The Emergence of Cooperation 1
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Cooperation is pervasive in nature. According to a strict Darwinian evolution perspective, costly co-operative behaviours should become less prevalent over time, to the point of extinction. How, then, does cooperation persist? Where did it originate from?

We first consider the case of the maintenance of costly cooperation. Costly cooperation is when a group of individuals (humans, cells, pyranha...) share resources (time, money, food...) for the benefit of all involved. A great example of costly cooperation is the website Wikipedia. It takes time for an individual to contribute, but if many do a terribly useful resource is created and many benefit. In terms of evolutionary forces, we think in terms of the expected number of offspring, fitness. An action is costly if it reduces an individual’s fitness and beneficial if it increases fitness.

A useful framework for thinking about cooperation is the Prisoner’s Dilemma (PD). Recall that in the PD, two criminals can either (C)ooperate with eachother or (D)efect. The PD matrix is

\[
\begin{array}{c|cc}
 & C & D \\
\hline
C & R & S \\
D & T & P \\
\end{array}
\]

where \( T > R > P > S \). Clearly, \( D \) is an evolutionary stable strategy. This means that a population consisting of defectors cannot be invaded by cooperators. Also, a population of cooperators can be invaded by defectors. The key assumption that makes this hold is that individuals engage in one-shot encounters. Once two pair off, they play the game once, receive their payoffs, and part ways. This is seldom the case in actual interactions. Typically a partner is encountered more than once, previous encounters are remembered, and strategies are altered accordingly. In this type of setup, can defectors still survive?

Let’s suppose that any two individuals in the population encounter eachother exactly \( m > 1 \) times. Denote the strategy of always defecting by \( \text{ALLD} \). Let’s consider another strategy, \( \text{GRIM} \), that starts with cooperating but as soon as the partner defects, \( \text{GRIM} \) always defects with that partner from that point onwards. How do these two strategies stack up against eachother? Here’s their payoff matrix:

\[
\begin{array}{c|cc}
 & \text{GRIM} & \text{ALLD} \\
\hline
\text{GRIM} & mR & S + (m - 1)P \\
\text{ALLD} & T + (m - 1)P & mP \\
\end{array}
\]

We can see that \( \text{GRIM} \) is an ESS if \( mR > T + (m - 1)P \). That is, the number of rounds must exceed a certain threshold value,

\[
m > \frac{T - P}{R - P}.
\]

So if the number of iterations of the game is large enough, \( \text{GRIM} \) can resist invasion by \( \text{ALLD} \). Hence, it is possible to have a population consisting of individuals that cooperate with eachother. The only requirement is that they must be exclusionary. If they encounter an uncooperative, they must defect against them. This is reciprocity; what goes around, comes around!