

# Adaptive Dynamics

Erol Akçay

Biol 417 – Spring 2019

March 14, 2019

In the previous few lectures we were mostly concerned with short-term evolutionary perspective: what happens during the competition between two (or sometimes more than two, but finite number of) specific genotypes of organisms. Now we will shift gears and look at long-term evolution. With this shift in perspective come a couple of subtle but biologically important changes in what we track. The first is that instead of genotypes, we will now focus on the evolution of phenotypes. The reason is two-fold: First, while it is possible to identify precisely two variants of a given genetic locus and keep track of their frequency in the short term, long-term evolution proceeds over many such competitions between different variants. So, it would become unwieldy to insist on tracking allele frequencies over evolutionary time. Second, and more importantly, over longer term, we are actually not even interested in allele frequencies in the long-term. We are interested how organisms change, and in particular how they might adapt to their environments (including social ones). Therefore, our state variable is now a phenotype, usually a continuous one.

Secondly, we might also want to keep track of some ecological variables: in the long-term, as the predominant phenotype in a population changes, we might expect the ecological equilibrium of the population to change as well, which can affect further evolutionary change on the phenotypes. We ignored this feedback in the short-term perspective, since basically we were looking at the same time-scale as ecological dynamics (our equations all described change over a single generation, just like our ecological equations). Now it is less supportable to ignore the feedback, since in the long-term perspective our “time-step” is really many generations of the organism we consider.

## Invasion fitness

First let us set the stage: we start with a population that is fixed for a phenotype  $z = z_r$  (subscript  $r$  for resident), and is at its ecological equilibrium, denoted by population size  $N_r^*$ . To this population, we introduce a rare mutant with a different phenotype  $z_m$ , and consider the fitness of the mutant  $w(z_m, z_r, N_r^*)$ . Now, since the population is at ecological equilibrium prior to the introduction of the mutant, we know that a neutral mutation that has the same phenotype as the resident will have (expected) fitness of 1:

$$w(z_r, z_r, N_r^*) = 1.$$

This means that a mutant for which  $w(z_m, z_r, N_r^*) > 1$  will increase in this population (at least in the short term), whereas a mutant for which the converse

Eshel (1996) is a classic and clear exposition of the distinction between short- and long-term perspectives on evolution.

Though we should and will insist that the long-term theory is consistent with the short-term one.

For instance, we might assume that ecological population dynamics might be described by logistic density dependence, where either the intrinsic growth rate or the carrying capacity (or both) might be functions of the phenotype,  $z_r$ . In general, the ecological dynamics might keep track of things other than population size (e.g., resource levels in the environment), but for now we'll just use the population size.

holds will decrease (again in the short-term). The quantity  $w(z_m, z_r, N_r^*)$  is called the invasion fitness of the mutant phenotype. The above facts imply that a phenotype  $z^*$  cannot be invaded by any other phenotype  $z$  if and only if:

$$w(z, z^*, N_{z^*}^*) < 1 \quad \forall z \neq z^* . \quad (1)$$

This is effectively a (stricter) version of the evolutionary stability condition we discussed in previous lectures (with the phenotype  $z$  playing the role of the strategy, and the addition of the ecological equilibrium condition).

### *Fitness and population growth rate*

Before continuing, it's worth remarking how the invasion fitness defined above relates to population growth in the short term. Suppose we have a monomorphic population for  $z_r$ . Its dynamics are given by:

$$\frac{dN_r}{dt} = N_r f(z_r, z_r, N) , \quad (2)$$

where  $f(\cdot, \cdot, N)$  is the per-capita contribution to the growth rate of a resident individual in a population size of  $N$  (which in a monomorphic population is equal to  $N_r$ ). Since  $f$  is the contribution to the *change* in population size, whereas  $w$  is the total number of offspring left by a single individual, we have:

$$f(z_r, z_r, N) = w(z_r, z_r, N) - 1 . \quad (3)$$

### *Small effect mutations*

Up to now, we haven't made any restriction to the mutant  $z_m$ . In practice, most adaptive dynamics theory makes the following (consequential) assumption:

$$z_m = z_r + \delta , \quad (4)$$

where  $|\delta| \ll 1$  is a small deviation. This assumption can be motivated by the fact that many phenotypes (like body mass, running speed, timing of activity) are produced by the interaction of many biological processes affected by thousands of underlying genes. Therefore, any mutation affecting one of these genes might be expected to alter the phenotype only in a small amount. If mutations are close to the resident values (and assuming that invasion fitness is a smooth function), then we can expand their invasion fitness around  $z_m = z_r$ :

$$w(z_m, z_r, N_r^*) \approx w(z_r, z_r, N_r^*) + \delta \left. \frac{\partial w(z_m, z_r, N_r^*)}{\partial z_m} \right|_{z_m=z_r} + \frac{1}{2} \delta^2 \left. \frac{\partial^2 w(z_m, z_r, N_r^*)}{\partial z_m^2} \right|_{z_m=z_r} . \quad (5)$$

Hence, the condition for a phenotype to be uninvadable is that the first derivative vanishes and the second derivative is negative:

You might recognize that in the ESS condition, we had a weak inequality and a second clause of the ESS that applies to the case of equality. That version makes more sense in the case of discrete strategies. Here, we will be dealing with continuous strategies and smooth functions, where the equality of other fitness values will generally correspond to degenerate, not structurally stable cases.

Of course this is an approximation: we know that single mutations can cause large phenotypic changes. But this approximation nonetheless holds for a great many traits, and as we will see, makes life much easier for us.

If the first derivative doesn't vanish, then either  $\delta > 0$  or  $\delta < 0$  can invade, and since  $\delta \gg \delta^2$ , the second derivative doesn't matter unless the first derivative vanishes.

$$\left. \frac{\partial w(z_m, z_r, N_r^*)}{\partial z_m} \right|_{z_m=z_r} = 0 \quad (6)$$

$$\left. \frac{\partial^2 w(z_m, z_r, N_r^*)}{\partial z_m^2} \right|_{z_m=z_r} < 0 . \quad (7)$$

Put another way, we want the invasion fitness to have a maximum at  $z_m = z_r$  (when its value equals 1). It is convenient to define the **selection gradient** as a function of the phenotype  $z$ :

$$S(z) \equiv \left. \frac{\partial w(z_m, z_r, N_r^*)}{\partial z_m} \right|_{z_m=z_r=z} . \quad (8)$$

Thus, a necessary condition for a phenotype  $z^*$  to be uninvadable is that  $S(z^*) = 0$ .

A phenotype  $z$  that solves  $S(z) = 0$  is sometimes also called a *candidate* ESS, since whether it is an actual ESS depends on the second order condition.

### Short-term basis of adaptive dynamics

The above results can be interpreted as pertaining to the “adaptive” part of “adaptive dynamics:” they tell us under what conditions will a phenotype be uninvadable, which is a reasonable definition of that phenotype being well-adapted. But we haven’t really touched the “dynamics” part yet. To really address dynamics, we would like to derive some equation for the long-term change in the phenotype. As we talked before, that change happens over successive competitions between particular alleles. In general, this is an intractable problem, but if we are willing to concede a couple of (not entirely harmless, but supportable in many cases) assumptions, we can get purchase on the question. First, though, the result:

$$\frac{dz}{d\tau} \propto S(z) . \quad (9)$$

where  $\tau$  is the measure of time in the longer, evolutionary time scale, and the  $\propto$  sign is to be understood as “is a positive constant times.” In other words, the phenotype change over evolutionary time will be in the direction of the selection gradient. Now, this result is intuitive: after all, we showed above that whether a phenotype slightly different than a resident one will invade or not will depend on the selection gradient (unless it vanishes). Is the selection gradient is positive, then phenotypes slightly larger than a resident can invade; if it’s negative, phenotypes slightly smaller will invade. Thus, we can expect the resident phenotype to be displaced in the direction of the selection gradient.

This argument is sound, but only under some simplifying assumptions. The reason is that the invasion fitness considered only a monomorphic population invaded by a mutant (so, just two types), and only when the mutant was rare. The latter guarantees invasion, but possibly not fixation, i.e., total displacement of the resident phenotype. The former implies we only know to look at cases where mutation is rare enough that one won’t have multiple mutations in the

populations at a given time. So let us assume, out of hand, that mutation rate is indeed low. What about invasion implying fixation? It turns out we can obtain that result under weak-effect mutations.

To see how, consider the short-term (ecological) dynamics of a population with a mutant and resident types. Now the mutant is no longer constrained to be rare, so we will write the per-capita contribution to growth rate as a function of a focal individual's own type, and the mean type of the population  $\bar{z}$ :

$$\frac{dN_m}{dt} = N_m f(z_m, \bar{z}, N) \quad (10)$$

$$\frac{dN_r}{dt} = N_r f(z_r, \bar{z}, N). \quad (11)$$

where  $N$  is the total population size. Thus, for the fraction of mutants,  $p$ , we can write:

$$\begin{aligned} \frac{dp}{dt} &= \frac{d}{dt} \frac{N_m}{N} = \frac{dN_m/dt}{N} - \frac{N_m(dN_m/dt + dN_r/dt)}{N^2} \\ &= \frac{1}{N} \left( \frac{dN_m}{dt} (1-p) - p \frac{dN_r}{dt} \right) = p(1-p)(f(z_m, \bar{z}, N) - f(z_r, \bar{z}, N)). \end{aligned} \quad (12)$$

Now, if  $z_m = z_r + \delta$ , we can write:

$$f(z_m, \bar{z}, N) \approx f(z_r, z_r, N_r) + \delta \left. \frac{d}{d\delta} f(z_m, \bar{z}, N) \right|_{z_m=z_r} \quad (13)$$

$$f(z_r, \bar{z}, N) \approx f(z_r, z_r, N_r) + \delta \left. \frac{d}{d\delta} f(z_r, \bar{z}, N) \right|_{z_m=z_r} \quad (14)$$

Notice that we have the total derivative w.r.t.  $\delta$  in the first order term. All three arguments of  $f$  in the first line are affected by  $\delta$ , whereas only the second and third arguments are affected by  $\delta$  on the second line. Thus, the per-capita contributions are:

$$f(z_m, \bar{z}, N) \approx f(z_r, z_r, N_r) + \delta \left[ \frac{\partial f}{\partial z_m} + \frac{\partial f}{\partial \bar{z}} \frac{d\bar{z}}{d\delta} + \frac{\partial f}{\partial N} \frac{dN}{d\delta} \right]_{z_m=z_r} \quad (15)$$

$$f(z_r, \bar{z}, N) \approx f(z_r, z_r, N_r) + \delta \left[ \frac{\partial f}{\partial \bar{z}} \frac{d\bar{z}}{d\delta} + \frac{\partial f}{\partial N} \frac{dN}{d\delta} \right]_{z_m=z_r}, \quad (16)$$

Note that  $\frac{dz_m}{d\delta} = 1$  by definition.

Note that two of the terms in the square brackets appear in both first-order terms, so they will cancel each other out, as will the zeroth order terms. Thus:

$$f(z_m, \bar{z}, N) - f(z_r, \bar{z}, N) \approx \delta \left. \frac{\partial f(z_m, \bar{z}, N)}{\partial z_m} \right|_{z_m=z_r} \quad (17)$$

The final step is to observe that the derivative is now evaluated at a population size  $N$  that might in principle be different than the resident equilibrium. However, we can again use the fact that the mutant is only slightly different than the resident to expand the derivative itself:

$$\frac{\partial f(z_m, \bar{z}, N)}{\partial z_m} \approx \frac{\partial f(z_m, \bar{z}, N_r^*)}{\partial z_m} + (N - N_r^*) \frac{\partial^2 f(z_m, \bar{z}, N)}{\partial z_m \partial N} \quad (18)$$

For small  $\delta$ , the difference  $N - N_r^*$  can be expected to be of order  $\delta$  (i.e.,  $N - N_r^* < k\delta$  for some constant  $k$ ), which means the second term in (18) will contribute a term of order  $\delta^2$  when plugged back into equation (17), which we can ignore. Hence:

$$\frac{dp}{dt} \approx p(1-p)\delta \left. \frac{\partial f(z_m, \bar{z}, N_r^*)}{\partial z_m} \right|_{z_m=z_r} = p(1-p)\delta S(z_r) \quad (19)$$

In other words, if a mutant can invade (if the selection gradient is positive) it will also be able to go to fixation, or substitute the resident phenotype. This removes the pesky possibility that the invasion of mutants will result in polymorphisms that might throw a wrench in long-term evolution. Again, it's worth pointing out that this result is a consequence of assuming that the resident is only slightly different than the mutant. To put it another way, this theory applies strictly speaking only in the limit of small genetic variation, but ends up being a useful approximation even for appreciable genetic variation in many cases.

## Convergence stability

Above, we discussed uninvadability, which is a notion of evolutionary stability that pertains to whether a population will move from a given phenotype. If a phenotype  $z^*$  is uninvadable in the above sense, long-term evolutionary dynamics (given by (9)) starting from  $z^*$  will not move from there. In other words  $z^*$  is an equilibrium of the dynamics in (9). But at this point, we know that equilibria can be stable or not, depending on whether trajectories starting off an equilibrium but close to it converge to the equilibrium or not. Thus, there is an additional stability concept we need to be concerned about. This concept is called *convergence stability*.

Fortunately, we know from the very beginning of the class how to determine the stability of equilibria in continuous time one-dimensional dynamics: an equilibrium  $z^*$  that solves  $S(z^*) = 0$  is convergence stable when:

$$S'(z^*) < 0, \quad (20)$$

which means that the selection gradient has to cross the zero-axis from above. Remember that  $S(z)$  itself is a partial derivative of the invasion fitness, so effectively we have a second order condition (one involving second derivatives):

$$S'(z) = \left[ \frac{\partial^2 w(z_m, z_r, N_r^*)}{\partial z_m^2} + \frac{\partial^2 w(z_m, z_r, N_r^*)}{\partial z_m \partial z_r} \right]_{z_m=z_r=z} < 0. \quad (21)$$

Note that condition (21) has the additional cross-derivative relative to condition (7). So it is possible to satisfy (7) but not (21) and vice versa. Thus, an uninvadable phenotype might not actually be attainable through adaptive dynamics, or the phenotype that adaptive dynamics converge to might not be uninvadable.

To distinguish it from evolutionary stability of the short-term perspective. This is in part why we avoided calling uninvadability evolutionary stability, since convergence stability is also a type of evolutionary stability. Many papers, however, will use evolutionary stability for uninvadability (and ESS for uninvadable phenotypes), so it's not wrong to use ESS for uninvadable.

## References

Eshel, I. 1996. On the changing concept of evolutionary population stability as a reflection of a changing point of view in the quantitative theory of evolution. *Journal of mathematical biology* 34:485–510.