

EVOLUTION AND THE THEORY OF GAMES

STEFAN GERITZ, HELSINKI, 2011

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47. Evolutionary stability is about immunity of a resident population of a given strategy against invasion by an initially rare mutant strategy. Invasion is essentially a population dynamical concept. So far we have been rather implicit about the connection between games and the underlying population dynamics.

The standard population dynamical embedding of games is the so-called *replicator equation*: let $x_1, \dots, x_k \in X$ be strategies, and let $p_1, \dots, p_k \geq 0$ with $\sum_i p_i = 1$ be the corresponding relative frequencies in a given population. Then the expected payoff to a player with strategy x_i against a randomly selected opponent is

$$w_i \stackrel{\text{def}}{=} \sum_{j=1}^k \pi_1(x_i, x_j) p_j$$

and the expected payoff to a randomly selected player against a randomly selected opponent is

$$\bar{w} \stackrel{\text{def}}{=} \sum_{i=1}^k \sum_{j=1}^k \pi_1(x_i, x_j) p_i p_j$$

The replicator equation is the equation

$$\frac{dp_i}{dt} = p_i(w_i - \bar{w}) \quad (i = 1, \dots, k)$$

describing the continuous change of the relative frequencies p_i . The replicator equation describes a purely frequency-dependent process, which is also its greatest weakness, because many populations are also regulated by density-dependent processes.

Whole carriers have been based on the replicator equation, but here we shall not pursue this equation any further. Instead we have a look from a different direction that is typical of a fairly new approach to evolutionary games and which is called *adaptive dynamics*.

48. Adaptive dynamics is a bottom-up approach in which we first describe the population dynamics and from that derive fitness, as opposed to what happens in

the replicator equation where we start with the fitness and from that construct a population dynamics.

Consider a resident population of strategies x_1, \dots, x_k and corresponding population densities n_1, \dots, n_k . The resident population dynamics we can generally represent by the differential equations

$$\frac{dn_i}{dt} = n_i f(x_i | E_{\text{res}}) \quad (i, \dots, k)$$

where $f(x_i | E_{\text{res}})$ is the *per capita* growth rate of strategy x_i in the environment E_{res} generated by the resident population as a whole:

$$E_{\text{res}} = h(n_1, \dots, n_k | x_1, \dots, x_k)$$

for some function h . We call E_{res} also the “feedback environment”, because while E_{res} affects the growth of each strategy separately, all strategies and their population densities together determine E_{res} thus closing the feedback loop from population growth to population growth.

Next, consider an initially rare mutant strategy y with corresponding population density m . As long as the mutant is sufficiently rare, its effect on E_{res} is negligible, but the effect of E_{res} on the mutant’s *per capita* growth rate $f(y | E_{\text{res}})$ is not negligible. Like with linear stability analysis, the fate of the mutant (i.e., whether it invades or not) is described by the linear equation

$$\frac{dm}{dt} = m f(y | E_{\text{res}})$$

Integration from zero to t and division by t gives

$$\frac{1}{t} (\log m(t) - \log m(0)) = \frac{1}{t} \int_0^t f(y | E_{\text{res}}(\tau)) d\tau$$

Suppose that for $t \rightarrow \infty$ the right hand side converges to

$$s_{E_{\text{res}}}(y) \stackrel{\text{def}}{=} \langle f(y | E_{\text{res}}) \rangle \stackrel{\text{def}}{=} \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t f(y | E_{\text{res}}(\tau)) d\tau$$

which is the time average *per capita* growth rate of the mutant. We call $s_{E_{\text{res}}}(y)$ the **invasion fitness of strategy y in the environment E_{res}** .

It is clear that if $s_{E_{\text{res}}}(y) > 0$, then the mutant invades, and if $s_{E_{\text{res}}}(y) < 0$, then the mutant does not invade. The case $s_{E_{\text{res}}}(y) = 0$ cannot be decided without involving non-linear properties of the resident-mutant population dynamics.

A resident population $(n_1, \dots, n_k | x_1, \dots, x_k)$ is evolutionarily stable if $s_{E_{\text{res}}}(y) < 0$ for all $y \notin \{x_1, \dots, x_k\}$.

49. A few words about coexistence of resident strategies: we say that the resident strategies x_1, \dots, x_k coexist if the corresponding population densities n_1, \dots, n_k

stay bounded away from zero and from plus infinity, i.e., if there exist real numbers a and A such that $0 < a \leq n_i \leq A < \infty$ for all $t \geq 0$ and all $i \in \{1, \dots, k\}$.

For any resident population with coexisting strategies x_1, \dots, x_k and resident environment E_{res} we have that $s_{E_{\text{res}}}(x_i) = 0$ for all i . We call this the “principle of selective neutrality of residents.”

To see why this is true, integrate the resident dynamics and divide by t , which gives

$$\frac{1}{t} \left(\log n_i(t) - \log n_i(0) \right) = \frac{1}{t} \int_0^t f(x_i | E_{\text{res}}(\tau)) d\tau$$

Since $\log n_i(t)$ is bounded from below by $\log a$ and from above by $\log A$, letting $t \rightarrow \infty$ gives

$$0 = \lim_{t \rightarrow \infty} \frac{1}{t} \int_0^t f(x_i | E_{\text{res}}(\tau)) d\tau = s_{E_{\text{res}}}(x_i)$$

which is what we wanted to show.

50. Consider the evolution of virulence, i.e., the additional death rate due to a viral infection. Let S be the population density of susceptibles, i.e., population density of uninfected individuals, and let I_i denote the population density of individuals infected by a virus with a virulence x_i . A simple model for the resident dynamics with viral types x_1, \dots, x_k is

$$\begin{cases} \frac{d}{dt} S &= \alpha(N)S - \delta S - S \sum_{j=1}^k \beta(x_j) I_j + \sum_{j=1}^k \gamma(x_j) I_j \\ \frac{d}{dt} I_i &= \beta(x_i) S I_i - (\delta + x_i) I_i - \gamma(x_i) I_i \quad (i = 1, \dots, k) \\ N &= S + \sum_{j=1}^k \varepsilon(x_j) I_j \end{cases}$$

where N is a weighed total population density of susceptible and infected individuals; $\alpha(N)$ is the birth rate (note: only susceptibles give birth); δ basic death rate; $\beta(x)$ is the infectiousness of an individual with a virus of type x ; $\gamma(x)$ is the recovery rate.

The only thing that matters for us is the equation

$$\frac{dI_i}{dt} = I_i f(x_i | E_{\text{res}})$$

where

$$f(x_i | E_{\text{res}}) = \beta(x_i) S - \gamma(x_i) - \delta - x_i$$

Apparently, the feedback environment is given by the population density of susceptibles, i.e.,

$$E_{\text{res}} = S$$

Hence, the invasion fitness of an initially rare mutant virus with virulence y is

$$s_{E_{\text{res}}}(y) = \langle f(y|E_{\text{res}}) \rangle = \beta(y)\langle S \rangle - \gamma(y) - \delta - y$$

and so y can invade (resp. not invade) if

$$(*) \quad s_{E_{\text{res}}}(y) > (<) 0 \quad \Leftrightarrow \quad \frac{\gamma(y) + \delta + y}{\beta(y)} < (>) \langle S \rangle$$

$\langle S \rangle$ we find by applying the principle of selective neutrality of residents, i.e., we find it from the equations

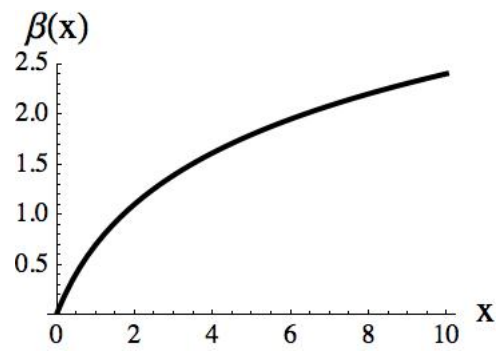
$$0 = \beta(x_i)\langle S \rangle - \gamma(x_i) - \delta - x_i$$

for $i = 1, \dots, k$, which is a system of k equations in one unknown variable $\langle S \rangle$. This tells us two things: firstly, only one virus type can robustly exist, because with two or more resident types the system of equations tends to be over-specified; and secondly,

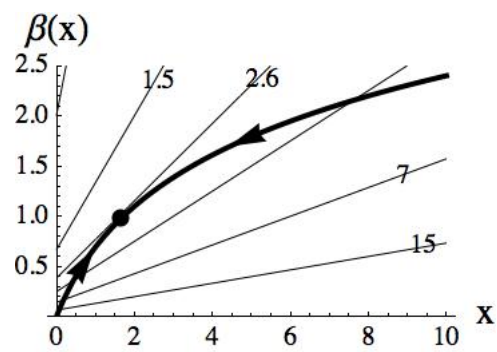
$$\langle S \rangle = \frac{\gamma(x) + \delta + x}{\beta(x)}$$

for any resident type x . Substitution of the above into $(*)$ shows that with each successful invasion and subsequent change of the resident viral type the long-term average of the density of susceptibles decreases. Eventually this will lead to the establishment of a viral type x^* that minimizes $\langle S \rangle$. Since no other type can produce a lower value of $\langle S \rangle$, no other type can invade, and hence x^* is evolutionarily stable.

This result may not be too nice for us, but at least it puts a break on the evolution of virulence, i.e., the virus does not evolve to infinite lethality. To see how this works, suppose that $\gamma(x) = \gamma$ is constant, and that $\beta(x)$ is a concave function of x as in the following figure:



Superimposed onto this graph we plot lines of constant $\langle S \rangle$, i.e., given by the equation $\beta = (\gamma + \delta + x)/c$ for various values of $c = \langle S \rangle$:



It now can be immediately seen what value of x minimizes $\langle S \rangle$.