Fitness☆

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Nomenclature

W	Absolute fitness of a class of variant
w	Relative fitness of a class of variant
s	Selection coefficient of a class of variant
$\overline{w}$	Mean fitness of a population
ϕ	Value of a continuous trait or the presence of a class of variants
$\overline{\phi}$	Mean value of a continuous trait or the relative frequency of a class of variant in the population
δ	Change in ϕ during a time period that is due to factors other than directional selection
N	A vector of the number of individuals with each state in a class of variants
A	A matrix of the probability of a transition from each state to each of the other states in a class of variants
B	A matrix of the per capita rate of a transition from each state to each of the other states in a class of variants
C and D	Matrices of the probability of a transition from one class to another class in a population
$s_x(y)$	Invasive fitness of a new class x under the environment of a resident population y
$H(x)$	Shannon's entropy of the uncertain system x
$I(x;y)$	Mutual information of y on uncertain system x
x_t	Environmental state at time t
π_t	Representation of different classes of variants in a population at time t
π	The value that π_t averaged over time approaches as time goes on
G_{max}	The highest conceivable growth rate of a population in the uncertain environment
G_{min}	Long-term growth rate of a population with no information on the uncertain environment
$H'(x)$	Fitness cost of uncertainty on the environment x
$I'(x;y)$	Fitness value of information y on environment x
$D(\hat{\pi}\|\pi)$	Kullback-Leibler divergence from π to $\hat{\pi}$.
c	Cost of the behavior to the actor in kin selection
b	Benefit to recipient of the behavior in kin selection
r	Genetic relatedness between the actor and the recipient in kin selection

Glossary

Allele One of two or more alternative versions of a heritable trait, often corresponding to a DNA sequence difference at a particular locus (place) in the genome.

Class General term for an identifiable variant of a heritable trait, which may be present in multiple copies in the population. For example, a given allele is a class representing a variant DNA sequence for a particular locus (place) in the genome. There may be many copies of the allele in many individuals, but they all belong to the same class.

Evolutionarily stable strategy (ESS) A class (typically representing some form of strategy) or a particular mix of classes that cannot be replaced by any other classes because no other class or combination of classes will have a fitness advantage over it (relative to an environment).

Genotype While this term has several possible meanings, here we use it to mean the particular genetic variants carried by an individual: that is which allele or alleles it has in its genome.

Kin selection Selection based on inclusive fitness, which includes the fitness advantage due to helping relatives to reproduce so that they increase the representation of shared alleles in the population.

Malthusian parameter Per capita growth rate of the number of copies in a class (e.g., individuals with a particular heritable trait, or number of copies of a given allele in a population).

Polymorphism Occurrence of more than one class of variants (e.g., multiple alleles of a gene, or different strategies for a behavioral response) in a population.

Background

The term "fitness" can have a range of meanings in biology, sometimes referring to a relatively general concept, at other times as a label for a specific parameter. This variation in meaning can lead to some confusion, partly due to the changing roles the term fitness has played in evolutionary biology over time (Dawkins, 1982). Fitness had long been used to describe the way that organisms are evidently suited to their particular mode of life, or the way that parts of an organism work together (Paley, 1809). Herbert Spencer introduced the phrase "survival of the fittest" as equivalent to "natural selection" (Spencer, 1896). Alfred Russel

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Wallace adopted the phrase, equating it to Darwin's description "preservation of favoured races in the struggle for life" (Wallace, 1867), and he recommended Darwin do the same, in order to avoid some of the misunderstandings associated with the phrase natural selection, which some readers took to imply a conscious choice (akin to artificial selection). Darwin concurred, and used the phrase survival of the fittest in some of his later works, though he preferred the term natural selection (Darwin, 1868). So, at its most basic, fitness is the capacity of organisms to survive and reproduce in the environment in which they find themselves.

Under this broad concept, the fitness of an individual is considered to be reflected in the number of its descendants. But it is not clear how this broad concept of fitness should be measured in practise, because there is no obvious point in time at which descendants should be tallied. In a finite population every allele in the genome can be traced to a single ancestor at some point in the past, leaving little obvious leverage for comparing fitness between individuals or genetic variants. An alternative and more practical measure would be to measure fitness differences by comparing differences in lifetime production of offspring. However, the actual reproductive output of an individual is dependent not only on its own characteristics but also chance events, therefore fitness should be expressed as the probability distribution of the number of offspring. Classical models in population genetics suggest that natural selection maximizes the expected number of offspring as long as the relative expected number of offspring of different genetic variants stay constant over time and space, which usually requires constant (or infinitely large) population size and a stable environment (Fisher, 1930). When these assumptions are relaxed, natural selection no longer maximizes the expected number of offspring, but maximizes some more complicated form of fitness. For instance, under fluctuating environment, natural selection maximizes the geometric mean of the expected number of offspring over generations (Orr, 2009).

In most usages in evolutionary theory, fitness does not describe a property of a unique individual, but the property for a class of variants. Here we mean "class" in the sense of a group that all share the same feature, so our focus might on a specific allele, or a haplotype consisting of several base changes inherited as a unit (e.g., a mitochondrial variant), or individuals with the same trait of interest, or a phenotype consisting of several traits, or a life history strategy. For example, the use of antimalarial drugs places selective pressure on *Plasmodium* (malaria) parasites: any allele that confers resistance will be favored by selection, so individuals carrying this allele have a fitness advantage over susceptible individuals. Under these conditions, we expect the allele with the fitness advantage to steadily increase in the population (Roper *et al.*, 2004). Note that this is a statement about expected outcomes. We cannot predict the reproductive success of a particular *Plasmodium* individual based on whether or not it has the resistant allele —a susceptible individual may thrive if it is lucky enough to avoid being exposed to pyrimethamine, and a resistant individual may fail to reproduce when the mosquito it is carried in gets squashed by an irate human before it can achieve infection. But we can say that on balance, when considered across the whole population, over the period of observation, the favored allele had a higher rate of inclusion in subsequent generations that would be expected under random sample (Nair *et al.*, 2003).

Influence of Environment on Fitness

Fitness is always considered relative to a given environment. We would rarely consider an allele to have an absolute advantage under all sets of environmental conditions. For example, the fitness advantage of the resistance allele in populations of *Plasmodium* would disappear if pyrimethamine were not present in the environment (and may even be reversed if there is a cost to resistance). The "environment" of a class of variants can be considered to have many different levels.

On the genomic level, when a class is a specific allele, the "environment" of the class includes the other alleles in the genome in which it resides. No gene acts in isolation, but in combination with other genes, so the selective advantage of an allele depends on the presence of other alleles. Selection on one allele can carry linked neutral or nearly neutral alleles to fixation (hitchhiking: Maynard Smith and Haigh, 1974). Similarly, selection against a deleterious allele will removed linked alleles from the population (background selection: Charlesworth *et al.*, 1993). Both hitchhiking and background selection will result in a reduction in observed variation around a site under selection, thus one way of detecting alleles under selection is to detect chromosomal regions of reduced variability, which is interpreted as sign of a "selective sweep" that has driven linked alleles to fixation. For example, selection on the pyrimethamine resistant allele has led to reduced variation for 100 kb of linked sequence (Nair *et al.*, 2003).

The fitness of an allele can also depend on unlinked alleles in the same genome, or between nuclear and organelle genomes in the same cell, due to interactions between gene products. For example, some mitochondrial genes will be advantageous in combination with particular nuclear alleles, but have fitness costs when combined with other nuclear alleles, which can lead to cytonuclear conflict (Rand *et al.*, 2004). There may even be sex-specific differences in fitness costs and benefits of alleles. For example, some mitochondrial alleles lead to poor sperm performance, but because mitochondria are passed through the female line, alleles deleterious in males can persist for many generations (Gemmell *et al.*, 2004).

Because interactions with other alleles can have positive or negative effects on an allele's fitness, the "environment" of an allele against which fitness is tested will also include other alleles segregating in the population. In a sexual population, each generation is formed by sampling the alleles from one generation and reassorting them into individuals in the next generation. But alleles are not simply filtered through a "substitutional sieve" that preferentially lets those of higher fitness through to the next generation (Dobzhansky, 1937). The passage of an allele to the next generation will depend on whether it tends to have a fitness advantage when combined with other common alleles in the population, such that particular combinations of alleles will tend to result in higher rates of reproduction. This means that alleles that do not work well with other common alleles will tend to have reduced representation in subsequent generations. As a consequence, co-adapted alleles tend to accumulate in populations. Alleles within a

population are selected to work well with each other, but if lack of gene flow prevents those alleles being tested against variants in a neighboring population, then alleles that have high fitness in one population may have low fitness when combined with alleles in another population. This leads to hybrid individuals, who have a parent from each population, to have lower fitness than the offspring of parents from the same population, potentially generating selection for isolating mechanisms that prevent interbreeding, thus leading to the formation of genetically isolated species (see Hua and Bromham, 2017).

The fitness of some alleles may depend on characteristics of the population in which they are found. Some alleles may be beneficial under high population density, but lose this fitness advantage under low densities. Furthermore, when considering the fitness of particular behavioral strategies, the "environment" includes the frequency of other strategies in the same population. For example, the fitness of alleles influencing foraging behaviour in *Drosophila melanogaster* can be frequency dependent: in low nutrient environments, alternative alleles of the same gene that promote "roving" (moving around) or "sitting" (remaining) are both advantageous when rare, as rare strategies allow access to resources with less competition from others following the same strategy (Fitzpatrick *et al.*, 2007).

Three Alternative Ways of Defining Fitness

We have discussed general conceptions of fitness, and the way that fitness is influenced by the complicated web of interactions with other alleles, other individuals in the population and many aspects of the environment. Formal concepts of fitness are mostly mathematical and statistical, and there is a range of different parameters that have been labeled as fitness. These mathematical definitions of different fitness parameters differ from the conceptual definition of fitness that we have just discussed (Otsuka, 2016). Below, we describe some bases of the most popular theories: the Price equation, Evolutionarily Stable Strategy (ESS) theory, and information theory. To make this discussion general to any population that can undergo evolution by natural selection, we are going to refer to the variants under selection as a "class." The "class" might refer to alleles, strategies, lineages, groups, or any other unit where we can compare the relative reproductive success of one class of heritable variants against others.

The Price Equation

The Price equation was derived by Price (1970), originally for the purpose of re-deriving W.D. Hamilton's work on kin selection (Hamilton, 1964), but it is now considered as a fundamental theorem that summarizes all the equations and theorems in population genetics. In population genetics, fitness, or more specifically, the absolute fitness (W) of a class of variants typically refers to the class's expected number of progeny multiplied by its chance of survival (Orr, 2009). Often, population geneticists normalize this fitness by the absolute fitness of the fittest class and call this relative fitness (w), so that the fittest class has a relative fitness of 1. Now the relative fitness of all the other classes can be written in a form of $1 - s$, where s is called the selection coefficient. The mean fitness of a population ($\overline{w}$) is then the weighted sum of the relative fitness of each class in the population and the weight is the frequency of each class. For example, if a class is a genotype and a population contains two different genotypes, then the mean fitness of the population is $\overline{w} = p_1 w_1 + p_2 w_2$, where p_1 and w_1 are the frequency and the relative fitness of one genotype and p_2 and w_2 are the frequency and the relative fitness of the other genotype. Similarly, if a class is a given value of a continuous trait (z), then the relative fitness is described as a function of trait value, $w(z)$, and the mean fitness of a population integrates the fitness over the total range of values that the trait could take $\overline{w} = \int p(z)w(z)dz$.

The Price equation describes the average change in the representation of a class ϕ in a population during a time period ($\Delta\overline{\phi}$). The class can be a given value of a continuous trait, such as body size or some measure of fitness itself, and $\overline{\phi}$ is the mean value of the trait or the mean fitness of the population. The class can also be a categorical type, such as the allele of interest, and $\overline{\phi}$ is the relative frequency of the category in the population. According to the Price's equation, $\Delta\overline{\phi}$ is the sum of two parts (Queller, 2017):

$$\Delta\overline{\phi} = \frac{1}{\overline{w}}[\mathrm{Cov}(w_i, , \phi_i) + E(w_i\delta_i)]$$

where i denotes a class of variants. The first part, $\frac{1}{\overline{w}}\mathrm{Cov}(w_i, , \phi_i)$, represents change in $\overline{\phi}$ due to directional natural selection. When ϕ is the relative fitness itself: $w_i = \phi_i$, the covariance between fitness and the class $\mathrm{Cov}(w_i, \phi_i)$ becomes the variance for fitness, and so the first part of the Price equation captures Fisher's fundamental theorem of natural selection that states natural selection increases the mean fitness of a population at a rate equal to the additive genetic variance for fitness (Fisher, 1930). The second part, $\frac{1}{\overline{w}}E(w_i\delta_i)$, where δ_i is the change in the value of ϕ_i during the time period, describes the expected change in $\overline{\phi}$ due to factors other than directional selection, such as mutation, migration, a change in the environment, and so on. Classical models in population genetics show that natural selection maximizes the expected number of offspring of a population $\overline{w}$, because these models assume constant relative fitness, that is, $\delta_i = 0$; in other words, the second part of the Price's equation is ignored.

In principle, the Price equation can predict changes in the representation of any kind of class in a population under natural selection as long as the class has heritability (Queller, 2017). For example, a class can be a suit of co-adapted alleles or traits, so that fitness depends on multiple alleles or traits. Then $\mathrm{Cov}(w_i, \phi_i)$ in the first part not only accounts for the covariance between fitness and each trait, but also the association among traits. The second part of the Price equation can be modified to account for changes in $\overline{\phi}$ due to various factors other than directional natural selection. For example, consider frequency-dependent selection on sex ratio. Class ϕ is a given value of the number of male offpsring relative to female offspring. Starting with an initial condition

where there are more females than males in the population, females who have more male offspring should have higher fitness in a random, multiple mating population, because their offspring will have higher reproductive success in total. However, when more males are produced, environment for these males changes because there is stronger competition for mates; in other words, δ_i becomes negative because some male offspring will not reproduce. As a result, there may be a point where the two parts of Price's equation cancels out, that is, $\Delta\overline{\phi} = 0$. Under this condition, natural selection keeps ϕ at an optimal point.

Evolutionarily Stable Strategy (ESS) Theory

The concept of the evolutionarily stable strategy was first formulated by John Maynard Smith, who applied game theory to study the evolution of animal behaviors (Maynard Smith, 1974). Game theory essentially looks for the existence of strategy equilibria given the expected payoff of each strategy. Here, the payoff is the fitness of the strategy, often estimated by the Malthusian parameter that was proposed by Ronald Fisher to describe the rate of increase in the number of individuals as an aggregate of individual fecundity and mortality (Fisher, 1930). This is also a measure on the logarithm scale of the absolute fitness used in population genetics. In principle, ESS theory can be generalized to any class of variants, such as a new mutation, a new trait value, or a new strategy, so hereafter we use "class" instead of "strategy."

We can write changes in the number of individuals for discrete time as:

$$\mathbf{N}(t+1) = \mathbf{A}\mathbf{N}(t)$$

or for continuous time as:

$$\frac{d}{dt}\mathbf{N}(t) = \mathbf{B}\mathbf{N}(t)$$

For a class of variants where each variant has multiple states, for example, age state often matters for a reproductive strategy because only mature individuals can reproduce, $\mathbf{N}(t)$ records the number of individuals at each state, and components of matrix **A** are demographic parameters, with the i, j-th components of matrix **A** describing the probability of a transition from state j to state i. For age state, matrix **A** is the classic Leslie matrix, in which the first row is the average number of female offspring born from mother of each age state and diagonal of the rest of the matrix is the fraction of individuals that survive from an age state to the next age state. Matrix **B** is similar to matrix **A**, except that its components are per capita rates. The Malthusian parameter for a given class is then the natural log of the dominant eigenvalue of matrix **A** or the dominant eigenvalue of matrix **B** (Metz *et al.*, 1992).

We can also calculate the Malthusian parameter of a population that consists of multiple classes. This is analogous to the mean fitness of a population used in population genetics. To do this, we combine the matrix **A** or **B** of each class into a larger matrix. For example, if there are two classes in the population, class 1 has matrix **A1** and class 2 has matrix **A2**, they are combined into one matrix as:

$$\begin{bmatrix} \mathbf{A1} & \mathbf{D} \\ \mathbf{C} & \mathbf{A2} \end{bmatrix}$$

where matrix **C** describes the probability of a transition from class 1 to class 2, and matrix **D** describes the probability of a transition from class 2 to class 1. These transition probabilities can have various forms, depending on the genetic bases of the two classes. For example, in a haploid population, the transition probabilities may reflect the mutation rate between classes. When the population can grow exponentially, natural selection will maximize the Malthusian parameter of the population; otherwise the population size will eventually reach equilibrium where the Malthusian parameter equals 0.

ESS theory is often used to ask two questions related to the relative fitness of classes in a population. First, can a new class invade an existing population? Second, if it can, will the new class replace or be replaced by any existing classes in the resident population, or will it coexist with the resident? To study the first problem, the theory introduces a new parameter $s_x(y)$, the invasive fitness of a new class x under the environment of a resident population y. Assuming that mutations are rare so that the resident population is always at its strategy equilibrium, when a new mutation enters the population, $s_x(y)$ equals the Malthusian parameter of the population that consists of both the new and the existing classes. If $s_x(y) > 0$, the new class has a positive probability to invade the resident population. If $s_x(y) < 0$, the new class is doomed to extinction (Metz, 2008).

As the new class forms a greater proportion of the population, its influence to the environment of the population gets larger. So to predict the fate of the new class in long run, we not only account for the influence of the resident classes to the environment, but also the influence of the new class on the environment. Organism's influence on the environment can be modeled by expressing the demographic parameters in the matrix **A** as a function of "feedback variables" that describe the source of the influence (Rueffler *et al.*, 2013). For example, under density dependence, the fraction of individuals that survives from an age state to the next age state may depend on the total number of individuals in the population due to competition. Here, the total number of individuals in the population is the feedback variable. At the strategy equilibria, the Malthusian parameter of the population equals 0, so one way to look for the existence of strategy equilibria is to prove that there are finite number of conditions under which the Malthusian parameter of the population equals 0 (Diekmann, 2004).

An ESS view of fitness is particularly helpful in cases where the fitness effects of classes have complicated interactions. For example, a non-transitive set of behaviors can form a loop, in which each class has higher fitness that one alternative class but lower fitness than another alternative class. This is like a "rock-scissors-paper" game (rock beats scissors, scissors beats paper, paper beats rock). In other words, if $s_x(y) > 0$ and $s_y(z) > 0$, no one class can replace the others when $s_x(z) < 0$ (Gyllenberg and Service,

2011). For example, *Escherichia coli* that can produce the antibacterial compound colicin (C) can have a fitness advantage over colicin-sensitive strains (S), but colicin-resistant strains (R) have a reproductive advantage over C by avoiding the cost of producing colicin. But the resistant strains (R) have a slower growth rate than sensitive strains (S). This is a non-transitive fitness loop because C beats S, S beats R and R beats C, leading to the potential for stable co-existence of the three strategies (Kerr *et al.*, 2002).

Another condition under which no one class can replace the others is when there are more than one "feedback variable" (Diekmann, 2004). For example, to study the evolution of annual versus biannual strategies in a population, we may express the Malthusian parameter of the population as a function of the relative frequency of the annual strategy in the population. If the survivability over the first winter is affected by the number of newborns and the survivability over the second winter is affected by the number of one-year-old individuals, then there are two feedback variables: the number of newborns and the number of one-year-old individuals. It has been shown that under this condition, populations with different frequencies of the annual strategy perform equally well (Diekmann, 2004). In contrast to the wide interest in finding a good proxy for fitness, the ESS theory suggests that the conditions under which natural selection will maximize the fitness of a population are actually limited.

Information Theory

The fundamental question in the information theory is how to reduce the error rate of data communication over noisy channels, or more abstractly, how to increase the amount of information on uncertain systems. To answer this question, we first need a measure of uncertainty: Shannon's entropy (Shannon, 1948). Given a variable x that could take N states, each with a probability p_i, the entropy of the variable is:

$$H(x) = -\sum_{i=1}^{N} p_i \log\ p_i$$

which counts the expected number of bits needed to code the variable x. Now we have a piece of information y on x. The value to attain the information is measured by how much uncertainty it reduces or how many bits it saves to code variable x, which we called mutual information (Cover and Thomas, 1991):

$$I(x;y) = H(x) - H(x|y)$$

If we treat environment as the uncertain system x and measure the value of information y on the environment in terms of the amount of increase in fitness, then it is more straightforward to account for uncertainty in the environment using information theory than the Price equation or ESS theory. With environmental uncertainty, long-term growth rate of a population becomes a more relevant proxy of fitness than the instantaneous Malthusian parameter because maximizing the growth rate at one time does not guarantee positive growth rate at another time. The long-term growth rate of a population can be intuitively defined as the arithmetic mean of the Malthusian parameter during each time step that is small enough that the environment during a time step is assumed constant (Donaldson-Matasci *et al.*, 2010). Mathematically, the long-term growth rate is the dominant Lyapunov exponent that describes the asymptotic rate of increase in population size (Metz, 2008).

Early work by Haldane (1957) and Kimura (1961) and recent studies on evolution under fluctuating environments (Donaldson-Matasci *et al.*, 2010; Rivoire and Leibler, 2011) suggest a tight link between fitness as formulated by information theory and the long-term growth rate of a population. To illustrate the link, we denote the environmental state at time t as x_t. The population will increase the representation of the class of variants that has the highest absolute fitness at time t in the population based on the information y_t they attain on x_t. The representation of different classes of variants at time t is denoted as π_t. The information can be directly acquired from the current environment, if π_t are mediated by phenotypic plasticity as a response to the current environmental cues, such that π_t does not depend on π_{t-1}. But more often, the information is inherited. The information on the current environment comes through the selective transmission of alleles or traits that are better suited to the previous environments than others, such that π_t depends on both π_{t-1} and the current environment. As time goes on, π_t averaged over time will approach a real number π. Our goal is to find the π that maximize the fitness or the long-term growth rate of the population.

It is intuitive that the maximum conceivable growth rate for a population occurs when the class of variants with the highest absolute fitness has 100% representation in the population at any point in time, so that the population is tuned perfectly to x_t. The worst situation is when traits associated with high fitness in past generations provide no information on likely success in the current environment. Under this situation, a population is most likely to survive over time if the relative frequency of different classes in the population is proportional to the relative frequency of different environmental states over time. Now, we denote the maximum conceivable growth rate as G_{max} and the long-term growth rate in the absence of information as G_{min}. The relationship between G_{max} and G_{min} follows (Rivoire and Leibler, 2011):

$$G_{min} = G_{max} - H'(x)$$

where $H'(x)$ is the fitness cost of uncertainty on the environment. When the information on the environment is imperfect, that is a population with π_{t-1} does not behave optimally under x_t, the maximum long-term growth rate of the population with $\hat{\pi}$, the optimal value of π is (Rivoire and Leibler, 2011):

$$G(\hat{\pi}) = G_{max} - H'(x) + I'(x;y)$$

where y is the imperfect information on the environment x and $I'(x;y)$ is the fitness value of information y on x. The selective

disadvantage of a population with an arbitrary value of π is related to $D(\hat{\pi}\|\pi)$ (Frank, 2012), the Kullback-Leibler divergence from π to $\hat{\pi}$, which is used in the information theory to measure the number of extra bits required to code variable π using a code optimized for $\hat{\pi}$ rather than the code optimized for π.

It has been shown that when π_t does not depend on π_{t-1}, and when the absolute fitness of the population in x_t is nonzero for only one class of variants, $H'(x)$ equals $H(x)$, the Shannon's entropy of the environment, $I'(x;y)$ equals $I(x;y)$, the mutual information on the environment, and the selective disadvantage of π equals $D(\hat{\pi}\|\pi)$ (Donaldson-Matasci *et al.*, 2010; Rivoire and Leibler, 2011). Under other conditions, the forms of $H'(x)$ and $I'(x;y)$ are more complicated, but $H(x)$ and $I(x;y)$ still defines the upper bounds of these values (Donaldson-Matasci *et al.*, 2010; Rivoire and Leibler, 2011).

Individual Fitness

The three different formulations we have discussed are related, in that each can be derived from each of the others (Demetrius and Ziehe, 2007; Frank, 2012). But these different formulations may be suited to answering different empirical questions. For example, the Price equation is a convenient way to investigate which features of organisms are correlated with fitness. ESS theory is well-suited to examining why populations may contain one or more alternative strategies. Information theory allows us to consider how environmental uncertainty affects fitness in the long run. These are all questions that biologists may wish to ask of real populations. In order to do so, we need to be able to measure the fitness relevant parameters, such as the Malthusian parameter, in real populations, in the lab or the field.

Field ecologists often measure fecundity and survivability by tracking marked individuals through their life span. So the major problem of estimating the Malthusian parameter of a class of variant or of a population in the field is how to translate discrete individual events—the birth, death, and reproduction of an individual—into the growth rate of the class or the population. For example, while any given individual will have a specific value for age at death that reflects both fitness and chance events, the survivability measures the proportion of individuals that survive to a given age in the population, so reflects the fitness of a given class of individuals.

Fisher (1930) showed that, without demographic and environmental stochasticity, the sum of the reproductive value of all individuals in the population increases at the population's asymptotic growth rate, regardless of whether the population is in stable age distribution. This suggests that if there is a measure of the reproductive contribution of each individual to the class or the population (Fisher, 1930), sometimes called the individual fitness (Sæther and Engen, 2015), then we can estimate the fitness of the class or the population by tracking some individuals of the class or the population through their life span. Using individual fitness is also a logic way to accounting for demographic and environmental stochasticity, because these sources of stochasticity must be reflected in the variation of individual fitness (Engen *et al.*, 2009).

Traditionally, individual fitness is measured by the number of offspring produced by an individual during its lifetime. However, using this individual fitness to estimate the fitness of the class or the population that the individual belongs to require additional assumptions, including constant population size and stable age distribution (Sæther and Engen, 2015). To avoid these assumptions, at least two new measures of individual fitness have been proposed. One measure defines individual fitness as the sum of the number of offspring an individual produced during a given time step (divided by 2 if sexual reproduction) and a dummy variable describing whether the individual is alive or not during the time step (Sæther and Engen, 2015). This measure is readily applicable to the Price equation by replacing w_i with the individual fitness and ϕ_i with the feature value of the individual. Another measure calculates individual fitness as the dominant eigenvalue of a matrix that is similar to the Leslie matrix, where the first row is the number of offspring produced at each age of the individual (divided by 2 if sexual reproduction) and the diagonal of the rest of the matrix is 1 if the individual is alive at the age and 0 if not alive (McGraw and Caswell, 1996). The geometric mean of individual fitness converges to a value as the number of individual increases, but the value is a biased estimate of the Malthusian population growth rate (McGraw and Caswell, 1996).

There are other measures of individual fitness, but they require estimating population growth rate or some demographic parameters of the population first. For example, one measure calculates individual contributions to population growth by comparing population growth rate estimated from datasets before and after removing the individual and its offspring that are produced during a given time step (Coulson *et al.*, 2006). These measures are still useful to remove demographic and environmental uncertainties because they can capture the variation in individual fitness either due to chance events that happen to different individuals during their lifespan or variation in the environment around an individual, such that some individuals happen to live in a good year and others in bad years.

Fitness Beyond the Individual

The fitness of a class of heritable variants, whether defined at the level of the genotype or the phenotype, is due to it having properties that increase its representation in the next generation. But, given that fitness concerns the expected outcomes for a class of heritable variants, not the fates of any given individual carrying the trait, an individual does not have to reproduce to increase the fitness of the class of variants. If an allele causes its carrier to help others with the same allele, even at personal cost, then it may result in a net fitness advantage if more copies of the allele are included in the next generation than would have been without the

altruistic action (Haldane, 1955). The more closely individuals are related, the more alleles they will share in common, hence the famous quote attributed to J.B.S. Haldane that he would risk his life to save two brothers from drowning, or eight cousins (Maynard Smith, 1975). This idea is captured in Hamilton's (1964) inclusive fitness, which writes the fitness effect of having a particular co-operative behaviour as

$$w = 1 - c + br$$

where c is cost of the behavior to the actor, b is the benefit to recipient, r is the genetic relatedness between the actor and the recipient. "1" is the baseline fitness as used in population genetics. In the ESS theory, this is the fitness of the resident population, but on the logarithm scale $\log(1) = 0$. The ESS theory predicts that a new variant can invade the resident population if its fitness is greater than the fitness of the resident population. So natural selection favors a particular co-operative behaviour when $1 - c + br > 1$, that is $br > c$ (Hamilton, 1964).

But individuals do not have to be close kin to share an allele whose fitness is increased by co-operation. If an allele within a population leads carriers of the same allele to co-operate to raise their net reproductive output, it will have a selective advantage. Such a situation is referred to as a "green beard" phenomenon: an allele that causes both green beards and propensity to help others with green beards could lead to evolution of altruism by providing a heritable basis for the fitness benefits of co-operation (Dawkins, 1979). For example, in the highly invasive fire ant *Solenopsis invicta*, a gene that codes for an odor-binding protein acts as a green beard: workers carrying the b allele help queens with the b allele to reproduce, and tend to kill queens that lack b (Keller and Ross, 1998). This is not strictly a case of kin selection, because it is irrelevant in this case whether the queens with the b allele are related to the workers or not, it is the presence or absence of the "green beard" olfactory cue allele that determines co-operation.

Individuals often inherit more than just genes from their parents. For example, if offspring tend to be located closer to their parental home than other members of the population are, then they inherit their environment as well as their genes. Since organisms also influence their own environment, natural selection can create feedback between the environment and the organism through niche construction. Organisms may change the physical structure of the world (e.g., termite mounds or birds nests), the physical form of other organisms (e.g., galls induced by wasps infecting trees), or the behaviour of other organisms (e.g., parasite manipulation of host behaviour). Influences on the environment may be neutral with respect to fitness or even deleterious (e.g., exhaustion of resources). But if there are heritable influences on environment that increase the fitness of a class of heritable variants by increasing its relative representation in subsequent generations, then we expect this "extended phenotype" to be under natural selection (Dawkins, 1982).

Because the fitness effect may extend beyond the physical boundaries of an individual organism, the fitness of a class of heritable variants depends not only on features of other classes of variants in the conspecific population, but also on the heritable features found in other species. These tangled fitness relationships blur the line of demarcation between individuals, and even between species. It is not always obvious when a mutually beneficial relationship between endosymbiont and host (e.g., termites and the bacteria that allow them to digest cellulose) becomes a dual genetic inheritance system (e.g., nuclear and mitochondrial genes). For example, braconid wasps reproduce by parasitizing caterpillars, but cannot do so without genes encoded in a virus that is amplified and transmitted in the wasps' eggs. The fitness of any alleles in the wasp genome depends on their co-transmission with viral genes, and vice versa (Louis *et al.*, 2013).

The consideration of combined fitness effects of alleles in different organisms leads us to the question of whether the concept of fitness can be applied to communities or ecosystems. In the informal sense, we might consider communities to have features that aid survival and propagation, such as robustness or resilience, and these features could be ultimately due to the net genetic information in the system (Van Valen, 1989). However, the formal theoretical sense of fitness concerns relative reproduction rate, and it is not clear what we might be comparing the fitness of an ecosystem to. To apply the theoretical framework of fitness to multi-species groups we would need to be able to define a system where communities compete for some key resource, that they have the capacity for reproduction (not just persistence) and that they have heritable traits that influence their chances of representation in subsequent generations.

See also: Behavioral Ecology: Kin Selection; Environmental Stress and Evolutionary Change. Evolutionary Ecology: Fecundity; Units of Selection; Natural Selection; Adaptation. General Ecology: Age-Class Models

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