The Evolution of cooperation in a multidimensional phenotype space

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Introduction

The emergence of cooperation (Axelrod 1984) in populations of selfish individual is a fascinating topic that has inspired much theoretical biology. An important model to study cooperation is the phenotypic model (Levin and Segel 1982, 1985), where individuals are characterised by phenotypic properties that are visible to others. The population is well mixed in the sense that everyone is equally likely to interact with everyone else, but the behavioral strategies can depend on distance in phenotype space. We say that cooperation is more abundant than defection if the average frequency of cooperators in the stationary state strictly exceeds $1/2$ (Antal *et al.* 2009). Antal *et al.* 2009 study the evolution of cooperation in a one dimensional phenotype space in the case of the Prisonner's Dilemma and find a condition that ensures that cooperation is more abundant than defection. We derive the corresponding necessary condition in the case of a phenotype space of any dimension by applying a perturbation method to study a mutation-selection equilibrium under weak selection. We express this condition in the large population size limit by using the ancestral process (Kingman 1982).

Model

We consider a population consisting of N haploid individuals numbered by the integers $1, 2, \ldots, N$. Individual k exhibits a n-dimensional phenotype represented by $\mathbf{x}(k) = (x_1(k), x_2(k), \ldots, x_n(k)) \in \mathbb{Z}^n$, where the i-th component $x_i(k)$ is an integer for $i = 1, \ldots, n$, for $k = 1, \ldots, N$.

- Each individual adopts a strategy among two strategies, cooperation denoted by C and defection denoted by D. We suppose that cooperators cooperate with those who are of the same phenotype and defect otherwise. Defectors always defect.
- Each individual I engages in pairwise interactions with all other individuals of the population in the same generation and accumulates a total payoff a_I. The result of an interaction is characterized by the 2×2 *payoff matrix*

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} R & S \\ T & P \end{pmatrix}. \end{array}$$

- The *fitness* of I is then assumed to be in the form

$$f_I = 1 + \delta \times a_I,$$

  where δ denotes the selection intensity.
- A discrete time Wright-Fisher model is considered where each of the N individuals of the next generation independently chooses a parent from the previous generation with a probability proportional to the parent's fitness.
- An offspring inherits the strategy of its parent with probability $1 - u$ or adopts a strategy chosen at random among the two available strategies with probability u.
- If the parent is individual k, then the offspring inherits the phenotype $\mathbf{x}(k)$ with probability $1 - v$, adopts the phenotype $\mathbf{x}(k) + \mathbf{e}_i$ with probability $\frac{v}{2n}$, or adopts the phenotype $\mathbf{x}(k) - \mathbf{e}_i$ with probability $\frac{v}{2n}$, for $i = 1, 2, \ldots, n$.

Method

In the stationary state, the average frequency of cooperators is given by

$$\mathbb{E}[X] = \frac{1}{2} + \frac{1-u}{u}\mathbb{E}[\Delta X_{\text{sel}}],$$

where $\mathbb{E}[\Delta X_{\text{sel}}]$ is the expected change in the frequency of cooperators due to selection. Given a population state $\mathbf{s} = (\mathbf{n}, \mathbf{m})$, this expected change is

$$\mathbb{E}\Big[\Delta X_{\text{sel}}(\mathbf{s})\Big] = \frac{1}{N}\left(\sum_{\mathbf{x}\in\mathbb{Z}^n} m_{\mathbf{x}}\omega_{C,\mathbf{x}} - m_{\mathbf{x}}\right).$$

Here $\omega_{C,\mathbf{x}}$ is the expected number of offspring of a cooperator whose phenotype is $\mathbf{x}$, for $\mathbf{x} \in \mathbb{Z}^n$, given by

$$\omega_{C,\mathbf{x}} = \frac{N f_{C,\mathbf{x}}}{\sum_{\mathbf{y}\in\mathbb{Z}^n}\Big(m_{\mathbf{y}} f_{C,\mathbf{y}} + (n_{\mathbf{y}} - m_{\mathbf{y}}) f_{D,\mathbf{y}}\Big)}.$$

Results

- In the case of a large population size $N \to \infty$, cooperation is more abundant than defection if

$$(R-S)g_n + (S-P)z_n > (R-S-T+P)\eta_n + (S+T-2P)h_n,$$

  for a phenotype space of any dimension $n \geq 1$. Here z_n, g_n, h_n and η_n are some identity measures given by the Laplace transform of the Modified Bessel function of index 0.
- In the case of a high population-scaled phenotype mutation rate $\nu = Nv \to \infty$ with a phenotype space of any dimension $n \geq 2$, this condition takes the form

$$R > P.$$

- In the case of a low population-scaled phenotype mutation rate $\nu = Nv \to 0$ with a phenotype space of any dimension $n \geq 2$, the condition becomes

$$R + S > T + P.$$

In the case of the simplified Prisoner's Dilemma where $R = b - c$, $S = -c$, $T = b$ and $P = 0$, where $b > c$, the evolution of cooperation is favored under the following conditions.

- In the case of a large population size $N \to \infty$, cooperation is more abundant than defection if

$$\frac{b}{c} > r_n,$$

  where r_n is the benefit-to-cost ratio given by

$$r_n = \frac{z_n - h_n}{g_n - h_n}.$$

- The best scenario for the evolution of cooperation (which minimizes the ratio r_n) is the case of a high population-scaled phenotype mutation rate $\nu \to \infty$, where $r_n = 1$.

Conclusions

※ In a large population with a high population-scaled phenotype mutation rate, the evolutionary process always chooses the strategy with the higher payoff against itself, because phenotypic identity also implies strategic identity. In particular in the case of the simplified Prisoner's Dilemma, cooperation is more abundant than defection.

※ In the case of a low population-scaled phenotype mutation rate, the condition that ensures the evolution of cooperation is the well-known condition for risk dominance in a cordination game (Hersanyi and Selten 1988). In particular in the case of the simplified Prisoner's Dilemma, defection is more abundant than cooperation.

References

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