Supplementary Online Material


Appendix E: Direct competition model

E.1 The model

We extend the birth-death model by allowing individuals to replace a random neighbour with one offspring when they reproduce. The dynamics of the global densities $p_M$ and $p_R$ then becomes

$$\frac{dp_M}{dt} = (b_M q_o/M - d + c(b_{MR} - b_{RM}) q_R/M) p_M$$
$$\frac{dp_R}{dt} = (b_R q_o/R - d + c(b_{RM} - b_{MR}) q_M/R) p_R$$

where $c$ is the competitive capacity, $b_{MR}$ is the average rate at which a $R$ individual is replaced by the offspring of a neighbouring $M$ individual, and $b_{RM}$ is the average rate of the reverse event. This yields the following expression for inclusive fitness

$$\Delta W_{IF} = \frac{q_o}{\bar{q}_M} \Delta(b_M - b_R) + b \Delta(q_o/M - q_o/R) + c(\bar{q}_M/R + \bar{q}_R/M) \Delta(b_{MR} - b_{RM})$$

In the following, we shall focus on the limiting case where the mutant is rare.

E.2 Relatedness

The equations for the dynamics of pairs $MM$ and $MR$ are (assuming $m = 0$ for the sake of simplicity)

$$\frac{dp_{RM}}{dt} = (\alpha_M + \alpha_R) q_R p_M - p_{RM}[2d + c(\phi b_{MR} + \phi b_{RM} + \bar{\phi} b_{MR} q_M/R + \bar{\phi} b_{RM} q_R/M - \bar{\phi} b_{MR} q_R/R)]$$
$$+ c b_{RM} \bar{\phi} q_R/MP_{MM}$$

$$\frac{dp_{MM}}{dt} = 2p_{oM} \beta_M - 2(d + c b_{RM} \bar{\phi} q_R/MM) p_{MM} + 2p_{RM} (\phi b_{MR} + \bar{\phi} b_{MR} q_M/R)$$

Evaluating those equations at neutrality, setting them to zero, and substracting them, we obtain using pair approximation and the fact that $\bar{q}_M/M - \bar{q}_M/R = \bar{q}_R/R - \bar{q}_R/M = \bar{\rho}$

$$0 = \frac{\bar{\phi} b c \bar{\rho}^2 - (d + c b - c \bar{\phi} d) \bar{\rho} + c \phi b + (1 - c) \phi d}{\phi}$$

If $c = 0$, the solution is $\bar{\rho} = \phi = 1/n$. If $c > 0$, the equation has two positive roots, only one of which is always less than 1 (note that $r < 1$ because $0 < q_{i/j} < 1$).

$$\hat{\bar{\rho}} = \frac{c + (1 - c \phi) q_{o/x} - \sqrt{(c + (1 - c \phi) q_{o/x})^2 - 4 c \phi (c + (1 - c) q_{o/x})}}{2 c \phi}$$

where $q_{o/x} = d/b$. It is easy to check that, for $c > 0$ and $b$ greater than the critical value for survival of the contact process

$$\lim_{b \to \infty} \hat{\bar{\rho}} = \lim_{c \to \infty} \hat{\bar{\rho}} = \frac{\phi}{\bar{\phi}} = \frac{1}{n - 1}$$

Thus, $\hat{\bar{\rho}}$ is discontinuous in $c = 0$ in the limit of high habitat saturation. This is a consequence of the pair approximation: the accuracy of pair approximation decreases when $c$ becomes small. For $c = 1$, we found that PA predicts well the qualitative trend, but underestimates the true value of relatedness when habitat saturation is low (figure E.1).
Nearest-neighbour relatedness

Local density of empty sites \( q_{o/x} = d/b \)

\[ \frac{1}{n-1} \]

extinction

\[
\text{Figure E.1: Effective relatedness } \tilde{r} = q_{M/M} - q_{M/R} \text{ computed from stochastic simulations of the neutral model on a random regular network with 10000 sites, under direct competition for increasing values of } c \text{ (filled circles: } c = 0 \text{; open circles: } c = 0.6 \text{; filled triangles: } c = 1 \text{; open triangles: } c = 1.6 \text{). The plain lines give the predictions of pair approximation (from top to bottom, } c = 1, c = 0.6, c = 0.3) \text{. The dotted line indicates the maximum value } 1/(n-1). \text{ Parameters } n = 4, d = 1, m = 0.}

E.3 DB vs BD processes

We now extend the analysis of Ohtsuki et al. (2006) to take into account the existence of empty sites. We use the same approximations as Ohtsuki et al. (2006), that is, we use weak selection and pair approximation, and we assume that we can replace the fecundities of an individual by the average fecundity based on pair approximation. The fecundity of a \( M \) individual in a \( MR \) pair will then be

\[ b_M^R = b + \bar{\phi} B q_{M/M} - C, \]

and the fecundity of a \( R \) individual in a \( RM \) pair is

\[ b_M^R = b + \bar{\phi} B q_{M/R}. \]

Likewise, we have

\[ b_M^M = b + \bar{\phi} B q_{M/M} - C \]

and

\[ b_R^R = b + \bar{\phi} B q_{M/R}. \]

Death-Birth process

Let us focus on a \( M \) individual. The individual dies at rate \( cb(1 - q_x(o)) \) and is replaced by a \( R \) individual with probability

\[ \frac{q_x(R) b_R^M}{q_x(R) b_R^M + q_x(M) b_M^M} \]

The resulting rate is non-linear with respect to \( x \), so we use an approximation of weak selection to compute the average. We obtain

\[ c p_{RM} \left[ b + \left( \frac{q_x(M)}{1 - q_x(o)} \right) (\bar{\phi} \Delta B \tilde{r} - \Delta C) \epsilon + O(\epsilon^3) \right] \]

where the average is taken over all \( M \) sites that have a \( R \) neighbour. Note that the factor \( \phi B \) in the \( b_M^M \) term has vanished due to the weak selection assumption.

Likewise, the rate at which a \( R \) individual is replaced by a \( M \) individual is

\[ c p_{RM} \left[ b - \left( \frac{q_x(R)}{1 - q_x(o)} \right) (\bar{\phi} \Delta B \tilde{r} - \Delta C) \epsilon + O(\epsilon^3) \right] \]

where the average is taken over all \( R \) sites that have a \( M \) neighbour. Putting everything together, we obtain

\[ \Delta(b_{MR} - b_{RM}) = \left[ \left( \frac{q_x(R)}{1 - q_x(o)} \right) \right]_{x=R \sim M} + \left[ \left( \frac{q_x(M)}{1 - q_x(o)} \right) \right]_{x=M \sim R} (\bar{\phi} \Delta B \tilde{r} - \Delta C) \quad (E.1) \]
The important point is that $\Delta (b_{MR} - b_{RM})$ has the same sign as $\tilde{\phi} \Delta B \tilde{r} - \Delta C$. When there is no empty sites, $q_e(o) = 0$, and therefore we can evaluate the averages as $\tilde{\phi} q_{R/RM}$ and $\tilde{\phi} q_{M/MR}$, so the factor between brackets is under pair approximation $\tilde{\phi}(q_{M/M} + q_{R/R})$. Because $q_{R/R} = 1$ and $q_{M/M} = \tilde{r}$ for a rare mutant, we find that $\tilde{\phi}(q_{M/M} + q_{R/R}) = 1$ using the fact that $\tilde{r} = 1/(n - 1)$ when there are no empty sites. This allows us to recover exactly the result of Ohtsuki et al. (2006) in the limit where the mutant is rare.

**Birth-Death** The rate at which an $M$ individual at site $x$ replaces an $R$ neighbour is given by

$$c q_x(R) b_{M}^R \sigma_x(M)$$

Likewise, the rate at which an $R$ individual at site $x$ replaces an $M$ neighbour is

$$c q_x(M) b_{R}^M \sigma_x(R)$$

Averaging over all sites, the contribution of direct competition to the inclusive fitness takes the form

$$c(q_{R/M} + q_{M/R})(b_{M}^R - b_{M}^M)$$

where

$$b_{M}^R - b_{R}^M = \tilde{\phi}B(q_{M/M} - q_{M/R}) - C - \phi B$$

yielding

$$\Delta (b_{MR} - b_{RM}) = \tilde{\phi} \Delta B \tilde{r} - \Delta C - \phi \Delta B \tag{E.2}$$

Compared to the DB process, there is an additional term $-\phi \Delta B$. Intuitively, one might think that this is because in the DB, the site being filled is empty and will therefore never provide help. However, this interpretation is not correct as the derivation of equation (E.1) for the DB process does not rely on this assumption, but only on a different way of selecting and replacing individuals. What the term $-\phi \Delta B$ in equation (E.2) really measures is the net effect of population regulation under BD competition.

**E.4 Invasion fitness**

Invasion fitness of a rare helping mutant in a selfish population is given by

$$\lambda_M = b_M q_o/M + c q_{R/M}(b_{MR} - b_{RM})$$

and the selection gradient takes the form

$$\Delta \lambda_M = q_o/\times \Delta b_M + b \Delta q_{o/M} + c \tilde{q}_{R/M} (\Delta b_{MR} - \Delta b_{RM})$$

In order to compute the ecological cost $\Delta q_{o/M}$, we will write down the equations for $dq_{M/M}/dt$ and $dq_{R/M}/dt$. Under the assumption that the mutant is rare, and using pair approximation, we obtain

$$\frac{dq_{M/M}}{dt}_{PA} = 2\tilde{\phi}b_M q_{o/M} + 2c\phi b_{MR} q_{R/M} - 2q_{M/M}(d + c\phi b_{RM} q_{R/M}) - q_{M/M} \lambda_M$$

$$\frac{dq_{R/M}}{dt}_{PA} = \tilde{\phi}(b_R + b_M) q_{R/o} q_{o/M} + \tilde{\phi}c b_{RM} q_{R/M} q_{M/M} - q_{R/M}(2d + c\phi b_{MR} + c\phi b_{RM} + c\phi b_{RM} q_{R/M} - c\phi b_{MR} q_{R/M}) - q_{R/M} \lambda_M$$

Assuming that the local densities are at quasi-equilibrium, we can set those equations to zero, and Taylor-expand them. Using the fact that $q_{R/R} = 1 - q_{o/\times} - q_{M/M}$, $q_{R/R} = 1 - q_{o/\times} - q_{M/R}$, $\Delta q_{M/M} = -\Delta q_{R/M} - \Delta q_{o/M}$, and that for a rare mutant $q_{M/R} = 0$, we obtain a system of two equations with two unknowns $\Delta q_{o/M}$ and $\Delta q_{R/M}$. Solving for $\Delta q_{o/M}$ then leads after some algebra to

$$b \Delta q_{o/M} = \tilde{\Phi}q_{o/\times} (\Delta b_M + c \tilde{q}_{R/M} (\Delta b_{MR} - \Delta b_{RM}))$$

where $T = \phi (1 + q_{o/\times} + \tilde{\phi} c q_{R/M})$, $\tilde{q}_{R/M} = 1 - q_{o/\times} - q_{M/M}$ and $\tilde{q}_{M/M} = \tilde{r}$ since the mutant is rare. We can then plug this result into the equation for $\Delta \lambda_M$ to obtain the invasion fitness of a rare mutant.
in the direct competition model. Finally, using the expressions for $\Delta(b_{MR} - b_{RM})$ derived previously for the DB and BD processes, we find that the sign of inclusive fitness is given by $\phi \Delta B \tilde{r} - \Delta C$ in the DB process, and by $\phi \Delta B \tilde{r} - \Delta C - \phi \Delta B \gamma$ in the BD process, where

$$
\gamma = \frac{c \bar{q}_{R/M} (1 - q/o \times T)}{1 - T} + (1 - q/o \times T)c \bar{q}_{R/M}
$$

When $q/o \times = 0$, $\gamma = 1$. On the verge of population extinction ($q/o \times = \phi$, see Appendix A in the main text), $\bar{q}_{R/M} = 0$, and therefore $\gamma = 0$. Because $\bar{q}_{R/M} = 1 - q/o \times - \bar{q}_{M/M}$, and $\bar{q}_{M/M} = \tilde{r}$ for a rare mutant, $\gamma$ is a function of $n$, $d/b = q/o \times$, and $c$. It is easy to show that $\gamma$ is a decreasing function of $q/o \times$.

In both the DB and the BD, the speed of selection is given by $(1 - T)q/o \times + c \bar{q}_{R/M} (1 - q/o \times T)$.

### E.5 Saturated habitat

We are now interested in the limiting case where $b \to \infty$. It is clear from the expression of $\Delta q/o/M$ that $\lim_{b \to \infty} b \Delta q/o/M = 0$, and since $q/o \times = d/b$, in the limit of high habitat saturation, invasion fitness reduces to

$c \bar{q}_{R/M} (\Delta b_{MR} - \Delta b_{RM})$.

Note that $\bar{q}_{R/M} = 1 - d/b - \bar{q}_{M/M}$, so that in the limit $b \to \infty$, $\bar{q}_{R/M} = 1 - \tilde{r} = 1 - 1/(n - 1) = (n - 2)/(n - 1) = (1 - 2\phi)/(1 - \phi)$. This scaling factor gives the speed of invasion. Lehmann (personal communication) has further shown that it also gives the magnitude of selection when the mutant is not rare.

### References