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3 Interactions and frequency-dependent selection [1]

So far, we assumed that fitness was an intrinsic quantity of an organism, which did not depend on the environment. In particular, it did not depend on the composition of the population. However, microorganisms interact in complex ways, e.g. by producing and secreting chemicals that can be useful or hurtful for others. For instance, one type of bacteria may produce a chemical that is useful to a second type of bacteria that is not able to produce it. But this production may entail a cost for the first type of bacteria. Then, the first type of bacteria is said to have a cooperative behavior.

To assess the impact of these effects in the simplest possible framework, we will look at the deterministic description. We will consider two types of individuals, denoted by A and B, and we will start from the differential equation we saw in the previous lecture (replicator equation), which describes the deterministic evolution of the population composition. Denoting by f_A the fitness of type A and by f_B the fitness of type B, the fraction x of A organisms in the population satisfies

$$\frac{dx}{dt} = (f_A - f_B)x(1-x)\,. \tag{1}$$

Interactions between types of individuals can be described in the framework of game theory. Let us consider a game such that:

- If an A individual interacts with another A, it obtains a payoff a;
- If an A individual interacts with a B individual, it obtains a payoff b;
- If a B individual interacts with an A individual, it obtains a payoff c;
- If a B individual interacts with another B, it obtains a payoff d.

Let us assume that these payoffs are all nonnegative. Let us further assume that there is no spatial structure and that all individuals interact with all others. Finally, let us assume that the fitness of an individual in the population is equal to the average payoff it receives from interacting with all other individuals. The respective fitnesses of types A and B then read

$$f_A = ax + b(1-x) \;\text{ and }\; f_B = cx + d(1-x)\,. \tag{2}$$

Importantly, they depend on the composition of the population via x. This leads to the replicator equation

$$\frac{dx}{dt} = \left[(a-b-c+d)\,x + b - d\right]x(1-x)\,. \tag{3}$$

In addition to the usual fixed points $x^* = 0$ and $x^* = 1$ corresponding to fixation of one type, there is a new fixed point in this case, provided that $a-b-c+d \neq 0$:

$$x^* = \frac{d-b}{a-b-c+d}\,. \tag{4}$$

This new fixed point is of interest only if it satisfies $0 < x^* < 1$, which requires either ($b < d$ and $a > c$), or ($b > d$ and $a < c$).

To understand the behavior of the system, we can perform a linear stability analysis around each of the fixed points. In other words, for each fixed point x^*, we write $x = x^* + \epsilon$ with $\epsilon \ll 1$, and we expand Eq. 3 to first order in ϵ, to assess if perturbations around x^* will tend to grow exponentially or to decay exponentially. We find that:

- $x^* = 0$ is stable if and only if $b < d$.
- $x^* = 1$ is stable if and only if $a > c$.
- $x^* = (d - b)/(a - b - c + d)$ is stable if and only if $a - b - c + d < 0$. Because we need either ($b < d$ and $a > c$), or ($b > d$ and $a < c$) for it to be between 0 and 1, the condition for it to be both between 0 and 1 and stable is ($b > d$ and $a < c$).

Thus, to summarize, we have the following cases:

- If $a > c$ and $b > d$, 0 is unstable, 1 is stable and $(d - b)/(a - b - c + d)$ is not between 0 and 1. Then, there is fixation of A (it is said that A dominates B).
- If $a > c$ and $b < d$, 0 is stable, 1 is stable and $(d - b)/(a - b - c + d)$ is between 0 and 1 and unstable. Then, there is bistability: either A or B fixes, depending on the initial conditions.
- If $a < c$ and $b > d$, 0 is unstable, 1 is unstable and $(d - b)/(a - b - c + d)$ is between 0 and 1 and stable. Then, there is coexistence: the fraction of A converges toward $(d - b)/(a - b - c + d)$, which is between 0 and 1.
- If $a < c$ and $b < d$, 0 is stable, 1 is unstable and $(d - b)/(a - b - c + d)$ is not between 0 and 1. Then, there is fixation of B (it is said that B dominates A).

So far, we have assumed that $a - b - c + d \neq 0$. If instead $a - b - c + d = 0$ but $b - d \neq 0$, then Eq. 3 reduces to the non-frequency-dependent case and we have either fixation of A or fixation or B. Finally, if $a = c$ and $b = d$, then Eq. 3 reduces to $dx/dt = 0$: this is the neutral case (no selection).

We observe that, with interactions and frequency-dependent selection, long-term coexistence between types becomes possible in some parameter regimes, and that initial conditions can impact the fate of the system in some parameter regimes. We conducted this analysis in the deterministic description, but it is possible to treat such a system in a stochastic description. Furthermore, we assumed that the population was well-mixed. However, spatial structure can impact the outcome in these models.

References

[1] A. Traulsen and C. Hauert. Stochastic evolutionary game dynamics. In H.-G. Schuster, editor, *Reviews of Nonlinear Dynamics and Complexity*, volume II. Wiley-VCH, 2009.