A Gentle Introduction to The Price Equation

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1 Introduction

The **Price Equation** is a very general way to describe selection processes. It is often used to explore multi-level selection (which is why we are interested in it). It looks simple but can be confusing. We will present several derivations of the equation, and some applications, in order to get a nuanced feeling for what the equation says.

2 Preliminaries[1]

We start by presenting a simple model of the evolution of a biological system, called *replicator dynamics for viability selection.* This has nothing to do with the Price equation, so you can skip it, if you want. However, we will use the formula derived here for our first derivation of the Price equation. In any case, this derivation is a good way to get your feet wet.

Assume a population with n haploid individuals. All reproduction in the model is asexual. There are two genotypes: A and B. Generations are discrete - everyone is born at the same time and reproduces at the same time. Reproduction produces zygotes, that have some probability which depends on their genotype of surviving into adulthood. This is how selection is modeled. The new generation of adults then produces the next generation of zygotes. Let p be the frequency of the A genotype in the population at time t :

$$p = \frac{\text{number of A zygotes}}{n}$$

This means that there are np zygotes of type A. So the B zygotes number $n(1-p)$.

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[1] This section follows a discussion in Richard McElreath and Robert Boyd *Mathematical Models of Social Evolution: A Guide for the Perplexed* (2007). I highly recommended this book.

From now on, we will use the convention of using a prime to indicate the value of variables in the next stage of evolution. Thus, p' is the frequency of A's in the next step.

We represent the chances of survival of zygotes of the two types by $V(A)$ and $V(B)$. For example, $V(A) = 0.5$ means that only half of the A zygotes survive. Using all these notational definitions we can write down an expression for the number of A adults:

$$\text{number of A adults} = npV(A)$$

This expression should be easy enough to understand. This type of calculation will appear many times in what follows, so make sure you understand it fully. Can you write an expression for the number of B adults? It is:

$$\text{number of B adults} = n(1-p)V(B)$$

Now that we know the number of A adults, we can calculate the frequency of A among adults, denoted p' :

$$\begin{aligned} p' &= \frac{\text{number of A adults}}{\text{number of A adults} + \text{number of B adults}} \\ &= \frac{npV(A)}{npV(A) + n(1-p)V(B)} \end{aligned}$$

The n's of course cancel out. The expression $pV(A) + (1-p)V(B)$ is simply the average fitness in the population. Make sure you understand why! For the most part we will try to avoid referring to population size, so when we need to compute population averages we will base the calculation on frequencies. Since fitness is often denoted by the letter w , and since we conventionally use a bar to signify averages, this value is usually written $\bar{w}$. Using this notation we can express the value of p' like this:

$$p' = \frac{pV(A)}{\bar{w}}$$

Now suppose that each adult, whether A or B, produces z zygotes when it reproduces. We guess that this means that p'' , the frequency of A among the zygotes at $t+1$will remain unchanged (since A and B reproduce at the same rate). We can verify this by writing down the expression for p'' :

$$p'' = \frac{z(\text{number of A adults})}{z(\text{number of A adults}) + z(\text{number of B adults})}$$

The z's of course cancel out, and $p'' = p'$ .We can use these expressions to calculate the frequency p any number of generations into the future (taking into account V , of course). Another way to represent what is going on in the population is to look at how the frequency p changes each generation:

$$\begin{aligned}\Delta p &= p'' - p \\ &= \frac{pV(A)}{\bar{w}} - p\end{aligned}$$

To simplify this expression we do a little algebra, starting by multiplying the rightmost p by $\frac{\bar{w}}{\bar{w}}$, which equals 1.

$$\begin{aligned}\Delta p &= \frac{pV(A)}{\bar{w}} - \frac{p\bar{w}}{\bar{w}} \\ &= \frac{pV(A) - p(pV(A) + (1-p)V(B))}{\bar{w}} \\ &= \frac{p\left[V(A) - pV(A) - (1-p)V(B)\right]}{\bar{w}} \\ &= \frac{p\left[(1-p)V(A) - (1-p)V(B)\right]}{\bar{w}} \\ &= p(1-p)\frac{V(A) - V(B)}{\bar{w}}\end{aligned}$$

This expression gives the change in the frequency of A as a result of selection. It is important to try to understand it in qualitative terms. $\frac{V(A)-V(B)}{\bar{w}}$ is the increase of A over B. Naturally, A is expected to increase in frequency if $V(A) > V(B)$ while B should spread if $V(B) > V(A)$. What about the $1/\bar{w}$ factor? It is not enough to know that each A has (say) m offspring more than B. To know how the *frequency* of A changes we need to factor in how many A's and B's there are. If there are many B's, and a solitary A, for example, A's advantage is probably dwarfed. Normalizing by the average fitness of the entire population fixes this issue. The term $\frac{V(A)-V(B)}{\bar{w}}$ gives the proportional increase (or decrease) of A over B.

Note also that the advantage of A compared to B does not remain constant. Assuming $V(A) > V(B)$, as generations pass there are more A's relative to B's. So their contribution to each subsequent generation is magnified (e.g., not only does each A have twice as many offspring as each B, but there are also twice as many A's in the population). But what about the change in their *frequency* (or proportion) relative to the B's? This will in fact become smaller (make sure you understand why). In the extreme case, when $p = 1$ and $1-p = 0$ no further change in the frequency of A's will occur (of course), though the population will continue to grow in size. When $p = 0$ and $1 - p = 1$, the reverse happens - the number of A's will not increase, no matter how large $V(A)$ is. More generally, as p grows relative to $1-p$, the rate of increase in p slows down. The fastest changes happen when $p = 1-p = 0.5$. At this point the change in the frequency of A *due to natural selection* is maximized. The term $p(1-p)$ captures this. In fact it is the *variance* of the two genotypes in the population. The strength on natural selection is directly proportional to the variance in the population.

Exercises

1. If the population mean fitness is $\bar{w}$, and the population size is N, what is the population size in the next generation?
2. Given a haploid population of size N, the frequency of allele A is p, how many individuals carry the A allele?
3. A random process involves picking on member of the population, and checking if it is an A. Success is counted as 1 and failure as 0. The frequency of A's in the population in p . Calculate the expected outcome of this trial, and the variance. (This setup is called a binomial distribution.)
4. Prove that the maximal value of $p(1-p)$ is at $p = 0.5$.
5. What do we mean when we say that a gene "spreads" in a population?

3 First derivation: simple version[2]

Let p be the frequency of allele A in the population, $V(A)$ the average fitness of allele A, and $\bar{w}$ the average fitness of the population. As we saw in the previous section, the frequency of A in the next step, p' , is,

$$p' = p\frac{V(A)}{\bar{w}}$$

Subtracting p from both sides, and multiplying by $\bar{w}$ gives:

$$\bar{w}\triangle p = pV(A) - p\bar{w} \tag{1}$$

We will now try to message the last equation so that its mathematical structure is more explicit. Assume each individual in the population has a unique id number, i (i will go from 1 to n). We will use the following notation:

w_i is the fitness of individual i

p_i is the frequency of allele A in individual i.

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[2] This section is also based on McElreath & Boyd (2007), chp. 3.

(What does "the frequency of an allele in an individual" mean? If organisms are haploid $p_i = 1$ if the organism carries A, and 0 otherwise. For diploids $p_i = 1$ if homozygote for A, 0.5 for heterozygotes, and 0 otherwise. In other words, "the frequency of an allele in an individual" is the probability of transmitting the allele to descendants, or (saying same thing in yet another different way), the proportion of the allele in the gamete pool of the individual. This number is the weight we need to assign to i when we go over each individual to determine p. We'll have to see later why the wording "the frequency of an allele in an individual" makes sense.)

Using these definitions we can write down formulas for $\bar{w}$ and p in terms of w_i and p_i.

$$\bar{w} = E(w_i) = \frac{1}{n}\sum w_i$$

$$p = E(p_i) = \frac{1}{n}\sum p_i$$

Exercises

6. To see why this expression for p is correct, give an expression for p in terms of c_i, the number of A alleles a diploid individual i carries. What's the relation between c_i and p_i?

We can also give an explicit expression for $V(A)$, the average fitness of allele A. To give an expression for $V(A)$ we take the sum of the fitnesses of all individuals weighted by the frequency of A, divided by the total number of A alleles in the population (again it might be easier to start by writing an expression using c_i):

$$V(A) = \frac{\sum p_i w_i}{\sum p_i}$$

We now substitute the expressions for $\bar{w}$ and p into eqn. (1) giving:

$$\bar{w}\triangle p = \left\{\frac{1}{n}\sum p_i\right\} V(A) - \left\{\frac{1}{n}\sum p_i\right\}\left\{\frac{1}{n}\sum w_i\right\}$$

Let's get rid of $V(A)$ by substituting the expression for $V(A)$ into the equation:

$$\bar{w}\triangle p = \left\{\frac{1}{n}\sum p_i\right\}\left\{\frac{\sum p_i w_i}{\sum p_i}\right\} - \left\{\frac{1}{n}\sum p_i\right\}\left\{\frac{1}{n}\sum w_i\right\}$$

We can now at last do a bit of math, and simplify the equation, giving:

$$\bar{w}\triangle p = \left\{\frac{1}{n}\sum p_i w_i\right\} - \left\{\frac{1}{n}\sum p_i\right\}\left\{\frac{1}{n}\sum w_i\right\}$$

The first term of the right hand side is the average, or expectation, of $p_i w_i$. The second is the product of the expected value of the allele frequency, p_i, and the expected value of individual fitness, w_i. This structure reminds us of the definition of covariance, cov(x,y)=E(xy)-E(x)E(y). Putting all this together we get the **Price equation** that describes in very general terms the response to selection:

$$\boxed{\bar{w}\triangle p = E(p_i w_i) - E(p_i)E(w_i) = \text{cov}(w_i, p_i) \qquad (2)}$$

Another way of expressing this equality is to recall that by the definition of the regression coefficient we have that $\text{cov}(x, y) = \text{var}(x)\beta(y, x)$ and that $\text{cov}(x, y) = \text{cov}(y, x)$. Substituting into the Price equation gives:

$$\bar{w}\triangle p = \text{var}(p_i)\beta(w_i, p_i)$$

This expression shows how the evolutionary change depends on the variance in allele frequencies and the regression of fitness on the genotype (i.e., on how well the genotype predicts fitness). The role of selection is captured by the regression coefficient of fitness on allele frequency ($\beta(w_i, p_i)$), that is on how well the allele frequency in an individual predicts the individual's fitness. It helps to divide both sides of equation (2) by $\bar{w}$ giving:

$$\triangle p = \text{cov}(\omega_i, p_i)$$

Instead of absolute fitness w_i, here ω_i is the *relative fitness.* Put this equation into words! ("The change in frequency....")

Notes:

1. The derivation started from an a haploid model. The result, it turns out, applies to any ploidy (diploid, haplodiploid).
2. A nice property of the last expression is that $\text{var}(p_i)$and $\beta(w_i, p_i)$ can potentially be empirically determined or estimated.
3. Eqn. (2) is not the full Price equation: An important term is missing. But it is still important to understand what this equation tells us about selection. We'll understand the simplifying assumptions later.

4 Full derivation[3]

We now derive the full Price equation from more generic assumptions. In the process we will see how selection can operate on many levels.

We consider a population of "particles" of many different types. We make no assumptions about the particles, only that they replicate (so they can refer to "genes" or alleles for example). The particles are grouped into subpopulations labeled $g = 1, 2, 3...$Within each subpopulation the particles themselves are labeled $i = 1, 2, 3...$The ith particle in group g is labeled ig and w_{ig} copies of it are made in a time unit. We will follow the fate of one kind of particles (e.g., one allele), which we will denote S. We further define the notation in the following table:

	Subpopulation g	Entire population
Number of particles	n_g	N
Frequency of S	p_g	p
Mean number of copies	$w_g = \frac{1}{n_g}\sum_i w_{ig}$	$\bar{w} = \sum_i \frac{n_g}{N} w_g$

We will add a prime to each variable to denote the value of the variable in the next generation. The frequency of S after on generation is:

$$p' = \sum_g \frac{n'_g p'_g}{N'}$$

This is simply the sum of the number of S individuals in each group, divided by the population size.

Note that $n'_g = w_g n_g$ and $N' = \bar{w}N$. Substituting we get:

$$p' = \sum_g \frac{w_g n_g}{\bar{w}N} p'_g$$

This equation shows us how to calculate the change in the frequency of S in the entire population by tallying what happens in each subpopulation (indicated by g).

Substract p from both sides and multiply by $\bar{w}$ to get:

$$\bar{w}\triangle p = \sum_g \frac{n_g}{N} w_g p'_g - p\bar{w} = \sum_g \frac{n_g}{N} w_g p'_g - p\left\{\sum_g \frac{n_g}{N} w_g\right\}$$

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[3] McElearth & Boyd (2007), chp. 6.

This is nasty, so we add and subtract $\sum_g \frac{n_g}{N} w_g p_g$to the last expression, and rearrange::

$$\bar{w}\triangle p = \left(\sum_g \frac{n_g}{N} w_g p_g - p\sum_g \frac{n_g}{N} w_g\right) + \left(\sum_g \frac{n_g}{N} w_g p_g' - \sum_g \frac{n_g}{N} w_g p_g\right)$$

Simplify the expressions in parenthesis:

$$\bar{w}\triangle p = \sum_g \frac{n_g}{N} w_g (p_g - p) + \sum_g \frac{n_g}{N} w_g (p_g' - p_g)$$

Recall that the expectation of a random variable is essentially the same thing as a weighted average, which is what we have in the last equation where each subpopulation g is weighted by its relative size. So another way to write the equation is:

$$\bar{w}\triangle p = E\left(w_g(p_g - p)\right) + E\left(w_g(p_g' - p_g)\right)$$

Reacall that $\mathrm{cov}(x, y) = E(xy) - E(x)E(y) = E\left\{x\left(y - E(y)\right)\right\}$. This means that $E\left(w_g(p_g - p)\right) = \mathrm{cov}(w_g, p_g)$. So, finally, the general form of the Price Equation:

$$\boxed{\bar{w}\triangle p = \mathrm{cov}(w_g, p_g) + E\left(w_g \triangle p_g\right) \qquad (3)}$$

What does this mean? The first thing we notice is that the evolutionary change is composed of two elements: a covariance term, and an expectation term. The first term is the inter-group term; the second the intra-group term. The covariance is between the frequency of the allele S in g and the mean fitness of individuals in g. This we have already seen in the simple version of the equation, and is easy to understand. This is about change that is directly due to selection. The better the trait predicts fitness the more quickly it will spread.The second term (the expectation term) is a little harder to understand. It tells us something about the *transmission* of group g (inheritance). The product is of the average fitness in group g times the change in frequency of the S allele in group g. It will take us awhile to understand exactly what this expectation means in biological terms.

It is easy to see that if the frequency of S in each group doesn't change ($\triangle p_g = 0$) the expectation term disappears and we are back to the simple version of the equation we initially developed. When is this the case? Suppose each *subpopulation* is a single individual organism (so we have a population of individuals, each itself a population of genes). If organisms reproduce asexually $\triangle p_g = 0$, since each organism transmits its exact genetic repertoire to its descendants (assuming no mutations!). Changes due to selection happen because of what happens to individuals, not because what happens to genes *inside* individuals. We now see that the same holds if the organisms are sexually reproducing as well: the frequency of the allele in the gametes should roughly equal its frequency in the parents. This is what we assumed in the first derivation.[4]

When is this not true? $\triangle p_g \neq 0$ if the frequency of S in offspring is different than in the parent. This will happen in situations where some alleles can get more or less than their share of the "bounty." For example, an allele might have a frequency of 0.5 (i.e., the individual is a heterozygote), but instead of being in only half the gamete manage to sneak into all of them, so $p'_g = 1$. This can happen due to *meiotic drive* and mutations. [What about assortative mating?] The second thing to keep in mind is that the equation shows us how to calculate the response of S in the entire population to selection by tallying what happens in each subpopulation..

Multi-Level Selection Comes to the Scene

Consider again eqn. (3):

$$\underline{\bar{w}\triangle p} = \mathrm{cov}(w_g, p_g) + E\left(\underline{w_g \triangle p_g}\right)$$

The two underlined expressions look almost the same. The left one is about the *whole* population. The underlined term on the right is the average fitness in group g times the change in frequency of the allele in group g. But we can use the Price equation to calculate the underlined value on the right hand side, since the Price equation applies to any population whatsoever. So we just <u>expand</u> eqn. (3) by substituting the right hand side of the Price equation into the expectation term, but this time the groups that make up each subpopulation g are the individuals ig :

$$\bar{w}\triangle p = \mathrm{cov}(w_g, p_g) + E\left(\underline{\mathrm{cov}(w_{ig}, p_{ig}) + E(w_{ig}\triangle p_{ig})}\right)$$

If we again assume there is no meiotic drive and mutations can be ignored (at the bottom level), we can simplify:

$$\bar{w}\triangle p = \mathrm{cov}(w_g, p_g) + E\left(\underline{\mathrm{cov}(w_{ig}, p_{ig})}\right)$$

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[4] There are nuances here that might be confusing: If each group is an individual, it is natural to think about all its descendants making up g', which will have the same p'_g. But in the diploid case, if each g is an individual, sexual reproduction means we need to keep track of two parents: if we put all the descendants of g in g' we'll end up counting them twice (for the father as well as the mother). In the general case this is not a problem (can you see why?), and the frequency of the allele in offspring should match the parents. We'll have to say more about these bookkeeping issues later. You may also be wondering about a more fundamental issue, namely that the model does not explicitly deal with reproduction (sex) *between* groups.

Formally this is simple, but what does it actually mean? This expression shows us how to calculate the response to selection, by first averaging across individuals within groups (to get the second cov), and then across the groups that make up the population (to get the expectation). Earlier we expressed the same quantity while ignoring the population structure. The numerical value remains the same, of course. We can tell that we are now thinking about two levels of organization just by looking at the second term on the right hand side (the expectation term). If you try to think how such a value is calculated you immediately see you need two levels, since you need multiple cov values, to take the average of. In this case we assumed that we have a population of subpopulations of individuals (each *ig* denotes a single individual comprised of genes; see figure 1). But we can of course repeatedly expand the equation for any number of levels, halting when we take the expectation term to be zero.

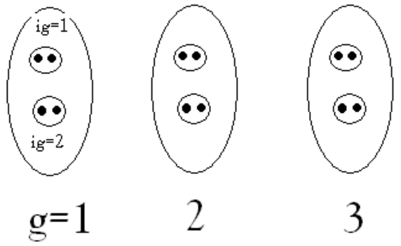

Figure 1: Population structure

Group selection

Let's express the two-level Price equation using regression coefficients:

$$\bar{w}\triangle p = \text{cov}(w_g, p_g) + E\left(\underline{\text{cov}(w_{ig}, p_{ig})}\right)$$

becomes

$$\bar{w}\triangle p = \text{var}(p_g)\beta(w_g, p_g) + E(\text{var}(p_{ig})\beta(w_{ig}, p_{ig}))$$

Recall that the regression coefficients tells us the effect of selection. By expanding the Price question we now see the effect of selection at each of the two levels. The left term refers to selection *between* groups (aka *group selection*), and the right term, which we are already familiar with, is concerned with selection between individuals. Using this decomposition we can try to think qualitatively about what happens when selection operates simultaneously on two levels. If having an allele is beneficial to individuals, and having many copies of the alleles is beneficial for a group, clearly selection on both levels will favor the allele. This will usually be the case: if being taller is better, probably having many tall members is good for the group (see question 7). The two beta expressions will be positive, and the effect of selection is additive. Try to figure out which term is likely to be bigger than the other. It may also be the case that there is no selection between the groups; again it is clear that what benefits individuals will spread. In which biological situations are the two terms going to have opposite signs? When, for example, is an allele detrimental to the individuals carrying it, while providing a benefit to the group (thus making the first beta positive and the second negative)? We need a trait that makes the group "fitter" at the expense of individual organisms. When this happens we talk about *biological altruism.* In the simplest terms, altruism happens when individuals reduce their own fitness by helping others, thereby increasing the fitness of groups with altruists compared to groups with less altruists. Since in such cases the terms will have opposite signs, what determines whether the trait will spread will be their relative magnitude.

The second thing the equation tells us is that for selection to be effective there has to be variance. If $\mathrm{var}(p_g)$ is very small, the first term disappears. Put into words: If groups have similar frequency of the altruism allele, altruism will not evolve.

Exercises

7. Return to the definitions and explain in your own words what w_g means. Does it make sense to call this *group fitness*?
8. So some groups fare better *because* of altruists. Or is it *individuals* in those groups that fare better? Explain how you interpret $\beta(w_g, p_g)$.
9. Does the Price equation say anything about selection *between* groups? What does selection *between* groups mean?
10. Think of the inheritance graph. Is there *group level* inheritance?

5 One more time[5]

You think you had enough? How about deriving the Price equation one more time? We will first write the equation (in its simple and full forms) using different symbols, and describe it slightly differently. This time we will be more explicit about what constitutes a group, and how groups change between generations. Don't worry, we are still talking about the same thing. Keep

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[5] The derivation in this section is from Frank (1995).

thinking of the form of the equations, and the biological processes they describe. So here is the simple form one more time:

$$\bar{w}\triangle\bar{z} = \text{cov}(w, z) = \beta(w, z)\text{var}(z)$$

where w as usual is fitness and z is a quantitative character (e.g. the length of the proverbial giraffe's neck). What this formulation says is that the change in the average value of the character, $\triangle\bar{z}$, depends on the covariance between the character and fitness. We already know that this is the same as the regression coefficient of fitness on the character, multiplied by the variance in the character. Compare this with the derivations so far: There we talked about frequency of alleles, here we assume a quantitative trait, with continuous values.[6] Now we can do something nifty. Assume the trait we want to track is the fitness of the individual, w. So $z = w$. Surely we can do that, since the equation applies to any quantitative trait. Here is what we get:

$$\bar{w}\triangle\bar{w} = \text{cov}(w, w) = \beta(w, w)\text{var}(w)$$

The beta coefficient is of course 1. This means that the change in mean fitness is *proportional* to the variance in fitness. This is a remarkable result, which we glimpsed a few times already but is worth putting in italics: *The change in mean fitness depends on the variance in fitness in the population.* This is result is called *the fundamental theorem of natural selection* and is attributed to R.A. Fisher.[7]

We of course already know that the equation as written above is incomplete. It misses those pesky genetic effects captured by the expectation term in the full equation. So let's get cracking.

Assume a population, where each element is labeled by index i. Each element has the character z_i . In contrast with what we did before, here i is not unique. Many elements can be labled i. The frequency of elements labeled i in the overall population is denoted q_i. The average value of z in the population is $\sum q_i z_i$(this is simply the arithmetic mean).

A descendant population has the traits z'_i and and frequencies q'_i.The change in average character value is:

$$\triangle\bar{z} = \sum q'_i z'_i - \sum q_i z_i \tag{4}$$

But who exactly are the individuals q'_i? By writing down the last equation we have not identified them! We simply defined some values and wrote down a formula for their arithmetic difference. Calling this $\triangle\bar{z}$ is a little suspicious!

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[6] So which formulation is more general?

[7] But this is not what he meant. Price explained why. Fisher's theorem deals only with the portion of fitness that depends on additive genetic variance, and excludes dominance, epistasis, and other genetic effects. See Frank (1995).

So here is the tricky part: We define q_i' to be the frequency (proportion) in the second population of the descendants of the elements i in the parent population. Let w_i be the fitness of the i elements (the mean fitness of group i, if you will). This is just the contribution of each i parent to the descendant population, or the average number of descendants of i elements. Using these definitions we can express q_i'as

$$q_i' = \frac{q_i w_i}{\bar{w}} = \frac{q_i w_i}{\sum q_i w_i}$$

where $\bar{w}$ is the mean fitness of the parent population, $\sum q_i w_i$, same as in the previous section. (If you are not sure why this works, check that q_i' calculated in this way is indeed the proportion of the descendants of i in the second generation.)

The next tricky part is that we define z_i' in a similar way: The i refers to the parent population. But how can that be you surely say: The descendants of i elements do not necessarily all have the same value for the trait! Quite right: z_i' will refer to the *average* character value of the descendants of the elements i. Put differently, but amounting to the same thing, collect all the elements in the second generation that have the same phenotype, y_j. We then go over each of these collections, and sum the fraction of its members that originated from i . This amounts to weighing each element in the descendant population that derives from i by the fraction of the total fitness of i that it represents. Putting this in symbols, denote by q_{ji} the fraction of the i-th parental subpopulation descendants that end up having the phenotype y_j. Note that $\sum_j q_{ji} = 1$. Using this notation we can express z_i' thus:

$$z_i' = \sum_j q_{ji}' y_j$$

And the average trait value in the descendant population is:

$$\bar{z}' = \sum q_i' z_i'$$

We define $\triangle z_i = z_i' - z_i$.

Equation 4 is true with these definitions of q_i' and z_i'. So by substituting and rearranging:

$$\triangle \bar{z} = \sum q_i (w_i/\bar{w})(z_i + \triangle z_i) - \sum q_i z_i = \sum q_i (w_i/\bar{w} - 1) z_i + \sum q_i (w_i/\bar{w}) \triangle z_i$$

Using standard definitions we can now get to the the full Price equation (figure 2 gives a visual representation of the process we analyzed algebraically):

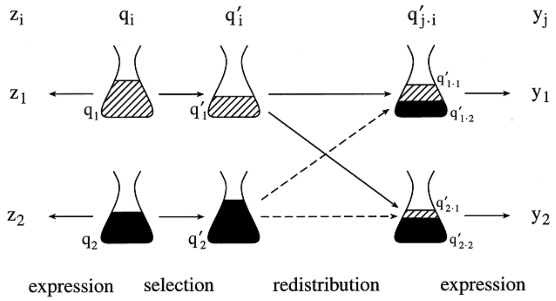

Fig. 1. Example of a selective system using the notation of the Price Equation. The initial population, the left column of beakers, is divided into subpopulations indexed by i, where q_i is the fraction of the total population in the i-th subpopulation. In this drawing, the two different kinds of transmissible material, solid and striped, are in separate subpopulations initially, but that is not necessary. Each subpopulation expresses a character value (phenotype), z_i. Any arbitrary rule can be used to assign trait values. Selection describes the changes in the quantities of the transmissible materials, where the primes on symbols denote the next time period. Thus $q'_i = q_i w_i / \bar{w}$ is the proportion of the descendant population derived from the i-th subpopulation of the initial population. The transmissible material may be redistributed to new groupings during or after the selective processes. The $q'_{j\cdot i}$ are the fractions of the i-th parental subpopulation, after selection, that end up in the j-th descendant subpopulation, thus $\Sigma_j q'_{j\cdot i} = 1$. The new mixtures in the j-th descendant subpopulations express trait values y_j according to whatever arbitrary rules are in effect. This allows full context-dependence (non-additivity) in the phenotypic expression of the transmissible material. Descendant trait values are assigned to the original subpopulations by weighting the contributions of those subpopulations, $z'_i = \Sigma_j q'_{j\cdot i} y_j$. Thus the average trait value in the descendant population is $\bar{z}' = \Sigma_i q'_i z'_i$.

Figure 2: Scenario represented by the Price equation (from Frank, 1995)

$$\boxed{\bar{w}\triangle z = \operatorname{cov}(w_i, z_i) + E\left(w_i \triangle z_i\right)}$$

The first term, as we noted before, is change due to selection. The second is the change due to transmission. The covariance captures the change in the character caused by differential reproductive success (does anything about causality follow from the derivation?), while the expectation term is a fitness weighted measure of change in character values between ancestor and descendant. The second term is easier to understand in this formulation than it was before. The expectation is an average of the change in the character from parents to offspring. Remember that for each parent, Δz_i is the average change in character across all i's offspring. Now we take a (weighted) average of these values across the population. This tells us whether there is *transmission bias*. If, for the entire population, the average trait among offspring equals the trait value in their parent, the expectation term vanishes. If transmission is highly non-reliable, however, a strong correlation betwen trait value and fitness may still not be enough for natural selection to affect the trait.

6 And another

Now that we have seen these derivations worked out in excruciating detail, let's go over the derivation in *Evolution and the Levels of Selection* (what follows reproduces Box 1.1 in the book)

$$\begin{aligned}\Delta\bar{z} &= \bar{z}_0 - \bar{z} \\ &= \frac{1}{n}\sum \frac{w_i}{\bar{w}}{}_i z_i' - \frac{1}{n}\sum_i z_i\end{aligned}$$

Multiplying both sides by $\bar{w}$ gives:

$$\bar{w}\Delta\bar{z} = \frac{1}{n}\sum_i w_i z_i' - \frac{1}{n}\sum_i \bar{w} z_i$$

Using the equality $z_i' = z_i + \Delta z_i$ to substitute for z_i' gives:

$$\begin{aligned}\bar{w}\Delta\bar{z} &= \frac{1}{n}\sum_i w_i(z_i + \Delta z_i) - \frac{1}{n}\sum_i \bar{w} z_i \\ &= \frac{1}{n}\sum_i w_i z_i + \frac{1}{n}\sum_i w_i \Delta z_i - \frac{1}{n}\sum_i \bar{w} z_i \\ &= \frac{1}{n}\sum_i z_i(w_i - \bar{w}) + \frac{1}{n}\sum_i w_i \Delta z_i\end{aligned}$$

Applying the standard statistical definitions of covariance and expectation gives:

$$\bar{w}\triangle z = \mathrm{cov}(w_i, z_i) + E\left(w_i \triangle z_i\right)$$

7 Applying the Price Equation

We will see many examples of applying the Price equation. Here is one worked out example that is relevant to the evolution of altruism. One of the paradigmatic explanations for the evolution of altruism was Hamilton's analysis of *inclusive fitness* and *kin selection*. In the most simplistic terms the idea is that it "pays" in evolutionary terms to give up some of your fitness in order to help others that are closely related to you (and hence carry many of the same genes). Provided, that is, that the cost to you is less than the total benefit they receive. This conclusion is summarized in *Hamilton's Rule* which states that altruistic behavior (genes) will evolve if:

$$rb > c$$

where r is the coefficient of relatedness, namely the chance that the recipient and donor share an allele due to common descent, b is the benefit to the recipient, and c is the cost to the donor.

We will derive this rule from the Price equation, which describes selection processes more generally, by adding several conditions that together make Hamilton's rule true.[8]

Additive fitness effects

Our first added assumption is that fitness effects are additive. Each time you receive help you get the same benefit (and similarly for costs). There are no diminishing returns. Formally:

$$w_i = w_0 + y_i b - h_i c$$

w_0 is the baseline fitness all organisms share, y_i is the probability of i receiving aid, and h_i is the probability of i giving aid.

Now we take this expression and substitute it into the (simple) Price equation from section 3:

$$\bar{w}\triangle p = \mathrm{cov}(w_0 + y_i b - h_i c, p_i)$$

Using the properties of covariance, we can rewrite this as:

$$\bar{w}\triangle p = \mathrm{cov}(w_0, p_i) + b\mathrm{cov}(y_i, p_i) - c\mathrm{cov}(h_i, p_i)$$

Since w_0 is constant the first term is zero, which leaves us with:

$$\bar{w}\triangle p = b\mathrm{cov}(y_i, p_i) - c\mathrm{cov}(h_i, p_i)$$

For altruism to spread we require that $\Delta p > 0$, which will happen if,

$$b\mathrm{cov}(y_i, p_i) > c\mathrm{cov}(h_i, p_i)$$

Or,

$$b\frac{\mathrm{cov}(y_i, p_i)}{\mathrm{cov}(h_i, p_i)} > c \qquad (5)$$

This looks just like Hamilton's rule, except that r is missing, and instead we have the ratio of covariances. This expression is very useful: It tells us when a gene for altruism will evolve. And it does it without saying anything about relatedness or common descent. (Try to put into words the meaning of the mathematical expression!) This might be a good place to stop. But it is not Hamilton's rule as we know it. For that we need to add several more assumptions.

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[8] This derivation is from McElreath & Boyd (2007), chapter 3.

Additive genetics

Our next assumption is that the likelihood of providing help is a linear function of the number of altruism alleles. Essentially we are assuming an ultra simple genotype-phenotype mapping (dominance, for example, is ruled out). Ouch!

$$h_i = a + kp_i$$

In exactly the same way w_0 gave the baseline fitness, a gives the baseline level of helping.

What's the likelihood of individual j helping out i ? It is simply,

$$y_i = a + kp_j$$

Using these:

$$\text{cov}(h_i, p_i) = \text{cov}(a + kp_ip_i) = k\text{cov}(p_i, p_i)$$

We know that $\text{cov}(x, x) = \text{var}(x)$, so we conclude that,

$$\text{cov}(h_i, p_i) = k\text{var}(p_i)$$

The same reasoning applies for the recipient so,

$$\text{cov}(y_i, p_i) = k\text{cov}(p_j, p_i)$$

Substituting these into (5) gives:

$$b\frac{k\text{cov}(p_j, p_i)}{k\text{var}(p_i)} > c$$

By using the definition of regression coefficient, this inequality reduces to,

$$b\beta(p_j, p_i) > c \tag{6}$$

This is Hamilton's rule, under the assumptions of additive fitness effects and additive genetics.

What does this inequality mean? It means that the spread of the altruistic allele depends on how well p_i predicts p_j. A little reflection should make it clear that this has something to do with the frequency p . But a little more reflection shows that even if p is high in the population, increasing the likelihood that both individuals will have genotypes with high p , this does not increase the predictive value of p_i. What we need in order for β to be great than zero is that there be positive *assortment* – essentially that helpers tend to help other helpful individuals. There are various scenarios in which this will be the case, not all of them depending on common descent, which is what Hamilton's rule talked about. For that we need yet another assumption.

No selection for altruism (!)

To find out what is required for Hamilton's rule to hold, given the previous results, we need to figure out when does $\beta(p_j, p_i)$ equal r , the coefficient of relatedness.

We define r as the fraction of alleles *identical by descent* in i and j . To calculate how well p_i predicts p_j (this is the regression coefficient), we need to find out two things in addition to r : (1) The fraction of the alleles that the two individuals share by common descent that are altruism alleles; (2) The fraction of the alleles not identical by descent that are altruism alleles. These numbers allow us to give an expression predicting p_j based on p_i.

The second of the two numbers we need is easy to figure out: It is simple the frequency of altruism alleles in the population, p .

It is a little tricky to figure out the first number, the fraction of the alleles that the two individuals share by common descent that are altruism genes. If r of j's genes are identical by descent with i's, and i does not have any altruism allele, then clearly the fraction of the alleles that the two individuals share by common descent that are altruism genes is zero. Similarly, If r of j's alleles are identical by descent with i's, and i is homozygous for the altruism allele, clearly the fraction of the alleles that the two individuals share by common descent that are altruism alleles is one (since all the alleles that the individuals share must by altruism alleles, the only kind i has to "share") . In the heterozygous case, where $p_i = 0.5$, it turns out that the fraction of the alleles that the two individuals share by common descent that are altruism alleles is 0.5 (can you see why?). Taken together, this means that the second number we needed to factor in in simply p_i . Something in the reasoning in this paragraph should not smell kosher. Can you tell what? Call this the goat.

Combining all these numbers together and doing some algebra allows us to calculate the regression coefficient $\beta(p_j, p_i)$ we need from equation (6) using r , p_i , and p . Simplifying the expression we get we find out that $\beta = r$. Substituting in equation (6) gives that standard version of Hamilton's rule, $br > c$.[9]

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[9] Here are the details we skipped over.
It is not hard to show that
$\beta(p_j, p_i) = \frac{E(p_j|P_i) - p}{p_i - p}$
From the discussion in the text we get:
$E(p_j|p_i) = rp_{j(IBD)} + (1-r)p_{j(not-IBD)t} = rp_i + (1-r)p$

Great! We managed to derive Hamilton's rule. But what about the goat? It is time to take the goat out![10]

The smelly goat is the assumption that the fraction of the alleles that the two individuals share by common descent that are altruism genes is equal to p_i. This works only if altruism alleles simply diffuse from generation to generation according to Mendel's laws. This is true only if there is *no selection for altruism*. If there is favorable selection, the ratio would increase, and if there is selection against it should decrease (that's what selection is all about!). So in deriving Hamilton's rule for the evolution of altruism we assumed no selection for altruism! That's kind of underhanded, don't you think?

In fact, this assumption is acceptable, provided we make some other assumptions (do you see a pattern here?). If selection is weak enough, its affects can be ignored when computing r for individuals that are close relatives. Hamilton's rule is an approximation that holds under these assumptions (and the earlier assumptions we made abut additive fitness affects and additive genetics, which can also be seen as simplifying assumptions).

Exercises

11. **Charlesworth's Paradox**: Consider a species of bird in which offspring can decide to stay and help their parents care for next season's offspring, or to go out and establish their own nests. A situation arises each generation allowing an individual to sacrifice its own life to save the lives of its four younger full siblings ($b = 4$; $c = 1$; $r = 0.5$). According to Hamilton's rule this altruistic behavior should evolve. But clearly it cannot: an individual with the mutation will sacrifice itself, and the allele will be destroyed. Discuss.
12. Does r tell us how closely related (genetically) two specific individuals are?

8 Concluding Remarks

Several things make the Price equation potentially confusing. The first stumbling block if you are not accustomed to this sort of analysis is the pervasive use

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Substituting this expression into the expression for β and simplifying, we conclude that $\beta = r$.

[10] What are all these goats doing here? There is a famous Jewish joke... This guy comes to the rabbi and says that his house is too crowded, what with his wife and twelve kids, and only one room, with a leaky roof. Do you have a goat, the rabbi asks. Well sure, the guy answers. Good, says the rabbi, take the goat inside to live with the family, and come back in two weeks time. The guy comes back after two weeks, smelly and not too happy. Rabbe, it is much much worse, he says. Now take the goat back out, commands the rabbi. The guy comes back after another week. Rabbi, he says, the house is so spacious now that the goat is gone.

of frequencies rather than the number of individuals carrying a gene or allele. By now you should fill comfortable with this approach, and the basic formulas for averages and so on should not look alien.

Natural selection changes the frequency of alleles a population so it is natural to use frequencies when writing down expressions that describe this evolutionary change. This is one manifestation of the frequently made assertion that natural selection is a population level process the understanding of which involves "population thinking." The Price equation is one illustration of the centrality of statistical vocabulary to our understanding of evolutionary processes. Expressing our results using frequencies allows us for the most part to ignore population size when expressing the evolutionary relationships. We do not need an extra parameter giving the population size. When in doubt, try to refer to the population size explicitly. Note, however, that throughout we assumed that the population size is big enough so that sampling errors (often referred to as drift in the biological context) can be ignored.

Another thing that can be confusing is the move from expressions that explicitly refer to averaging processes of summing the number of descendants etc. to expressions that employ the notions of expection, variance and covariance. This is especially difficult if you do not have a qualitative feeling for the meaning of these concepts (think: average, spread, and similarity). Thinking of regression coefficients (and hence, prediction) rather than covariance can help. The move from expressions about explicit sums to expressions that utilize the statistical functions can also be confusing, since the latter express relationships that apply to whole groups as single entities. When in doubt, make sure you know which groups each statistic refers to and the number of "nesting" levels of the population.

Two observations to complete this discussion. The Price equation deals with any selection process. Indeed, we can *define* selection using it. It says noting in particular about biological or genetic evolution, and is not tied to any particular biological scenario. This gives it immense power, but also means that it is quite possible to apply it incorrectly to the real world. This leads us to the second and final observation. The Price equation is *analytic*. It is not a synthetic proposition. We derived it based on straightforward definitions, and universal mathematical principles. The equation simply provides a useful way of interpreting the meaning of the straightforward definitions we started from. This however is not the case once you put the equation into words, thereby interpreting the mathematical relationships. If you merely say: "I define 'selection' to be the covariance blah blah blah," you might be safe. If you say: "the covariance blah blah blah *is* selection," you are making a claim with empirical content. More fundamentally, the belief that the rules of probability theory and statistics, or any other mathematical manipulation, describe the actual wold is synthetic.[11]

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[11] This observation is emphasized by McShea & Brandon (2010).

9 Answers

1. $\bar{w}N$

3. The variance is $p(1-p)$.

4. Consider the function $p(1-p)$. To find the maximum we take the derivative, and determine where it is equal to zero. This gives the equation $1-2p=0$ which is satisfied when $p=0.5$. To make sure that this is indeed a maximum we can take the second derivative, or simply note the shape of the paraboa (i.e., that it is upside down). .

5. We mean that the frequency of the gene increases relative to other genes (more correctly, alleles).

6. $c_i=0$ for aa individuals, 1 for Aa and aA, and 2 for AA individuals. The total number of A alleles in the population is $\sum c_i$. The total number of alleles in the population is $2n$ (because of diploidy). Combining the two we get $p=\frac{\sum c_i}{2n}=\frac{1}{n}\frac{\sum c_i}{2}=\frac{1}{n}\sum\frac{c_i}{2}=\frac{1}{n}\sum p_i$

11. Here we have strong selection against altruism, nullifying the assumption we made in deriving Hamilton's rule.

12. No. We saw that r is a statistic: it summarizes information about the population, namely how well does donor genotype predict the recipient's genotype.