Evolution of Cooperation and Cheating

In this project, we investigate a simple model for the evolution of cooperative behaviour. The obvious problem with cooperation is that it is vulnerable to cheating. Selfish individuals ("defectors"), who take the benefit offered by others but fail to return the benefits to others at their own cost, are at an advantage in a population of cooperators. Many models of game theory address the joint dynamics of cooperators and defectors and investigate which mechanisms can protect a population of cooperators from the invasion of defectors. In this project, however, we are concerned with the evolution of the very strategies "cooperator" and "defector". We thus assume that the level of cooperative investment is a continuous variable x, which is evolving, and which is scaled such that x = 0 invests nothing into the common good or into helping others (but accepts what they give) and x = 1 gives maximal investment.

For simplicity, we consider only pairwise interactions between individuals that encounter each other at random. Both parties share the same benefit, which is an increasing function of the sum of their investments, and both parties pay a cost, which is an increasing function of their own personal investment. In a population with only strategy x, the payoff (=benefit minus cost) to an individual is

$$P(x,x) = B(2x) - C(x)$$
 (1)

where *B* and *C* are respectively the benefit and cost functions, which are both increasing with B(0) = 0 and C(0) = 0 (no investment implies no benefit and no cost). The payoff of a rare mutant *y* is

$$P(y,x) = B(x+y) - C(y)$$
⁽²⁾

because it will (almost surely) encounter a resident partner.

The number of offspring of an individual is an increasing function of the payoff received, and also depends on population density (otherwise the population would grow exponentially). We assume that the number of offspring can be written in the product form W(P)F(N), where P is the payoff to the individual and N is the size of the resident population, and that all parents die after reproduction such that the population in the next year is made up of only the offspring. The number of mutants then changes according to

$$M(t+1) = W(P(y,x))F(N(t))M(t)$$
(3)

whereas the number of residents is

$$N(t+1) = W(P(x,x))F(N(t))N(t)$$
(4)

Because the resident population is in equilibrium, N(t+1) = N(t). From equation (4), we have F(N(t)) = 1/W(P(x, x)). (Doing this, we assume that the equilibrium density is not zero, i.e., that every strategy is viable.) Substituting this into equation (3), we obtain

$$M(t+1) = \frac{W(P(y,x))}{W(P(x,x))}M(t)$$
(5)

The mutant invades if the ratio W(P(y,x))/W(P(x,x)) is greater than 1.

For the function W(P), we take

$$W(P) = \begin{cases} 0 & \text{if } P < -a \\ a+P & \text{if } P \ge -a \end{cases}$$
(6)

where *a* may be positive or negative.

The last assumption is not restrictive: Under biologically realistic conditions (which do not permit a negative value of W), one can transform an arbitrary function W into the form of equation (4) using non-linear scaling of B and C.

The behaviour of the model depends on the shape of functions B and C in equation (1). Explore the adaptive dynamics of the cooperative investment x for different functions B and C. The monomorphic singularities can be analysed analytically, but illustrate the results also with PIPs (it is worth to check linear functions and then perturb them). Investigate under which conditions evolutionary branching or evolution to a single evolutionarily stable strategy occurs, and explore the evolution of dimorphic populations by constructing isocline plots in an example with evolutionary branching.