Adaptive Dynamics Course
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Evolution of resistance in host-pathogen systems

In this project, we consider a pathogen that causes lifelong infection of its hosts, and assume that hosts may develop resistance against this pathogen (i.e., are able to defend against getting infected) but only at some cost. The question is how much resistance the host should evolve.

> The following background will hopefully further motivate this project but is not necessary for the immediate job. From basic models of epidemiology, such as the SIR model, you may be aware of the phenomenon of herd immunity. Herd immunity means that if a large enough fraction of the population is resistant or immune to the pathogen, then there is no epidemic outbreak, because the expected number of secondary infections during the lifetime of a primary infection (i.e. till recovery or death of the infected host) is less than 1 and is thus not enough to replace the primary infected host. The point here is that not every individual need to be resistant for herd immunity, and it is possible to enjoy protection from herd immunity without being resistant to the disease. When resistance is costly, there is an incentive to rely on herd immunity and avoid paying the cost. This is a form of cheating, because such non-resistant individuals enjoy benefit from others' costly resistance. Of course if cheaters are too frequent, then herd immunity collapses. Yet we may expect the evolution of resistant and cheating strategies, and this is what the present project will elaborate on.

A basic ecological model of a lifelong infection is given by

$$\begin{aligned} \frac{dx}{dt} &= r(x+y) - q(x+y)x - \beta xy \\ \frac{dy}{dt} &= \beta xy - \alpha y - q(x+y)y \end{aligned} \qquad (1)$$

where x and y are respectively the number of susceptible and the number of infected hosts. It is assumed that susceptible and infected individuals reproduce alike and newborns are free of the infection; hence all the $r(x+y)$ newborns, where r is the birth rate, are added to the susceptibles. The death rate, $q(x+y)$, depends linearly on total population size such that in absence of the pathogen, the host population grows according to the logistic model. β is the infection rate and α is the rate of death caused by the disease, called virulence.

We assume that different strains of the host differ in how much they are resistant to the disease. More resistance implies a lower rate of contracting the disease and therefore a smaller value of β (full resistance is achieved when $\beta = 0$). Resistance implies a cost: we assume that more resistant strains have lower birth rates such that $r(\beta)$ is an increasing function. The full dynamics for n different host strains is thus given by

$$\begin{aligned}\frac{dx_i}{dt} &= r(\beta_i)(x_i + y_i) - q\left(\sum_{j=1}^{n} x_j + y_j\right)x_i - \beta_i x_i \sum_{j=1}^{n} y_j \\ \frac{dy_i}{dt} &= \beta_i x_i \sum_{j=1}^{n} y_j - \alpha y_i - q\left(\sum_{j=1}^{n} x_j + y_j\right)y_i\end{aligned} \tag{2}$$

for $i = 1,...,n$.

When necessary for numerical work, assume the trade-off function $r(\beta)$ is either linear [$r(\beta) = a\beta + c$] or is given by

$$r(\beta) = c - \frac{1}{a(\beta - b)} \tag{3}$$

assuming $a > 0$. You can use the left branch of this equilateral hyperbola (with $b > 0, c > 0$ and $\beta < b$) for a convex trade-off function or the right branch (with $b < 0, c > 0$) for a concave trade-off function.

In the adaptive dynamics analysis, find examples for evolutionary branching and explore the coevolution of two host strains (will one of them evolve to be a cheater?). Investigate the effect of virulence (α) on the adaptive dynamics.