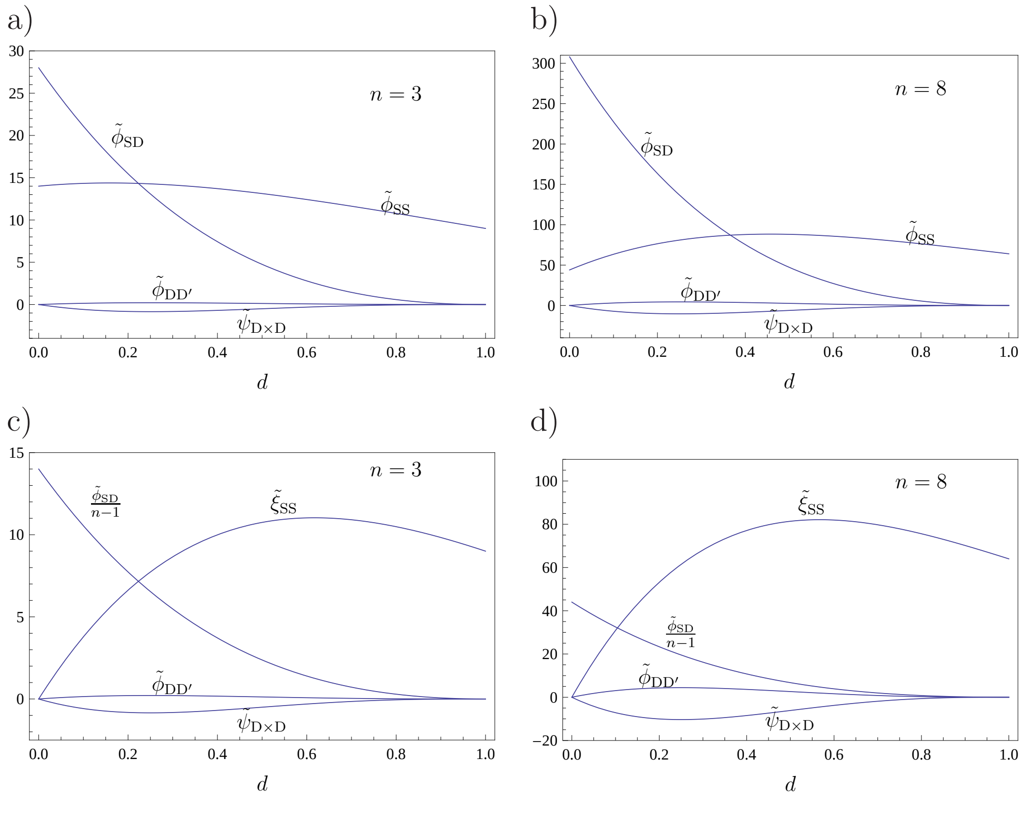

Figure 1: Effect of the fecundity derivatives on evolutionary stability. Coefficients of $\tilde{D}_2(s_{\rm res})$ given (a,b) by equation (3.12) and (c,d) by equation (3.13) as a function of d when (a,c) $n = 3$ and (b,d) $n = 8$.

4 Does spatial structure inhibit branching?

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, Wakano and Lehmann (2014) have shown that a branching point (evolutionarily attracting singular strategy, which is not uninvadable) in a well-mixed model changes to be evolutionarily stable (uninvadable) as the migration rate decreases below a threshold value. We can generalize this result in the form of the following theorem.

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

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

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

According to Theorem 3 (Equation 3.9), if a singular strategy s is convergence stable we have $F_{\mathrm{SS}}+(n-1)F_{\mathrm{SD}} < 0$, 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. □

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 evolutionarily stable and convergence stable in a well-mixed model becomes 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.

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

$$F_{\mathrm{S}} = 0,\ F_{\mathrm{SS}} + (n-1)F_{\mathrm{SD}} < 0,\ \textit{and}\ F_{\mathrm{SS}} < 0. \tag{4.2}$$

If

$$F_{\mathrm{DD'}} \leqslant 0 \tag{4.3}$$

or

$$F_{\mathrm{DD'}} \leqslant F_{\mathrm{SD}} \tag{4.4}$$

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

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

holds for $0 < d < 1$.

Proof. According to (3.13)

$$\begin{aligned}\tilde{D}_2(s_{\mathrm{res}}) = {} & \underbrace{\tilde{\xi}_{\mathrm{SS}}}_{\geqslant 0} \underbrace{\left(\frac{F_{\mathrm{SS}}}{F^0_{\mathrm{res}}}\right)}_{<0} + \underbrace{\frac{\tilde{\phi}_{\mathrm{SD}}}{n-1}}_{\geqslant 0} \underbrace{\left(\frac{F_{\mathrm{SS}} + (n-1)F_{\mathrm{SD}}}{F^0_{\mathrm{res}}}\right)}_{<0} \\ & + \underbrace{\tilde{\phi}_{\mathrm{DD'}}}_{\geqslant 0} \underbrace{\left(\frac{F_{\mathrm{DD'}}}{F^0_{\mathrm{res}}}\right)}_{\leqslant 0} + \underbrace{\tilde{\psi}_{\mathrm{D\times D}}}_{\leqslant 0} \underbrace{\left(\frac{F_{\mathrm{D}}}{F^0_{\mathrm{res}}}\right)^2}_{\geqslant 0} < 0\end{aligned} \tag{4.6}$$

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

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

□

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 $F_{\mathrm{SS}} + (n-1)F_{\mathrm{SD}}$, and evolutionary stability by the sign of equation (3.11) involving the derivatives F_{SS}, F_{SD}, $F_{\mathrm{DD'}}$ and F_{D}. The two latter derivatives thus only affect evolutionary stability, and not convergence stability. The corresponding coefficients of $\tilde{D}_2(s_{\mathrm{res}})$, $\tilde{\phi}_{\mathrm{DD}'} \geqslant 0$ and $\tilde{\psi}_{\mathrm{D}\times\mathrm{D}} \leqslant 0$ (3.12) are zero for $d = 0$ and $d = 1$, so they affect evolutionary stability for intermediate values of d. Therefore, when $\frac{F_{\mathrm{DD}'}}{F^0_{\mathrm{res}}}$ is positive and large compared to $\left(\frac{F_{\mathrm{D}}}{F^0_{\mathrm{res}}}\right)^2$, $D_2(s)$ can be positive for intermediate values of d, even though branching does not occur for $d = 1$, $F_{\mathrm{SS}} < 0$.

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

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

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 $s \in [0, 2]$. For this model $F_{\mathrm{S}} = -2(s-1)$ and $F_{\mathrm{SS}} + (n-1)F_{\mathrm{SD}} = -2$, which means that $s = 1$ is a singular strategy, and convergence stable for all d. Furthermore, $F_{\mathrm{SS}} = -2$, so that the singular strategy is evolutionarily stable in the well-mixed model. Since for $s = 1$ we have $F_{\mathrm{D}} = 0$ and $\frac{F_{\mathrm{DD}'}}{F^0_{\mathrm{res}}} = \frac{2b}{(n-1)^2}$ is positive, 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 point for intermediate values of d. The threshold value for b, above which branching is possible, is, however, unrealistically large, and increases with n. Finding such cases in reality would be unlikely. Nevertheless, this example shows that spatial structure can promote branching with some fecundity functions, and thus it is not possible to prove that spatial structure would always inhibit evolutionary branching.

5 Examples

5.1 Pairwise games

Assume that individuals in the deme play pairwise games among each other and that the total payoff from these games determines the fecundity 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 com-

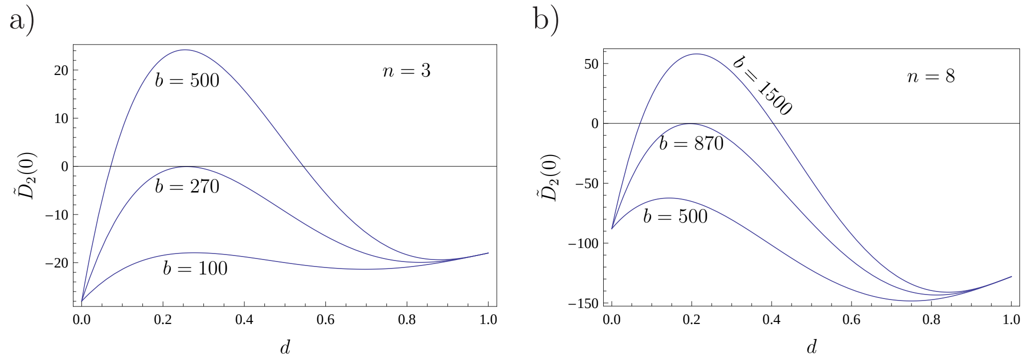

Figure 2: Spatial structure can promote evolutionary branching with some fecundity functions. The expression $\tilde{D}_2(s_{\text{res}})$ determining evolutionarily stability given by equation (3.11) of the singular strategy $s_{\text{res}} = 1$ as a function of d for the fecundity function (4.8) with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

binations of games take place. In some games the role of individuals matters. In such a situation, let $G_i(s_{\text{self}}, s_{\text{opponent}})$ denote the payoff of the 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 vector $\mathbf{s} = (s^{(1)}, s^{(2)})$ for playing strategy $s^{(1)}$ in role 1 and playing $s^{(2)}$ in role 2. When player 1 with the list $\mathbf{s_1} = (s_1^{(1)}, s_1^{(2)})$ is matched with player 2 with the list $\mathbf{s}_2 = (s_2^{(1)}, s_2^{(2)})$ and if their roles are determined randomly, the 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).

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

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 $b_1 = 6, b_2 = -1.4, c_1 = 4.56, c_2 = -1.6$, evolutionary branching occurs in the well-mixed situation (Figure 1A by Doebeli et al. (2004)).

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

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

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

We are interested in how the introduction of spatial structure affects conditions of evolutionary branching. The first-order and second-order derivatives of F are written in terms of G as follows;

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

where

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

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

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

5.2 Public-goods game

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

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

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

$$F_{\mathrm{S}} = \frac{f'(s_{\mathrm{res}})}{n} - g'(s_{\mathrm{res}}), \quad F_{\mathrm{D}} = \frac{f'(s_{\mathrm{res}})}{n}. \tag{5.7}$$

The boundary strategy $s=0$ is evolutionarily repelling, if $F_S = \frac{f'(0)}{n} - g'(0) > 0$, 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

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

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

Another common way to think about benefit in a public-goods game is 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 a minor change as

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

The first order derivatives are given by

$$F_{\mathrm{S}} = -g'(s_{\mathrm{res}}), \quad F_{\mathrm{D}} = \frac{f'(s_{\mathrm{res}})}{n-1}, \tag{5.10}$$

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 island model studied here.

6 Discussion

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 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 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 become adults are randomly chosen among the offspring present in each patch after dispersal. We have derived explicit conditions for evolutionary singularity, 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 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 unless the derivative $F_{\mathrm{DD}'}$ is positive and large. However, spatial structure can occasionally promote evolutionary branching with some fecundity functions. In fact, in the example in Section 4.2, evolutionary branching can occur only for intermediate values of d. In other words, although evolutionary branching is not possible in a well-mixed setting, it does occur in a spatial setting. The parameter values for which this scenario happens are, however, not very realistic.

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

Structured metapopulation models (Metz and Gyllenberg, 2001; Gyllenberg and Metz, 2001) typically also have an island structure (global dispersal), but incorporate more realistic local population dynamics than Wright's 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 singular strategies (e.g., Alizon and Taylor, 2008; Nurmi and Parvinen, 2008, 2011; Parvinen, 2011; Seppänen and Parvinen, 2014). In some cases spatial structure still inhibits evolutionary branching. For example, see Figure 4 of Parvinen (2011), in which evolutionary branching of cooperation does not occur for low dispersal rates. For a counterexample in the context of resource specialization, see Figure 8b of Nurmi and Parvinen (2008), according to which a branching point can become evolutionarily stable when the emigration probability is increased. Note, however, that in that model not all patches are ecologically equal, as the resource distribution is different among 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 in Wright's island model with ecologically different patches.

In summary, by deriving conditions for convergence stability and evolutionary stability (and thus also for evolutionary branching) in terms of derivatives of the fecundity function, we have derived much simpler expressions than before. We believe that those expressions provide accessible tools for researchers interested in evolution in Wright's island model. Finally, these 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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A The metapopulation fitness, R_{m}

The metapopulation reproduction number (metapopulation fitness) is the expected number of dispersing mutant juveniles that are produced by the mutant colony of one dispersing mutant juvenile (Gyllenberg and Metz, 2001; Metz and Gyllenberg, 2001). Consider a mutant juvenile that has just emigrated from a patch. It will survive dispersal with probability p. Next we 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 arrives in a random patch. Its proportion of the whole amount of juveniles in this patch is approximately

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

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

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

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 means that there are $n-i$ residents. The proportion of mutant juveniles competing in this patch in the next generation is

$$\begin{aligned} p_i &= \frac{(1-m)i\gamma F^i_{\text{mut}}}{(1-m)i\gamma F^i_{\text{mut}} + (1-m)(n-i)\gamma F^i_{\text{res}} + mnp\gamma F^0_{\text{res}}} \\ &= \frac{(1-m)iF^i_{\text{mut}}}{(1-m)iF^i_{\text{mut}} + (1-m)(n-i)F^i_{\text{res}} + mnpF^0_{\text{res}}}. \end{aligned} \tag{A.3}$$

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

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

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

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

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

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

where the last equality holds because γ is large:

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

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

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

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

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

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

$$R_{\text{m}} = E^T\omega. \tag{A.10}$$

See also Ajar (2003).

B Consistency between metapopulation fitness and invasion fitness

The metapopulation reproduction ratio measures growth of the mutant population between dispersal generations. We can also consider dynamics in real time. The transition matrix $\mathbf{T}$ gives the transition probabilities for 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 only. Altogether we get the next generation matrix

$$\mathbf{\Gamma} = \mathbf{T} + \begin{pmatrix} E^T \\ 0 \\ \vdots \\ 0 \end{pmatrix} \tag{B.1}$$

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

$$r = \ln\left(\lambda_d(\mathbf{\Gamma})\right) \tag{B.2}$$

Theorem 8. *The invasion fitness and the metapopulation reproduction ratio are consistent:* $r = 0$ *if* $R_{\mathrm{m}} = 1$

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

$$\mathbf{\Gamma}\omega = \mathbf{T}\omega + \begin{pmatrix} E^T\omega \\ 0 \\ \vdots \\ 0 \end{pmatrix} = \mathbf{T}\omega + \begin{pmatrix} R_{\mathrm{m}} \\ 0 \\ \vdots \\ 0 \end{pmatrix} \tag{B.3}$$

If $R_{\mathrm{m}} = 1$, equation (B.3) becomes

$$\mathbf{\Gamma}\omega = \mathbf{T}\omega + \alpha_0 = \omega, \tag{B.4}$$

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

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 already observed that when $s_{\mathrm{mut}} = s_{\mathrm{res}}$, 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

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

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

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

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

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

In this part of the Appendix, our aim is to provide a proof for Theorem 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 explained in A, the vector ω needed in the calculation of metapopulation fitness is obtained by solving a system of linear equations. Therefore, we first use the implicit function theorem to obtain an explicit expression for the first derivative of metapopulation fitness. Second, by taking advantage of symmetry properties of the fecundity function, we obtain the equation presented in Theorem 1. Throughout the appendix we will use the notations

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

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

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

$$D_{\mathrm{m}}(s_{\mathrm{res}}) = \frac{\partial}{\partial s_{\mathrm{mut}}} R_{\mathrm{m}} \bigg|_{s_{\mathrm{mut}}=s_{\mathrm{res}}} = E^T_{\mathrm{res}}\omega' + E'^T\omega_{\mathrm{res}}. \tag{C.2}$$

Vectors E and ω have an intuitive meaning. The elements E_i describe the 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 sojourn time). The metapopulation fitness (reproduction number) $R_{\mathrm{m}} = E^T\omega$ is the average number of successful emigrants of a mutant colony. The first component of the fitness gradient ($E^T_{\mathrm{res}}\omega'$) describes how a (first-order) 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 second term ($E'^T\omega_{\mathrm{res}}$) 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.

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

$$D_{\mathrm{m}}(s_{\mathrm{res}}) = \left(\frac{\partial}{\partial s_{\mathrm{mut}}} L_1^T \mathbf{T}\right)\omega_{\mathrm{res}} + E'^T\omega_{\mathrm{res}} \tag{C.3}$$

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

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

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

$$E^T_{\mathrm{res}}(I - \mathbf{T}_{\mathrm{res}})^{-1} = L_1^T. \tag{C.5}$$

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

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

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

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

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

Therefore

$$\frac{\partial}{\partial s_{\mathrm{mut}}}L_1^T\mathbf{T} = \frac{1}{F_{\mathrm{res}}(0)}\left[K_1L_1+K_2L_2\right]. \tag{C.8}$$

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

$$E' = \frac{d}{F_{\mathrm{res}}(0)}\left[(F_S-F_D)L_1+F_DL_2\right] \tag{C.9}$$

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

D Proof of second-order results (Theorem 4)

In this part of the appendix, we prove Theorem 4, which gives an explicit 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 C, we first use the implicit function theorem, and then use symmetry properties of the fecundity function.

Differentiating $R_{\mathrm{m}} = E^T\omega$ (Equation A.10) two times we obtain

$$\frac{\partial^2}{\partial s_{\mathrm{mut}}^2}R_{\mathrm{m}}\Big|_{s_{\mathrm{mut}}=s_{\mathrm{res}}} = E^T\omega''+2E'^T\omega'+E''^T\omega, \tag{D.1}$$

where $E'' = \frac{\partial^2}{\partial s_{\mathrm{mut}}^2}E\big|_{s_{\mathrm{mut}}=s_{\mathrm{res}}}$. The second-order effects of a mutation on 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 fixed (third term), and finally first-order effects on both (second term).

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

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

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

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

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

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

□

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

$$\left.\frac{\partial^2}{\partial s_{\text{mut}}^2} np_i\right|_{s_{\text{mut}}=s_{\text{res}}} = A_1 i + A_2 i^2 + A_3 i^3, \tag{D.5}$$

where

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

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 supplement. We obtain $\frac{\partial^2}{\partial s_{\text{mut}}^2}\left(L_1^T\mathbf{T}\right)\omega_{\text{res}} = (A_1L_1^T + A_2L_2^T + A_3L_3^T)\omega_{\text{res}}$, and by using (E.7), (E.9) and (E.10) we get the first part ready. It is not shown separately, since we only need the sum in (D.2).

Concerning the second term, $\frac{\partial}{\partial s_{\mathrm{mut}}}\left(L_1^T\mathbf{T}\right)$ is given by (C.8) and E'^T is 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 $L_j(I-\mathbf{T}_{\mathrm{res}})^{-1}$, thereafter (C.8) and (E.13) for $\frac{\partial}{\partial s_{\mathrm{mut}}}(L_j\mathbf{T})$, and finally (E.7), (E.9) and (E.10) for $L_i^T\omega_{\mathrm{res}}$ to obtain an explicit expression (not shown separately).

The third term is obtained by differentiating E:

$$E''\omega_{\mathrm{res}} = \frac{d}{F_{\mathrm{res}}(0)}\left(C_1L_1 + C_2L_2 + C_3L_3\right)\omega_{\mathrm{res}}, \tag{D.7}$$

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

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

E Vectors L_1, L_2 and L_3

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

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

$$(L_1^T\mathbf{T})_i = \sum_{j=1}^{n} j t_{ji} = \sum_{j=1}^{n} j \binom{n}{j} p_i^j (1-p_i)^{n-j} = \mathrm{E}(\mathbf{X_i}) = np_i, \tag{E.1}$$

where $\mathbf{X_i}$ is a binomially distributed random variable with parameters n and 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

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

Analogously, we have

$$\begin{aligned}(L_2^T\mathbf{T})_i &= \sum_{j=1}^{n} j^2 t_{ji} = \sum_{j=1}^{n} j^2 \binom{n}{j} p_i^j (1-p_i)^{n-j} = \mathrm{E}(\mathbf{X_i}^2)\\ &= np_i + n(n-1)p_i^2.\end{aligned} \tag{E.3}$$

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

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

In a similar way, we have

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

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

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

$$1 = R_{\text{m}} = E^T \omega_{\text{res}} = dL_1^T \omega_{\text{res}}, \tag{E.6}$$

from which we get

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

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

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

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:

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

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

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

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

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

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

Furthermore, from (E.4) we have $L_2^T(I - \mathbf{T}_{\text{res}}) = (d-1)\,L_1^T + \left(1 - \frac{(1-d)^2(n-1)}{n}\right) L_2^T$. By multiplying with $(I - \mathbf{T}_{\text{res}})^{-1}$from the right we get an expression from which we can solve

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

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

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

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

F Connection to results based on trait distribution approach

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

$$\Delta\bar{s} = V(w_{\rm S}+R_2w_{\rm D}) \tag{F.1}$$

and the dynamics of the variance V is given by

$$\Delta V = Q_{\rm ES}V^2 \tag{F.2}$$

where

$$Q_{\rm ES} = \Delta w + \Delta r \tag{F.3}$$

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

$$\Delta r = 4R_2 \frac{(2R_2 + (n-2)R_3)w_{\mathrm{D}}^{p} + (1 + (n-1)R_2)w_{\mathrm{S}}^{P}}{1-m} w_{\mathrm{D}} \tag{F.5}$$

where R_2 and R_3 are the solutions of

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

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

The definitions of $w_{\mathrm{S}}, w_{D,} w_{\mathrm{SS}}, w_{\mathrm{SD}}, w_{\mathrm{DD}}, w_{\mathrm{DD'}}, w_{\mathrm{S}}^{P}, w_{\mathrm{D}}^{P}$ 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.

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 $w_{ki} = w_{ki}(s_{11}, s_{12}, ..., s_{1n}, s_{21}, ...)$ 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

$$w_{ki} = w_{ki}^{P} + w_{ki}^{A} \tag{F.8}$$

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

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

$$w_{ki}^{A} = \frac{dF_{ki}}{\bar{F}} \tag{F.10}$$

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,

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

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

$$w_{\mathrm{S}} = \left.\frac{\partial w_{ki}}{\partial s_{ki}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} \tag{F.12}$$

$$w_{\mathrm{SS}} = \left.\frac{\partial^2 w_{ki}}{\partial s_{ki}^2}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} \tag{F.13}$$

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

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

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

$$w_{\mathrm{S}}^P = \left.\frac{\partial w_{ki}^P}{\partial s_{ki}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} \tag{F.17}$$

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

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

$$\left.\frac{\partial F_{ki}}{\partial s_{ki}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} = F_{\mathrm{S}} \tag{F.19}$$

$$\left.\frac{\partial F_{ki}}{\partial s_{kj}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} = F_{\mathrm{D}}, \quad (i \neq j) \tag{F.20}$$

$$\bar{F} = F_{\mathrm{res}}^0 \tag{F.21}$$

$$\left.\frac{\partial \bar{F}}{\partial s_{ki}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} = 0 \tag{F.22}$$

$$\left.\frac{\partial F_k}{\partial s_{ki}}\right|_{s_{11}=s_{12}=\ldots=\bar{s}} = \frac{F_{\mathrm{S}}+(n-1)F_{\mathrm{D}}}{n} \tag{F.23}$$

Then a straightforward calculation shows the selection gradient satisfies

$$\frac{w_{\mathrm{S}}+R_2 w_{\mathrm{D}}}{d} = D_1(s_{\mathrm{res}}) \tag{F.24}$$

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

To rewrite Q_{ES} , fitness derivatives w_{SS}, w_{SD}, w_{DD}, $w_{\mathrm{DD'}}$, 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 $F_{\mathrm{DD'}}$. Using the singular condition $F_{\mathrm{S}} = 0$ and using the similar rules as above, we obtain these six functions. Note that $w_{\mathrm{DD'}} \neq 0$ even if $F_{\mathrm{DD'}} = 0$. Then a very lengthy but straightforward calculation shows

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

where the explicit form of $D_2(s_{\mathrm{res}})$ is identical to ours shown in Theorem 4 when $F_{\mathrm{S}} = 0$. Wakano and Lehmann (2014)'s Appendix D only provided how to obtain $D_2(s_{\mathrm{res}})$ 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 that it is identical to our Theorem 4 when $F_{\mathrm{S}} = 0$. On the other hand, when game payoff only slightly changes fecundity, $Q_{\mathrm{ES}} \simeq \Delta w$ holds and a simple expression in terms of derivatives of the fecundity function and relatedness coefficients that approximately holds for a broader class of updating rules can be derived (their eq.37-39).

Conceptually speaking, the trait distribution approach considers the mean and variance of a distribution $(s_{11}, s_{12}, ..., s_{1n}, s_{21}, ...)$ 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.