Out-of-Equilibrium Competitive Dynamics

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1 Introduction

The largest eigenvalue of a transition matrix determines the long-run growth rate of that population. So as $t \rightarrow +\infty$, $\frac{n(t)}{\lambda_1} = c_1 * w_1$, where $n(t)$ is the population vector at time t, λ_1 is the dominant eigenvalue with eigenvector w_1, and c_1 is a constant. If you combine two different species, with different transition matrices, in one system, the one with the larger dominant eigenvalue will outgrow the other in the long run. The dominant eigenvalue sets the asymptotic growth rate, and the fate of two (infinitely large) competing heterogeneous populations is deterministically set by the asymptotic growth rate [1].

What would happen, however, if one or more of the assumptions of long-run equilibrium were relaxed in this competitive scenario? We could put a cap on the population. In addition, we could set the initial conditions of the population to something different than the two populations' eigenvectors. This is exactly what is examined in Aguirre and Manrubia's paper [1]. They studied what would happen if two quasispecies were introduced into the same finite space and forced to compete for survival. Such a situation would occur when various viruses infect a host cell and attempt to take over. Only the virus that can replicate itself the most will win out. Most cells can only accommodate 1000 of these invaders before it bursts, so there is a definite population cap that the viruses expand towards. Had the population cap been infinite, the quasispecies with the larger dominant eigenvalue would always win out, population-wise. However, in a system with a finite population and two rapidly changing quasispecies, there is no guarantee that the population with the larger asymptotic growth rate will win out.

Let us examine the transition properties of each quasispecies in this model, to better understand why the out-of-equilibrium dynamics of the competition are not necessarily deterministic. Each population has a finite number of fecundity classes to reside in. If an individual is in the 5th fecundity class, for example, it will have 5 offspring every time it reproduces. Random mutation will affect the fecundity class into which each individual is born. If the individual is born with fitness-increasing mutations, it will have a fecundity that is one larger than its parent; this happens with probability q. There is also a probability p, which is typically larger than q, that the individual will experience detrimental mutations and slip down one fecundity class from its parent. All remaining individuals stay in their parent's fecundity class. The probability of remaining in the same fecundity class as your parent is referred to as the $neutrality$ of a population, and has value $\eta = 1 - p - q$.

In the case of a maximum fecundity of three, the transition matrix would look like:

$$\begin{pmatrix} \eta + 1 & 2p & 0 \\ q & 2\eta + 1 & 3p \\ 0 & 2q & 3 - 3p + 1 \end{pmatrix}$$

For any larger maximum fecundity, you can see that the transition matrix will be tri-diagonal, as the offspring can only move up a class from where their parent is, stay in the same class, or move down a class. The $+1$ on the all the diagonal entries is to show that parents do not die when they have offspring and are carried over into the next generation.

If $f_\alpha(t)$ is our population distribution at generation t for quasispecies α, then

$$f_\alpha(t+1) = M_\alpha * f_\alpha(t)$$

where M_α is the transition matrix, whose form was described and illustrated above.

Populations are allowed to grow without bound until the total population of the system reaches a finite population cap N_{max}. When that occurs, competition between species begins. Competition in this model works by letting the populations grow without bound at generation t. Then, if the total population of the system exceeds N_{max}, the population of each quasispecies is scaled according to this equation:

$$f_\alpha(t+1) = \frac{M_\alpha * f_\alpha(t)}{N_{total}(t+1)} N_{max}$$

where $N_{total}(t+1)$ is the total number of individuals in all fecundity classes of all quasispecies in generation $t+1$.

2 Methods and Results

2.1 Finding λ

The transition matrix, as discussed above, is a tridiagonal matrix with dimensions F by F, where F is the highest fecundity class possible. One of the first items to examine would be the value of λ_1, the long-run growth rate, given F, p, and q. If M_α is the transition matrix for species α, $M_\alpha * w_1 = \lambda_1 * w_1$ defines the dominant eigenvalue λ_1 and eigenvector w_1. To find λ_1, we must set $det(M_\alpha - \lambda_1 * I)$ equal to 0, where

I is the F by F identity matrix. This is only tractable in the 2 fecundity class system, where you can use the characteristic equation $\lambda_1^2 - trace(M_\alpha) * \lambda_1 + det(M_\alpha) = 0$. In that case,

$$\lambda_1 = \frac{1}{2}(4 + \eta - 2p + \sqrt{4 - 4\eta + \eta^2 - 16p - 4\eta p + 4p^2 + 8(1 + \eta + p)q}$$

In all cases where F is not equal to 2, a closed form solution for λ_1 is not possible due to the fact that setting $det(M_\alpha - \lambda_1 * I)$ equal to 0 creates a polynomial of degree greater than 2 for λ_1.

λ_1 is an accurate predictor of long-run equilibrium growth. Comparing the λ_1 values between two species shows which one will dominate the total population if the population were not capped in the system. If a population has reproduced over many populations, it is possible to obtain λ_1 without knowing p or q in the following way: Let $\tilde{f_\alpha}(t)$ be the average fecundity at generation t. You know that

$$N_\alpha(t+1) = (1 + \tilde{f_\alpha}(t)) * N_\alpha(t)$$

where $N_\alpha(t)$ is the total number of α species individuals at time t. This is true because there are $N_\alpha(t)$ parents that will carry over from generation t and each of them will have an average of $\tilde{f_\alpha}(t)$ offspring. So if the fecundity distribution is stable, $\lambda_1 = \frac{N_\alpha(t+1)}{N_\alpha(t)}$. So $\lambda_1 = 1 + \tilde{f_\alpha}(t)$ if the fecundity distribution is stable at generation t.

2.2 Examples of Transient Dynamics

Given p (the probability of moving down a fecundity class), q (the probability of moving up), F (the maximum fecundity), N_{max} (the maximum total population), and $f(0)$ (the initial fecundity distribution) for two populations, it is possible to model their transient dynamics and see who wins out in competition. In the following images, I have recreated Figures 1a, 1b, and 2a from the Aguirre paper.

In this system, $N_{max} = 1000$, $F = 20$, $p_\alpha = .1$, and $q_\alpha = .001$, resulting in an asymptotic growth rate for species α of 19.04. Species β has an asymptotic growth rate of 18.61 because $p_\beta = .2$ and $q_\beta = .05$. So species α would win out in the long run. In Figure 1, we show the total population of each species vs. the generation. In this figure, $f_\alpha(0) = 6$ and $f_\beta(0) = 3$, so species α starts out with a higher fecundity. With a better starting point and higher asymptotic growth, species α wins this competition fairly quickly.

Using the same parameters as Figure 1, but starting with different initial fecundity distributions, we arrive at Figure 2. Here, $f_\alpha(0) = 15$ and $f_\beta(0) = 15$, so both species start out the same. However, after 20 generations, species β begins to take over, due to its ability to mutate to higher fecundity distributions more quickly.

While Figures 1 and 2 show the generation by generation dynamics using certain initial conditions, Figure 3 simply shows who will win out in a competition for all initial

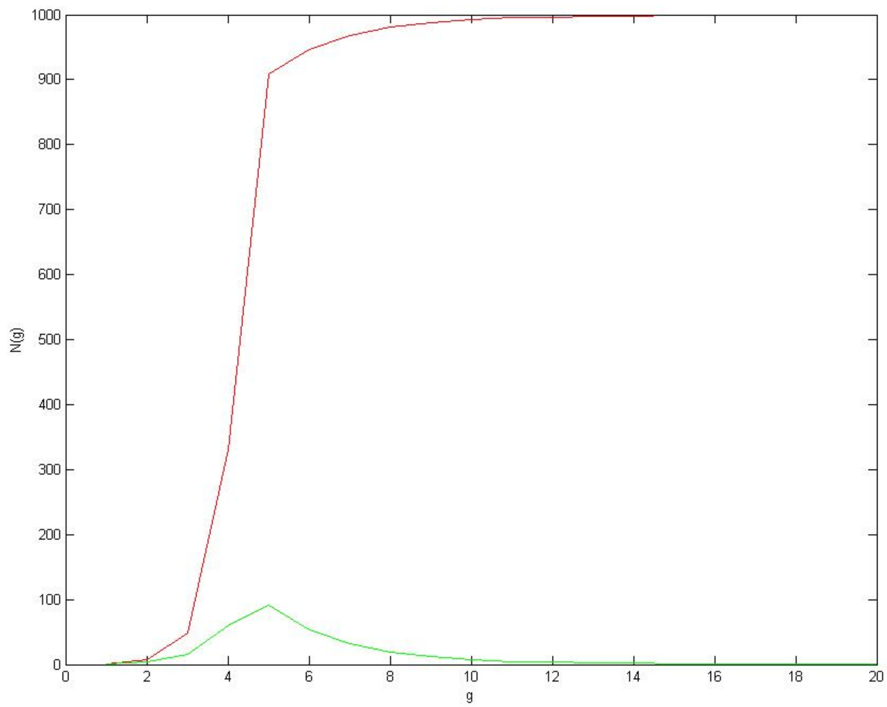

Figure 1: Here, $N_{max} = 1000$, $F = 20$, $p_\alpha = .1$, $q_\alpha = .001$, $p_\beta = .2$, and $q_\beta = .05$. $f_\alpha(0) = 6$ and $f_\beta(0) = 3$, so species α starts out with a higher fecundity. The purple line traces the population of species α and the gray line traces the population of species β. With a better starting point and higher asymptotic growth, species α wins this competition fairly quickly.

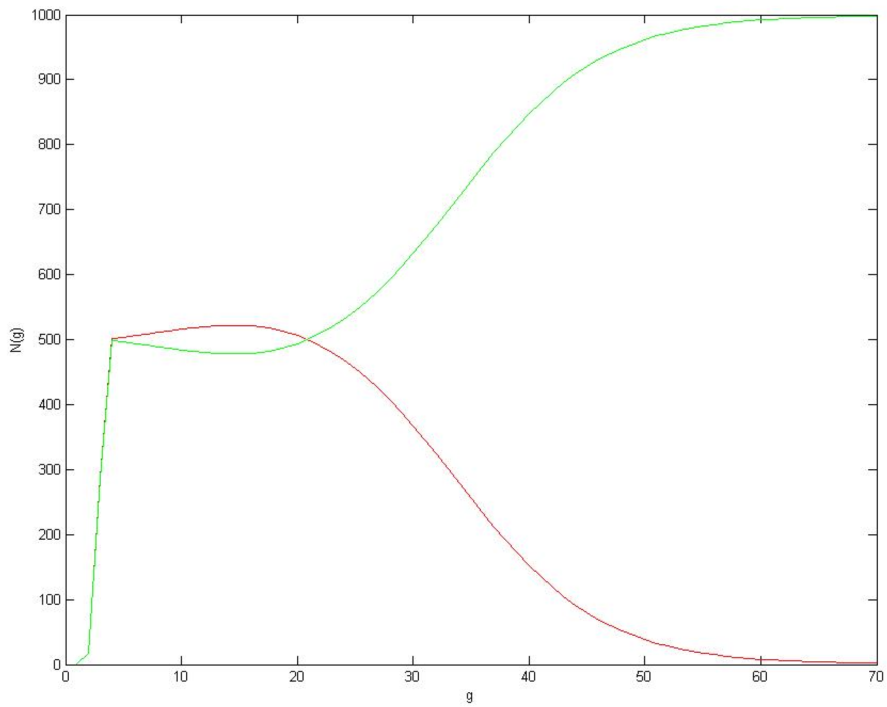

Figure 2: Here, $N_{max} = 1000$, $F = 20$, $p_\alpha = .1$, $q_\alpha = .001$, $p_\beta = .2$, and $q_\beta = .05$. $f_\alpha(15) = 6$ and $f_\beta(15) = 3$, so both species start with the same fecundity distribution. The purple line traces the population of species α and the gray line traces the population of species β. With mutations helping its population to outpace species α, species β ends up winning out here despite its lower asymptotic growth rate.

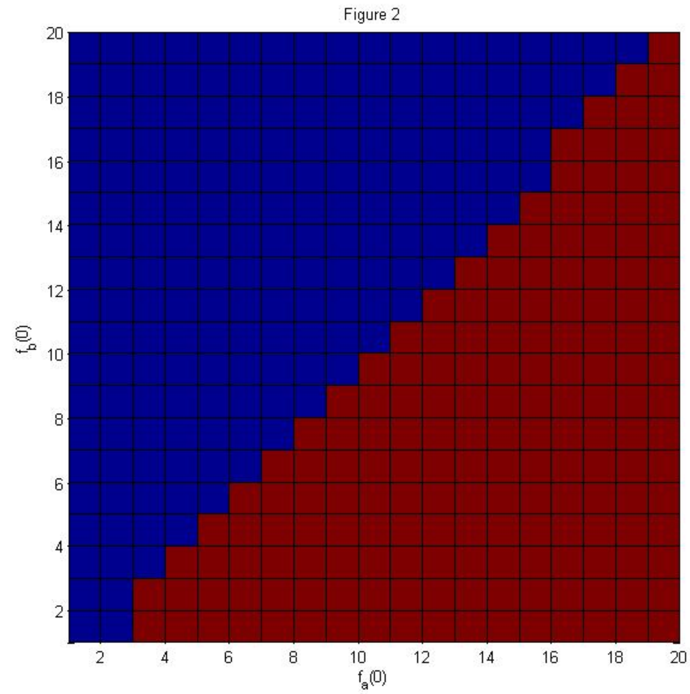

Figure 3: Here, $N_{max} = 1000$, $F = 20$, $p_\alpha = .1$, $q_\alpha = .001$, $p_\beta = .2$, and $q_\beta = .05$. $f_\alpha(0)$ is plotted on the x-axis and $f_\beta(0)$ is plotted on the y-axis. If a box is blue, that indicates that after 1000 generations, species β was winning. If a box is red, species α was winning after 1000 generations. As you can see by looking at the $f_\alpha(0) = f_\beta(0)$ diagonal, the lower the starting fecundities, the more likely β is to win because it is able to mutate to a higher fecundity distribution more quickly.

conditions. Using the same parameters (other than initial distribution) as Figures 1 and 2 above, Figure 3 plots who is winning the competition after 1000 generations. Blue boxes signify species β won and red box signify species α won. As you can see, even though species α has the higher eigenvalue (19.04 to 18.61 for species β), it often loses to species β due to the transient dynamics. Even along the $f_\alpha(0) = f_\beta(0)$ diagonal, species β wins out up to the point where $f_\alpha(0) = f_\beta(0) = 17$. Species β can simply mutate and evolve to a higher fecundity distribution faster than species α, and that makes all the difference in the short-run.

3 Discussion

An evolutionary biology class may teach you that natural selection always causes a more fit population to beat a less fit population in a competitive situation. However, this model shows that this may not be true in some cases. If a system's maximum population is capped and initial conditions for the fecundity of both species are varied, you find many situations in which the less fit population will drive the more fit population to extinction. This analysis hinges on the fact that the less fit population was more susceptible to mutation and tended to have a varied fecundity distribution more quickly than the more fit population. So the less fit population mutated faster, driving it to produce more offspring than the other population in the short-run, even though the less fit population has a smaller asymptotic growth rate and it would have produced fewer offspring in the long-run than the other population.

Such transient dynamics play a major role in real, biological systems. Few, if any, ecosystems are in a long-run equilibrium among species. The environment is typically in a state of constant flux, reacting to humans, the weather, evolution, etc. While it may be a good estimate to look at long-run population growth between species on the large scale, this ideal often breaks down given smaller systems (such as viruses in cells) or smaller time scales. If a population is eliminated in the short-run, it is pointless to argue that the population would have thrived in a competitive situation in the long-run. Thus, transient dynamics play a huge role in real world systems, and this model gives one way to evaluate the dynamics of a short-term competitive environment.

References

[1] Aguirre, J. and S.C. Manrubia, *Out-of-equilibrium competitive dynamics of quasispecies*. EPL Journal. February 2007.