# Unifying Evolutionary Dynamics

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Darwinian evolution is based on three fundamental principles, reproduction, mutation and selection, which describe how populations change over time and how new forms evolve out of old ones. There are numerous mathematical descriptions of the resulting evolutionary dynamics. In this paper, we show that apparently very different formulations are part of a single unified framework. At the center of this framework is the equivalence between the replicator–mutator equation and the Price equation. From these equations, we obtain as special cases adaptive dynamics, evolutionary game dynamics, the Lotka-Volterra equation of ecology and the quasispecies equation of molecular evolution.

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## Introduction

In 1906, W. F. R. Weldon, who invented the field of biometrics, noted that Darwinian evolution was essentially a mathematical theory that could only be tested using mathematical and statistical techniques. The founding fathers of evolutionary genetics, Fisher, Haldane and Wright used mathematical models to generate a synthesis between Mendelian genetics and Darwinian evolution. Kimura's theory of neutral evolution, Hamilton's kin selection and Maynard Smith's evolutionary game theory are all based on mathematical descriptions of evolutionary dynamics. Concepts like fitness and natural selection are best defined in terms of mathematical equations. The perspective of this paper is to show that apparently very different descriptions of evolutionary dynamics are part of a single unified framework (Fig. 1). We concentrate on deterministic dynamics, which represent the core of evolutionary theory. We do not consider stochastic, spatial or individual-based approaches, which are mathematically more diverse and hence less amenable to any attempt of unification. Obviously, stochastic approaches that include finite population size effects are always more realistic, but usually the basic understanding of a system can be derived by considering deterministic dynamics; stochastic extensions often work in a predictable way.

## The Quasispecies Equation

Let us start with the quasispecies equation of molecular evolution (Eigen & Schuster, 1977; Eigen *et al.*, 1989). The variable $x_i$ denotes the relative abundance of a genetic sequence, $i$, in a population. The fitness, $f_i$, of this sequence is

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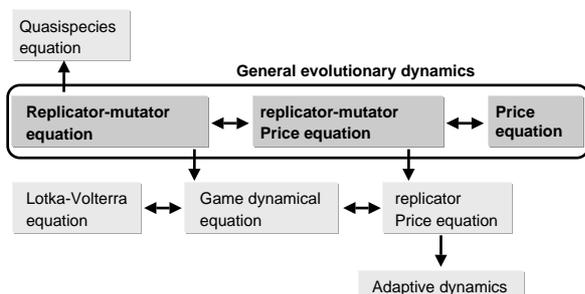*E-mail address*: k.page@cs.ucl.ac.uk (K.M. Page).

FIG. 1. General evolutionary dynamics are described by the equivalence between the replicator–mutator equation, the replicator–mutator Price equation (which uses the labeling system of the replicator–mutator framework) and the Price equation (which uses the labeling system of the Price equation). The game dynamical equation is obtained from the replicator–mutator equation by neglecting mutation. Similarly, the replicator Price equation is derived from the Price equation in the absence of mutation. The Lotka–Volterra equation, the game dynamical equation and the replicator Price equation are equivalent. Adaptive dynamics can be derived from the replicator Price equation. The quasispecies equation is a special case of the replicator–mutator equation for the case of constant fitness.

determined by its replication rate. The average fitness of the population is given by $\bar{f} = \sum_i f_i x_i$. There are $n$ genetic sequences. Replication is error-prone; the probability that replication of sequence $i$ gives rise to sequence $j$ is given by $q_{ij}$. These quantities describe the mutation matrix, $Q$. The rate at which $x_i$ changes over time is given by

$$\dot{x}_i = \sum_{j=1}^{n} x_j f_j q_{ji} - x_i \bar{f}. \tag{1}$$

The term, $-x_i \bar{f}$, ensures that $\sum_i x_i = 1$. The quasispecies equation describes the adaptation of a population on a constant fitness landscape. The underlying geometry is given by sequence space, which is a high-dimensional array of sequences arranged in such a way that neighboring sequences differ by a single-point mutation.

## Evolutionary Game Dynamics and Lotka–Volterra

Evolutionary game theory is a phenotypic approach to evolutionary dynamics (Maynard Smith, 1982). It describes the natural selection of strategies in evolutionary games, such as the Hawk–Dove game or the Prisoner's Dilemma.

The key aspect of evolutionary game theory is frequency-dependent selection: the fitness of an individual depends on the frequency of other strategies in the population, Let $x_i$ denote the frequency of strategy $i$, Its fitness, $f_i(\mathbf{x})$, is a function of the distribution of the population given by the vector $\mathbf{x} = (x_1, \ldots, x_n)$. Evolutionary game dynamics of discrete phenotypes are described by the replicator equation (Hofbauer & Sigmund, 1998; Taylor & Jonker, 1978):

$$\dot{x}_i = x_i[f_i(\mathbf{x}) - \bar{f}]. \tag{2}$$

For early treatments of frequency-dependent selection, see Haldane & Jayakar (1963), Sacks (1967), Wright (1969), Crow & Kimura (1970), Charlesworth & Charlesworth (1975, 1976a, b).

In ecology, the Lotka–Volterra equation describes the interaction among $n$ different species (Lotka, 1920; Volterra, 1926; May, 2001). The abundance of species $i$ is given by $y_i$. The reproductive rate (fitness), $f_i$, of each species depends on the abundance of other species. In general, we have $\dot{y}_i = y_i f_i(\mathbf{y})$. The Lotka–Volterra equation for $n-1$ species is equivalent to the replicatior equation for $n$ phenotypes. Let $y = \sum_{i=1}^{n-1} y_i$. The equivalence can be shown with the transformation $x_i = y_i/(1+y)$ for $i = 1, \ldots, n-1$ and $x_n = 1/(1+y)$ (Hofbauer & Sigmund, 1998).

## The Replicator–Mutator Equation

The quasispecies equation (1) lacks frequency-dependent selection, while the replicator equation (2) lacks mutation. Combining these two equations we obtain

$$\dot{x}_i = \sum_{j=1}^{n} x_j f_j(\mathbf{x}) q_{ji} - x_i \bar{f}. \tag{3}$$

This "replicator–mutator equation" describes both frequency-dependent selection and mutation. It has been used in population genetics (Hadeler, 1981), autocatalytic reaction networks (Stadler & Schuster, 1992), game theory (Bomze and Buerger, 1995) and language evolution (Nowak *et al.*, 2001). It is clear that the quasispecies equation and the replicator equation are special cases of the replicator–mutator equation.

## The Price Equation

In 1970, George Price derived an equation to describe any form of selection (Price, 1970, 1972; Frank, 1995). The "Price equation" was used by Hamilton in his seminal work on kin selection (Hamilton, 1970). It has been applied to problems in evolutionary genetics (Lewontin, 1974; Crow & Nagylaki, 1976), social evolution (Frank, 1998), group selection (Price, 1972; Michod, 2000), sex ratio (Frank, 1986) and ecological diversity (Loreau & Hector, 2001). Fisher's fundamental theorem of natural selection can be directly derived from the Price equation (Frank, 1998). For continuous time, the Price equation is of the form (Price, 1972)

$$\dot{E}(p) = Cov(f, p) + E(\dot{p}). \qquad (4)$$

The numerical value of an arbitrary trait of individual $i$ is given by $p_i$. The population average of this trait is given by $\bar{p} \equiv E(p) = \sum_i p_i x_i$. The covariance of trait $p$ and fitness $f$ is given by $Cov(f, p) = \sum_i x_i f_i p_i - \bar{f}\bar{p}$. The second term eqn (4) is the population average of the rate at which the trait values change over time. We have $E(\dot{p}) = \sum_i x_i \dot{p}_i$. If the trait values, $p_i$, do not change with time, we obtain the "covariance equation", $\dot{E}(p) = Cov(f, p)$.

## Equivalence

We will now show that the game-dynamical eqn (2) is equivalent to the Price eqn (4), while the replicator–mutator eqn (3) is equivalent to an expanded Price equation of the form

$$\dot{E}(p) = Cov(f, p) + E(\dot{p}) + E(f \Delta_m p). \qquad (5)$$

The additional term, $E(f \Delta_m p) = \sum_i x_i f_i \Delta_m p_i$, describes mutation among types, with $\Delta_m p_i = \sum_j q_{ij}(p_j - p_i)$ denoting the expected change in trait value when mutating from type $i$.

We have $\bar{p} \equiv E(p) = \sum_i p_i x_i$ and therefore $\dot{E}(p) = \sum_i p_i \dot{x}_i + \sum_i x_i \dot{p}_i$. From the replicator–mutator equation (3), we obtain

$$\dot{E}(p) = \sum_i p_i \left( \sum_j x_j f_j q_{ji} - x_i \bar{f} \right) + E(\dot{p})$$
$$= \sum_{ij} p_i x_j f_j q_{ji} - \bar{f}\bar{p} + E(\dot{p})$$

$$= \sum_{ij} p_j x_j f_j q_{ji} - \bar{f}\bar{p}$$
$$+ \sum_{ij} (p_i - p_j) x_j f_j q_{ji} + E(\dot{p})$$
$$= \sum_j p_j x_j f_j - \bar{f}\bar{p} + \sum_j x_j f_j \sum_i q_{ji}(p_i - p_j)$$
$$+ E(\dot{p}) = Cov(f, p) + E(\dot{p}) + E(f \Delta_m p)$$

This is the expanded Price equation with the additional mutation term. The term $Cov(f, p)$ describes selection (and in our framework would include epistatic and dominance interactions among genes and alleles). The term $E(\dot{p})$ describes changes in trait value, which may be consequences of changes in the environment or the trait being frequency-dependent (such as fitness). The term $E(f \Delta_m p)$ describes mutation among the different types. In the same way, we can derive the standard Price eqn (4) from the replicator eqn (2).

In general, the Price equation is dynamically insufficient (Lewontin, 1974; Barton & Turelli, 1987). To calculate how the population average of a trait changes with time, we need to consider a differential equation for the covariance, which in turn will include higher moments. Dynamic sufficiency can only be obtained in special cases. For our purpose, the trick is to consider $n$ traits that are indicator functions of the $n$ types: for $i = 1 \ldots n$ we have $p_j^{\langle i \rangle} = 1$ if $i = j$ and $p_j^{\langle i \rangle} = 0$ if $i \neq j$. The population average of $p^{\langle i \rangle}$ is $E(p^{\langle i \rangle}) = \sum_j x_j p_j^{\langle i \rangle} = x_i$. For the three terms on the RHS of the expanded Price equation (5), we obtain $Cov(f, p^{\langle i \rangle}) = x_i(f_i - \bar{f})$, $E(\dot{p}^{\langle i \rangle}) = 0$, and $E(f \Delta_m p^{\langle i \rangle}) = -x_i f_i + \sum_k x_k f_k q_{ki}$. Hence, the Price equation for trait $p^{\langle i \rangle}$ leads to the replicator–mutator equation for frequency $x_i$.

In Appendix A, we also show the equivalence between the replicator–mutator equation and the expanded Price equation for discrete time and for sexual reproduction with recombination. One can also show equivalence between the Price equation and a replicator–mutator equation describing continuous phenotypes.

In our framework, the Price eqn (4) does not include mutation, whereas the expanded Price eqn (5) does include mutation. It is interesting to note that Price does not mention mutation in his

original papers (Price, 1970, 1972). Nevertheless, Frank points out that the Price eqn (4) is an exact and complete description of evolutionary dynamics including both selection and mutation (Frank, 1995, 1998). The resolution of this apparent discrepancy lies in the different labeling systems. In our paper, we use the labeling system of the replicator–mutator framework: $x_i(t)$ denotes the relative abundance of type $i$ individuals at time $t$. In the original Price equation, however, $x_i(t)$ denotes the relative abundance of individuals at time $t$ that are derived from type $i$ individuals at time 0. Indeed, with this unusual labeling system the Price eqn (4) can be interpreted to include any form of mutation and selection. Hence, it makes sense to call eqn (4) "replicator Price equation" and eqn (5) "replicator–mutator Price equation" if one uses the labeling system of the replicator framework. In contrast, "Price equation" should refer to eqn (4) with the labeling system of Price. In this sense, the Price equation is equivalent to the replicator–mutator Price equation which is equivalent to the replicator–mutator equation.

## Adaptive Dynamics

Another framework for evolutionary change is given by adaptive dynamics (Nowak & Sigmund, 1990; Metz *et al.*, 1996; Dieckmann & Law, 1996; Dieckmann & Doebeli, 1999), which describes how continuous traits or strategies change under mutation and frequency-dependent selection. Adaptive dynamics assume there is a resident population which is surrounded by a cloud of mutants. Selection chooses the mutant with maximum fitness in the context of the resident population. In the limit of many mutants very close to the resident population, one obtains an equation using partial derivatives of trait values. Adaptive dynamics illustrate the nature of evolutionarily stable strategies (Hofbauer & Sigmund, 1998), which emerge as stable or unstable equilibrium points. There is also a connection to Wright's "adaptive landscape" and formulations of selection gradients (Lande & Arnold, 1983; Brawn & Vincent, 1987; Iwasa *et al.*, 1991; Turelli & Barton, 1994).

It turns out that adaptive dynamics can be derived from the Price equation. Let us assume

that the population is described by a continuous distribution, $x(p)$, of some trait variable, $p$. The fitness of individuals with a particular trait value $p$ depends on $x$ and is given by $f(p; x)$.

Let us start from the expanded Price eqn (5) but assume that the expect mutational change for trait $p$ is zero. Hence, $E(f\Delta_m p) = 0$, and we obtain the Price eqn (4). Observe, however, that we do not assume there is no mutation, we only assume that on average mutational events are equally likely to increase or decrease the trait value. Let us further assume that the trait values, $p_i$, do not change with time. Hence, $E(\dot{p}) = 0$ and we obtain the covariance equation, $\dot{E}(p) = Cov[p, f(p; x)]$. The fitness of individuals with a trait value $p$ is given by $f(p; x)$, where $x$ describes the distribution of the population. A first-order Taylor expansion of $f(p; x)$ around the population average $\bar{p} \equiv E(p) = \int x(p)p\,\mathrm{d}p$ is given by

$$f(p; x) \approx f(\bar{p}; x) + (p - \bar{p})\frac{\partial f(q; x)}{\partial q}\Big|_{q=\bar{p}}.$$

Hence,

$$\dot{E}(p) \approx Cov\left(p, f(\bar{p}; x) + (p - \bar{p})\frac{\partial f(q; x)}{\partial q}\Big|_{q=\bar{p}}\right)$$

$$= Var(p)\frac{\partial f(q; x)}{\partial q}\Big|_{q=\bar{p}}.$$

This equation describes the adaptive dynamics for trait $p$.

## Discussion

In summary, we have shown that different descriptions of evolutionary and ecological dynamics can be transformed into each other. At the center of the unified framework are the replicator–mutator equation and the Price equation, which emerge as equivalent formulations of general evolutionary dynamics. The replicator–mutator equation describes the dynamics of the distribution of a population, while the Price equation describes its moments. In specific limits, we obtain adaptive dynamics, evolutionary game dynamics and the quasispecies equation. Understanding the relationship among evolutionary equations is useful, because results for one system can be transferred to other systems, and specific problems are more easily

expressed in one framework than another. We also need to be aware that the different approaches are equivalent formulations of the same fundamental theory of biology.

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# Appendix A

### DISCRETE TIME

The replicator–mutator equations for discrete generations is of the form $x'_i = \sum_j q_{ji}s_j x_j/\bar{s}$. Here $s_i$ is the selection coefficient or discrete time fitness and $\bar{s} \equiv E(s) = \sum_i s_i x_i$. From $\Delta E(p) = \sum_i p'_i x'_i - \sum_i p_i x_i$, we obtain

$$E(s)\Delta E(p) = Cov(s,p) + E(s\Delta_m p)$$

$$+ E(s\Delta p) + E[s\Delta_m(\Delta p)].$$

Here $E(s\Delta_m p) = \sum_{ij}(p_i - p_j)q_{ji}s_j x_j$, $E(s\Delta p) = \sum_j \Delta p_j s_j x_j$ and $E[s\Delta_m(\Delta p)] = \sum_{ij}(\Delta p_i - \Delta p_j)q_{ji}s_j x_j$. The three expectation terms on the RHS can be incorporated into a single term using the definition $\Delta_{tot}p_j = \sum_i(q_{ji}p_i') - p_j$. Hence, we obtain

$$E(s)\Delta E(p) = Cov(s, p) + E(s\Delta_{tot}p).$$

In the same way, the replicator equation in discrete time, $x_i' = x_i s_i/\bar{s}$, leads to

$$E(s)\Delta E(p) = Cov(s, p) + E(s\Delta p).$$

### SEXUAL REPRODUCTION

For the case of sexual reproduction, the replicator–mutator equation is of the form

$$\dot{x}_i = \sum_{jk} x_j x_k F_{jk} Q_{jki} - \bar{f}x_i.$$

Here $F_{jk} = F_{kj}$ is the rate at which individuals $j$ and $k$ meet the reproduce. $Q_{jki} = Q_{kji}$ is the probability that mating between $j$ and $k$ results in an offspring of type $i$. For simplicity, we assume here that there is only one sex, and the mating interaction is symmetric. Extensions to other cases are possible.

We have $f_i = \sum_j F_{ij}x_j$ and $\bar{f} = \sum_i x_i f_i$. From this equation, we can derive the expanded Price equation $\dot{E}(p) = Cov(f, p) + E(\dot{p}) + E(F\Delta_m p)$, where $E(F\Delta_m p) = \sum_{jk} x_j x_k F_{jk}\Delta_m p_{jk}$ and $\Delta_m p_{jk} = \sum_i Q_{jki}[p_i - (p_j + p_k)/2]$. The reverse direction again uses indicator traits.