

Evolution of reproductive effort in viscous populations: the importance of population dynamics

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Supplementary Online Material

S1 Monomorphic population

In this appendix, I show how to compute the equilibrium density $q_{o/o\times}$, which proves useful in the simplification of the expression for the selection gradient. In the monomorphic population, the dynamics of pairs $o\times$ and $\times\times$ are given by

$$\begin{aligned}\frac{dp_{o\times}}{dt} &= dp_{\times\times} + p_{oo}((1-P)b\bar{\phi}q_{\times/oo} + P\sigma bp_{\times}) - p_{o\times}(d + (1-P)b(\phi + \bar{\phi}q_{\times/o\times}) + P\sigma bp_{\times}) \\ \frac{dp_{\times\times}}{dt} &= -2dp_{\times\times} + 2p_{o\times}b((1-P)(\phi + \bar{\phi}q_{\times/o\times}) + P\sigma p_{\times})\end{aligned}$$

where $\phi = 1/n$ is the inverse of the number of neighbours of each site on the network, and $\bar{\phi} = 1 - \phi$. Adding the second equation and twice the first equation yields at equilibrium

$$0 = 2p_{oo}((1-P)b\bar{\phi}q_{\times/oo} + P\sigma bp_{\times}) - 2dp_{o\times}$$

Using the fact that $p_{oo}q_{\times/oo} = q_{o/o\times}p_{o\times}$ and $p_{oo} = p_o - p_{o\times}$, we can rearrange this equation and obtain an exact expression for $q_{o/o\times}$ as a function of $q_{o/\times}$ and p_o . Using equation (1) in the main text, we can further express the equilibrium density $q_{o/o\times}$ in the monomorphic population in function of $q_{o/\times}$ only.

S2 Deriving the selection gradient

The computation of the selection gradient requires some tedious algebraic manipulations, so rather than providing the full derivation, I sketch the different steps of the derivation. Further details about the method used can be found in [van Baalen and Rand \(1998\)](#); [Lion and Gandon \(2009\)](#); [Lion \(2009\)](#).

The per-capita growth rates of R and M individuals are

$$\lambda_R = (1-P)b_Rq_{o/R} + P\sigma b_Rp_o - d_R$$

and

$$\lambda_M = (1-P)b_Mq_{o/M} + P\sigma b_Mp_o - d_M$$

In the neutral model ($b_M = b_R = b$, $d_M = d_R = d$), it follows that at equilibrium $q_{o/R} = q_{o/M} = q_{o/\times}$. In the model with selection, if the mutant is rare and the resident population is at equilibrium, we have $\lambda_R = 0$, and we can Taylor-expand the invasion fitness λ_M around the neutral point. This gives

$$\Delta\lambda_M = [(1-P)q_{o/\times} + P\sigma p_o]\Delta b + (1-P)b\Delta q_{o/M} - \Delta d$$

Note that although the global density p_o is fixed by the resident trait, the local density $q_{o/M}$ will depend on the reproductive effort of mutants.

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Equipped with this first expression for invasion fitness, we will now derive the expression of $\Delta q_{o/M}$. Let \mathbf{p} be the vector of pair densities $(p_{oM} \ p_{RM} \ p_{MM})^T$. The dynamics of \mathbf{p} is given by

$$\frac{d\mathbf{p}}{dt} = \mathbf{M}\mathbf{p}$$

where $\mathbf{M} = \mathbf{M}_0 + P\sigma\mathbf{M}_1$. From [van Baalen and Rand \(1998\)](#) and [Lion and Gandon \(2009\)](#), we know that

$$\mathbf{M}_0 = \begin{pmatrix} -(1-P)b_M(\phi + \bar{\phi}q_{M/oM} - \bar{\phi}q_{o/oM}) - (1-P)b_R\bar{\phi}q_{R/oM} - d_M & d_R & d_M \\ (1-P)(b_R + b_M)\bar{\phi}q_{R/oM} & -d_R - d_M & 0 \\ 2(1-P)b_M(\phi + \bar{\phi}q_{M/oM}) & 0 & -2d_M \end{pmatrix}$$

The mortality terms are simple to understand because mortality is density-independent in this model. Therefore, a term of the form $d_{RR}p_{RM}$ indicates the contribution to the dynamics of the death of a R individual in a RM pair. For reproduction events, some further explanation is needed. First, the matrix \mathbf{M}_0 only collects the contributions of *local* reproduction events, hence the factor $(1-P)$. Second, the first column of \mathbf{M}_0 derives from a bookkeeping of all possible reproductive events that may affect a pair oM . Consider for instance the transition $oM \rightarrow MM$, which yields the term in the lower left-hand side corner of the matrix. Then, the empty site can be filled either by the offspring of the individual in the pair (at rate $b_M/n = \phi b_M$) or by a M individual connected to the empty site of the oM pair, which occurs at rate $(n-1)/nq_{M/oM}b_M$. The factor 2 on the last line of \mathbf{M}_0 comes from the fact that pairs are counted in both directions ([Rand, 1999](#)), hence pairs MM are counted twice.

Computing \mathbf{M}_1 is a bit more complex, but we obtain the following expression

$$\mathbf{M}_1 = \begin{pmatrix} -(b_M p_M + b_R p_R) + \frac{q_{o/o}}{q_{o/M}} p_o b_M & 0 & 0 \\ \frac{q_{o/R}}{q_{o/M}} b_M p_R + b_R p_R & 0 & 0 \\ 2p_M b_M & 0 & 0 \end{pmatrix}$$

The term on the first row gives the rate at which a pair oM is altered by long-distance reproduction events; either the pair is destroyed when a random R or M individual reproduces to the empty site in the pair, or it is created from a oo pair through long-range reproduction of a mutant. This affects the dynamics of oM pairs by a term $b_M p_M p_{oo}$, which can be rewritten because $p_M = p_{oM}/q_{o/M}$. The term on the second row gives the rate at which a RM pair is created when a random resident individual reproduces into the empty site in a oM pair, or when a random mutant individual reproduces into the empty site in a oR pair. The contribution to the dynamics is then $b_M p_M p_{oR} + b_R p_R p_{oM}$ which can be rewritten using the same trick as above. Finally, the term in the third row gives the rate at which pairs MM are created through long-distance reproduction of mutants into the empty site of a oM pair. Assuming the mutant is rare, the expression of M_1 can be further simplified using $p_M \approx 0$ and $p_R \approx p_\times$ (the equilibrium density in the monomorphic population)

$$\mathbf{M}_1 = \begin{pmatrix} -b_R p_\times + \frac{q_{o/o}}{q_{o/M}} p_o b_M & 0 & 0 \\ \frac{q_{o/R}}{q_{o/M}} b_M p_\times + b_R p_\times & 0 & 0 \\ 0 & 0 & 0 \end{pmatrix}$$

At neutrality ($b_M = b_R = b$, $d_M = d_R = d$, and $q_{o/R} = q_{o/M} = q_{o/\times}$), the expression of the invasion matrix \mathbf{M} can be simplified, and we can compute the left and right eigenvector of the neutral matrix associated with eigenvalue 0. For the left eigenvector, we find $\mathbf{v} = (2 \ 1 \ 1)$, and we know the right eigenvector is the vector $\mathbf{u} = (q_{o/M} \ q_{R/M} \ q_{M/M})^T$ ([van Baalen and Rand, 1998](#); [Lion and van Baalen, 2009](#)). Further algebra yields

$$\mathbf{u} = \left(q_{o/\times} \quad \frac{bq_{o/\times}}{d}(P\sigma p_\times + (1-P)\bar{\phi}q_{R/oM}) \quad \frac{bq_{o/\times}}{d}(1-P)(\phi + \bar{\phi}q_{M/oM}) \right)^T$$

Note that this gives in particular an equation for the nearest-neighbour relatedness $r = q_{M/M}$ ([Lion and Gandon, 2009](#); [Lion, 2009](#)) as a function of $q_{M/oM}$.

Assuming that the local densities equilibrate on a fast time scale compared to the global density of mutants, the invasion matrix \mathbf{M} can be approximated as a constant matrix whose dominant eigenvalue is the per-capita growth rate of the mutant when rare, that is, the invasion fitness (van Baalen and Rand, 1998; Ferrière and Le Galliard, 2001; Lion and van Baalen, 2009). The selection gradient is then given by

$$\Delta\lambda_M = \frac{\mathbf{v} \Delta\mathbf{M} \mathbf{u}}{\mathbf{v}\mathbf{u}}$$

where $\Delta\mathbf{M} = \Delta\mathbf{M}_0 + P\sigma\Delta\mathbf{M}_1$ is the first-order effect of selection on the invasion matrix.

Assuming the mutant is rare and the resident population is on the monomorphic attractor, the only variables that will be affected by a change in reproductive effort are b_M , d_M , $q_{o/M}$ and the triple local densities $q_{i/oM}$. Using the expressions for \mathbf{u} , \mathbf{v} and \mathbf{M} , we obtain after some rearrangements and simplifications an expression for $\Delta\lambda_M$ as a function of Δb , Δd , $\Delta q_{o/M}$ and $\Delta q_{o/oM}$ (note that $\Delta q_{o/oM} = -\Delta q_{R/oM} - \Delta q_{M/oM}$). The coefficients of the Δ terms are all evaluated in the neutral model.

Along with equation (5) in the main text, this gives a system of two equations with two unknowns $\Delta\lambda$ and $\Delta q_{o/M}$. Solving the system yields an expression for $\Delta q_{o/M}$ that depends on $q_{o/\times}$, $p_o = 1 - p_\times$, $q_{o/o\times}$, $q_{R/oM}$ and $q_{M/oM}$. Further simplifications are possible, because p_o and $q_{o/o\times}$ can be expressed in terms of $q_{o/\times}$ (equation 1 in the main text, Appendix S1), because $q_{R/oM} = 1 - q_{M/oM} - q_{o/oM} = 1 - q_{M/oM} - q_{o/o\times}$, and $q_{M/oM}$ can be expressed in terms of nearest-neighbour relatedness $r \equiv q_{M/M}$ using the expressions of the eigenvector \mathbf{u} . Putting everything together we finally obtain equation (6) in the main text.

S3 Habitat degradation

I will now extend the previous model by adding a degraded state (u). Degraded state are created when an individual dies, and become empty at rate ν . The per-capita growth rate of individuals of type $i = R$ or M takes the same form as previously

$$\lambda_i = (1 - P)b_i q_{o/i} + P\sigma b_i p_o - d_i$$

It follows that, in a monomorphic population, equation (1) in the main text still holds true in this model. From the expression for invasion fitness λ_M , equation (9) in the main text follows readily.

Now, in order to describe the invasion dynamics in more detail, we need to track four pair densities p_{oM} , p_{RM} , p_{MM} and p_{uM} . I will restrict my attention to the limiting case $P = 0$. In this case we obtain the following invasion matrix

$$\mathbf{M} = \begin{pmatrix} -b_M(\phi + \bar{\phi}q_{M/oM} - \bar{\phi}q_{o/oM}) - b_R\bar{\phi}q_{R/oM} - d_M & 0 & 0 & \nu \\ (b_M + b_R)\bar{\phi}q_{R/oM} & -d_R - d_M & 0 & 0 \\ 2b_M(\phi + \bar{\phi}q_{M/oM}) & 0 & -2d_M & 0 \\ b_M\bar{\phi}q_{u/oM} & d_R & d_M & -\nu - d_M \end{pmatrix}$$

As previously, we can compute the eigenvectors of the neutral invasion matrix associated with eigenvalue 0 and we find

$$\mathbf{v} = \left(2\frac{d+\nu}{\nu} \quad 1 \quad 1 \quad 2 \right)$$

and

$$\mathbf{u} = \left(q_{o/M} \quad q_{R/M} \quad q_{M/M} \quad q_{u/M} \right)^T = \left(\frac{d}{b} \quad \bar{\phi}q_{R/oM} \quad \phi + \bar{\phi}q_{M/oM} \quad \frac{d}{d+\nu}(1 - \bar{\phi}q_{o/oM}) \right)^T$$

Using the perturbation analysis of Appendix S2, we find

$$\begin{aligned} \Delta\lambda_M = & \Delta b q_{o/M} [2(d + \nu)\bar{\phi}q_{o/oM} + \nu\bar{\phi}q_{R/oM} + 2\nu\bar{\phi}q_{u/oM} - 2d(\phi + \bar{\phi}q_{M/oM})] \\ & - \Delta d [2(d + \nu)q_{o/M} + \nu(q_{R/M} + 2q_{u/M})] \end{aligned} \quad (\text{S1})$$

after neglecting the terms in $\Delta q_{i/oM}$ with $i = o, R, M, u$. We can simplify things further by noting that, from the expression of \mathbf{u} , we have $q_{o/M} = d/b = q_{o/\times}$, $\bar{\phi}q_{R/oM} = q_{R/M}$, $\phi + \bar{\phi}q_{M/oM} = q_{M/M}$, $\bar{\phi}q_{o/oM} =$

$1 - (d + \nu)q_{u/M}/d$. Furthermore, we have $q_{R/M} = 1 - q_{o/M} - q_{u/M} - q_{M/M} = 1 - q_{o/\times} - q_{u/M} - q_{M/M}$. Assuming that, in the neutral model, $q_{u/M} \approx q_{u/\times}$ and $q_{u/oM} \approx q_{u/o\times}$, we are left with the task of computing the equilibrium density of $q_{u/o\times}$ in the monomorphic model. I show below that this yields an implicit expression in function of $q_{u/\times}$. After some rearrangements and simplifications, we obtain equation (10) in the main text.

Combining equations (9) et (10) in the main text, we find that the ESRE in a viscous population ($P = 0$) is the solution of

$$\frac{(\Delta b/b)}{(\Delta d/d)} = \frac{1 + q_{u/\times} + (k+1)q_{o/\times} - r}{1 + q_{u/\times} + (k+1)q_{o/\times} - r + k(q_{\times/\times} - q_{\times/u} - r)} \quad (\text{S2})$$

where $k = 2d/\nu$. Extensive simulations suggest that $q_{\times/\times} - q_{\times/u} < \phi$ (results not shown), and because $r > \phi$ (Lion and Gandon, 2009; Lion, 2009), we find that the right-hand side of equation (S2) is greater than 1. For a concave-down trade-off between b and d , this implies that the ESRE for $L = 0$ is lower than the ESRE for $P = 1$.

The equilibrium value of $q_{u/o\times}$ in the monomorphic population remains to be calculated. The starting point is the equation for the dynamics of p_{ou} pairs. At equilibrium, this gives

$$dp_{o\times} + \nu p_{uu} - (\nu + b\bar{\phi}q_{\times/ou})p_{ou} = 0$$

Using the fact that $q_{\times/ou}p_{ou} = q_{u/o\times}p_{o\times}$, $q_{u/\times}p_{\times} = q_{\times/u}p_u$, and $q_{o/\times} = d/b$, we obtain

$$\bar{\phi}q_{u/o\times} = q_{o/\times} + \frac{\nu}{d}(q_{u/u} - q_{o/u})\frac{p_u}{p_{\times}} \quad (\text{S3})$$

Now, the dynamics of uu pairs is simply

$$\frac{dp_{uu}}{dt} = dp_{u\times} - \nu p_{uu}$$

which gives at equilibrium

$$q_{u/u} = \frac{d}{\nu}q_{\times/u} \quad (\text{S4})$$

Furthermore, the dynamics of the global density of u sites is

$$\frac{dp_u}{dt} = dp_{\times} - \nu p_u$$

so we have at equilibrium, using the fact that $q_{\times/u}p_u = q_{u/\times}p_{\times}$

$$\frac{p_{\times}}{p_u} = \frac{\nu}{d} = \frac{q_{\times/u}}{q_{u/\times}} \quad (\text{S5})$$

It follows from equation (S4) and (S5) that

$$q_{u/u} = q_{u/\times} \quad (\text{S6})$$

Putting equations (S3)-(S6) together, we obtain

$$\bar{\phi}q_{u/o\times} = q_{o/\times} + q_{u/\times} - q_{o/u}$$

and because $q_{o/u} + q_{u/u} + q_{\times/u} = 1$, we have finally, using equations (S4) and (S5) once more

$$\bar{\phi}q_{u/o\times} = q_{o/\times} - 1 + \frac{2d + \nu}{d}q_{u/\times}$$

which can be used in equation (S1) to obtain equation (S2).

References

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