Appendix B from J.-F. Le Galliard et al., "Adaptive Evolution of Social Traits: Origin, Trajectories, and Correlations of Altruism and Mobility"

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Evolutionary Dynamics

Pseudoequilibrium Frequencies

We use the tilde and bar accents to denote the pseudoequilibrium state of the mutant during invasion and the equilibrium state of the resident, respectively. The pseudoequilibrium frequencies $\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$ are the steady states of equation (A3) when x is a resident type at ecological equilibrium and y is a rare mutant type, which gives

$$(\bar{\alpha}_x + \tilde{\alpha}_y'\bar{q}_{0|0})\tilde{q}_{0|y} - (\tilde{\delta}_y + \bar{\delta}_x + \tilde{\lambda}_y)\tilde{q}_{x|y} = 0,$$

$$2\tilde{\beta}_y\tilde{q}_{0|y} - (2\tilde{\delta}_y + \tilde{\lambda}_y)\tilde{q}_{y|y} = 0. \tag{B1}$$

Since $\tilde{q}_{y|0} \approx 0$ when the mutant is rare, this nonlinear system involves three unknowns ($\tilde{q}_{0|y}$, $\tilde{q}_{x|y}$, and $\tilde{q}_{y|y}$) and two equations. Together with the constraint $\tilde{q}_{0|y} = 1 - \tilde{q}_{x|y} - \tilde{q}_{y|y}$, equations (B1) can thus be used to evaluate the pseudoequilibrium frequencies of the mutant and hence the spatial invasion fitness defined by equation (3).

Pseudoequilibrium Frequencies of a Degenerate Mutant

In general, there is no analytical solution for the pseudoequilibrium frequencies of a mutant. However, assuming a degenerate mutant with the same phenotype as the resident, the nonlinear system (B1) can be solved analytically. The solutions of equations (B1) in this case are $\tilde{q}_{0|y} = \bar{q}_{0|x}$ and $\tilde{q}_{y|y} = \bar{q}_{y|y}$, where the detailed analytical expression for $\bar{q}_{y|y}$ (the relatedness in our model) is given by equation (6).

Selective Pressure on Mobility

The first component of the selection gradient in equation (1) can be approximated by a first-order Taylor expansion of the spatial invasion fitness with respect to m. Considering a slightly different mobility phenotype $m_y = m_x + \varepsilon$ and the first-order approximations $\tilde{q}_{0|y} = \bar{q}_{0|x} + a\varepsilon$ and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b\varepsilon$ leads to

$$\left.\frac{\partial s_x(y)}{\partial m_y}\right|_{m_y=m_x} = \bar{q}_{0|x}\left\{\left[\frac{d}{\bar{q}^2_{0|x}} - (1-\phi)u_x\right]a - \left.\frac{\partial C(m_y, u_x)}{\partial m_y}\right|_{m_y=m_x}\right\} + o(\varepsilon). \tag{B2}$$

The analytical evaluation of a using equations (B1) yields a complicated term affected directly by the mobility and altruism rate, death rate, cost of mobility, and neighborhood size but also indirectly by the effects of all model parameters on the habitat saturation statistics $\bar{q}_{x|x}$ and $\bar{q}_{0|0}$. Numerical sensitivity analyses of the selection components over a large range of parameter values indicate that a is primarily sensitive to changes in mobility rates through local contention $\bar{q}_{x|0}$, with a negative feedback of m on this selection component. For example, assuming a zero mobility cost, local aggregation becomes independent of mobility, whereas local contention increases monotonically with the mobility rate; thus, in this case, the eco-evolutionary feedback on mobility is mediated entirely by local contention and not by local aggregation. The conversion term (expression in brackets in front of a) is primarily sensitive to changes in altruism rate, life-history traits, and habitat structure.

Selective Pressure on Altruism

The second component of the selection gradient can be approximated by a first-order Taylor expansion of the spatial invasion fitness with respect to u. Assuming a slightly deviant mutant $u_y = u_x + \varepsilon$, $\tilde{q}_{0|y} = \bar{q}_{0|x} + a'\varepsilon$, and $\tilde{q}_{y|y} = \bar{q}_{y|y} + b'\varepsilon$, the first-order approximation results in the following expression (see also eq. [3] in Le Galliard et al. 2003):

$$\left.\frac{\partial s_x(y)}{\partial u_y}\right|_{u_y=u_x} = \bar{q}_{0|x}\left\{(1-\phi)\bar{q}_{y|y} + \left[\frac{d}{\bar{q}_{0|x}^2} - (1-\phi)u_x\right]a' - \left.\frac{\partial C(m_x, u_y)}{\partial u_y}\right|_{u_y=u_x}\right\} + o(\varepsilon). \tag{B3}$$