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EVOLUTION PROCESSES WITH CONTINUITY OF TYPES

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Abstract

The objective of this work is to study the long range evolutionary traits in a population with an infinite number of types; we are especially interested in the asymptotic rate of evolution, variance and type-distribution. In this paper we concentrate on an asexual population with the same probabilistic mutation force acting over all types in the population.

Most results are proved under the assumption that the mutation effect is also unchanged in time; some are extended to more general cases with time-changed distribution of mutation.

EVOLUTION; MUTATION; SELECTION; MUTATION-SELECTION BALANCE; RATE OF EVOLUTION; TIME HOMOGENEOUS PROCESS OF EVOLUTION; PERFECT PROCESS OF EVOLUTION; SEMI-MARKOV PROCESS OF EVOLUTION; DISTRIBUTION OF FITNESS; DISTRIBUTION OF MUTATION; ASYMPTOTIC DISTRIBUTION OF FITNESS

1. Introduction

The motivation for this work stems from the many investigations carried out on the combined effects of mutation and selection on a large population (see [3], [10], [11], [27], [32] and references therein).

Although most classical works concentrate on the situation in which very few, usually two or three, possible genotypes are involved, a deeper understanding of some aspects of the natural process appears to require study of a polygenic situation for which the development of an infinite-type model is the most feasible. This approach, justified by the large number of possible genotypes offered by the chromosomal system, has been pursued by Kimura and Crow [23], Kimura [19], Karlin and McGregor [17], Karlin [16], and lately, in connection with problems of biochemical evolution, by Kimura [21], [22], Kimura and Crow [24], Kimura and Ohta [25], Ewens [7] and others. Another approach, attributing quantitative variation in population both to phenotypic and genotypic features has already been treated by Fisher [9], Wright [31], and more recently by Bodner and Edwards [1], Kojima [26], O'Donald [28] and others. In all of these works, however, the genetic factor

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has been restricted to a one-locus two allele situation. Finally, polygenic models which allow qualitative features to be genetically inherited were used by Kimura [19] and by Slatkin [30].

This work attempts to analyze the combined effect of selection and mutation on an infinitely large, asexual population, in which quantitative differences in fitness are determined by a genetic variation on a continuum. Changes in the distribution of the fitness-factor are investigated with a special consideration given to the asymptotic behavior of the population in the long run.

In introducing an amount of a parental material as a basic unit of reproduction, the approach of this work is somewhat similar to that of Jirina's continuous-state branching processes (see, for example, Jirina [14], [15], Seneta and Vere-Jones [29] and reference therein). However, both the basic problem of this work and the mathematical methods used are quite different.

For biological applications and discussion, the reader is referred to [4]. Extensions of some of these results to a sexual model are given in [5].

2. The general model and basic properties

We consider an infinite population characterized by various inherited properties. The types of the population are identified with points of a certain measurable space $\langle E, \mathscr{B} \rangle$. The population is described by its frequency-measure over this space. Starting with μ_0 as the initial frequency measure of types in the population, the population is assumed to change over successive generations, under the influence of selection and mutation pressures. We formulate the problem in a quite general setting, but the bulk of the analysis concentrates mainly on the one-dimensional case $E = R^1$, where all types in the population may be ordered according to a single real parameter.

(i) *Selection.* At the first step, each individual in the population produces offspring replicating its type. In agreement with the traditional approach of population biology (e.g., Fisher [10], Haldane [11] and Crow and Kimura [3]), we postulate that each generation, the expected number of viable offspring produced by an x-type individual ($x \in E$), is proportional to a given value $\gamma(x)$, namely the fitness of this type. The fitness function $\gamma(x)$ is naturally assumed to be positive and integrable over $\langle E, \mathscr{B}, \mu_0 \rangle$, with

$$E_0\gamma(x) = \int \gamma(x)\mu_0(dx) < \infty. \tag{2.1}$$

For any class of types $A \subset E$, the frequency of offspring produced by an A-type individual, relative to the entire population, is

$$\frac{\int_A \gamma(x)\mu_0(dx)}{\int \gamma(x)\mu_0(dx)} = \frac{1}{E_0\gamma(x)} \int_A \gamma(x)\mu_0(dx). \tag{2.2}$$

(ii) *Mutation.* As a second step, each offspring in general may mutate (alter its type) governed by a given probabilistic law, which depends on the generation-time and on its parental type. Explicitly, let $\nu_t(\cdot \mid y)$ be the type-probability-measure of each offspring produced by a y-type parent in time t $(t=0,1,2,\cdots;\ y\in E)$. $\nu_t(\cdot \mid y)$ is called the *mutation probability-measure.*

Influenced by selection and mutation, the frequency-measure of all offspring types is given by:

$$\begin{aligned}\mu_1(A) &= (1/E_0\gamma(x)) \int_E \nu_0(A \mid y) \int_{dy} \gamma(u)\mu_0(du)\\ &= (1/E_0\gamma(x)) \int_E \nu_0(A \mid y)\gamma(y)\mu_0(dy),\end{aligned}$$

for all $A \in \mathscr{B}$.

In exactly the same way one may express the frequency-measure μ_{t+1} of the $t+1$ generation in terms of μ_t and $\nu_t(\cdot \mid y)$ $(y \in E)$

$$\mu_{t+1}(A) = (1/E_t\gamma(x)) \int_E \nu_t(A \mid y)\gamma(y)\mu_t(dy). \tag{2.3}$$

The sequence $\{\mu_t\}_t$ is thus recursively determined by μ_0 and by the mutation-distributions.

Definition. A sequence $\{\mu_t\}$ of frequency-measures over E, as determined by (2.3), is called an *asexual process of evolution.*

If for some T, $(T = 1,2,3,\cdots)$ $E_T\gamma(x) = \infty$, the process is said to explode in a finite time. If not, we speak of a *lasting process of evolution.*

In this work we exclusively consider lasting processes, which are manifestly most meaningful for biological applications.

When the types of the population are characterized by any (finite or infinite) number of continuously ordered biological features, the measure space E is naturally described as a vector space. In this case it is convenient to use the notations

$$F_t(x) = \int_{u \leqq x} \mu_t(du)$$

and

$$G_t(x \mid y) = \int_{u \leqq x} \nu_t(du \mid y)$$

for the distributions of types and mutations respectively in the tth generation. Henceforth the limitations of our analysis require the homogeneity assumption that in each generation all mutations are equi-distributed around their parental type; so that

$$G_t(x \mid y) = G_t(x - y), \quad t = 0,1,\cdots; x, y \in E. \tag{2.4}$$

Under this assumption (2.3) becomes

$$F_{t+1}(x) = (1/E_t\gamma(x)) \int_E G_t(x-y)\gamma(y)dF_t(y). \tag{2.5}$$

With some special forms of $\gamma(x)$ in mind it is convenient to describe the process by its generating functions (g.f.'s):

$$\phi_t(s) = \int_E s^x dF_t(x), \tag{2.6}$$

$$\psi_t(s) = \int_E s^x dG_t(x), \tag{2.7}$$

where $s = (s_1, \dots, s_n)$, $s^x = s_1^{x_1} \dots s_n^{x_n}$, and wherever the right hand sides are defined (i.e., when $F_t(x)$ is defined, $G_t(x \mid y) = G_t(x-y)$ and the integrals converge). In terms of generating functions, (2.5) may be expressed in the manner:

$$\begin{aligned} \phi_{t+1}(s) &= (1/E_t\gamma(x)) \int_E s^x d\left(\int_E G_t(x-u)\gamma(u)dF_t(u)\right) \\ &= (1/E_t\gamma(x)) \int_E \gamma(u) \int_E s^{x+u} dG_t(x)dF_t(u) \\ &= (\psi_t(s)/E_t\gamma(x)) \int_E \gamma(u)s^u dF_t(u). \end{aligned} \tag{2.8}$$

A recursive formula for $\phi_t(s)$ is readily obtained when $\int \gamma(u)s^u dF_t(u)$ can be expressed in terms of the g.f. $\phi_t(s)$. This, for example, is the case when $\gamma(u)$ is a polynomial function of u (with $\gamma(u) \geqq 0$). Thus, in the simplest, linear situation for $u \geqq 0$ $\gamma(u) = \alpha + \beta u$ (with $\alpha, \beta \geqq 0$), we get:

$$\phi_{t+1}(s) = \psi_t(s)\frac{\alpha\phi_t(s) + \beta s\phi_t'(s)}{\alpha + \beta\phi_t'(1)}.$$

A more important case, on which we concentrate throughout the sequel of this work, occurs when x is a single parameter which corresponds to the general Darwinian trait of *fitness*, i.e., the expected number of surviving offspring of an individual of a given type. Defining x, more precisely, to be a logarithmic function of this expectation, postulate (2.4) complied with the biologically plausible assumption (see [4]) that *relative* change in fitness due to mutation is equi-distributed over the whole population.

In this case we get

$$\gamma(x) = \lambda^x, \tag{2.9}$$

where $\lambda > 1$ is a measure for the intensity of selection in the population (see [4]), and (2.8) then reduces to

$$\phi_{t+1}(s) = \frac{\psi_t(s)\phi_t(\lambda s)}{\phi_t(\lambda)}. \tag{2.10}$$

Definitions. (a) A general process of evolution with $\gamma(x) = \lambda^x$ $(\lambda > 1)$ is called a *fitness process of evolution* or (in this work) simply a *process of evolution.*

In such a process, λ is called the *Malthusian parameter* (see Fisher [10]). The parameter x is referred to as the *fitness.* The value $E_{t+1}x - E_t x$ $(t = 0, 1, 2, \cdots)$, measuring one-generation changes in fitness, is called the *rate of evolution.*

(b) Any process in which $G_t(x) = G(x)$ for all $t = 0, 1, 2, \cdots$ is said to be *time homogeneous* in respect to mutation.

If for some n and all t, $G_{t+n}(x) = G_t(x)$, we speak of a *periodic process.* Later, we shall also be interested in the more general case in which eruptions of mutation are stochastically dependent on previous eruption, thus producing a semi-Markov process.

The main results proved in this work concern time homogeneous fitness processes; these are as follows.

(a) If the fitness in the initial population is bounded from above, then the rate of evolution tends to a limit which depends only on the mutation distribution.

This limit is finite iff the parent-offspring difference in fitness due to mutation is bounded from above. Furthermore, in this case the rate of evolution tends exactly to the supremum of this parent-offspring difference, independent of the initial distribution and of the Malthusian parameter.

(b) Under the assumption of (a), the variance of the centered distribution $F_t(x - E_t x)$ is bounded and tends to a finite limit.

(c) $F_t(x - E_t x)$ converges in law to a limit distribution $F(x)$, which depends only on the distribution of the mutation. Furthermore, under the assumption of a bounded fitness population, there is a 1–1 correspondence between the distributions of the mutation and the limit centered distribution $F(x)$. An explicit formulation for this correspondence will be developed in terms of the g.f.'s, and a criterion will be elaborated to determine whether a given distribution may be obtained as a limit distribution of a time homogeneous process.

(d) The support of the limit centered distribution is bounded from above (i.e., the limit *relative-fitness* is bounded from above) iff there is a positive probability for the maximal mutation.

(e) The *absolute fitness* tends (in law) to a limit distribution iff all possible mutations are deleterious but there is a positive probability for each offspring to suffer no mutation.

In this case, although the limit *mutation selection balance* distribution depends on the distribution of the deleterious mutation, the limit fitness of the population as a whole is independent of it; here we have defined population fitness as the average number of surviving offspring per individual. Furthermore, the population limit fitness is always equal to the maximal fitness in the initial population multiplied by the (positive) probability of an offspring not to be mutated.

3. Fitness processes, regularity and limit rate of evolution

Theorem 3.1. A fitness process is lasting (non-exploding) iff one of the following conditions is satisfied:

(i) $\phi_t(s) < \infty$ for all $1 \leqq s < \infty$ and $t = 0, 1, 2, \cdots$;

(ii) $\phi_0(s)$ and all $\psi_t(s)$ are finite for $1 \leqq s < \infty$.

Proof. By definition the process does not explode iff:

$$E_t\gamma(x) = E_t\lambda^x = \phi_t(\lambda) < \infty, \quad t = 0, 1, 2, \cdots. \tag{3.1}$$

This is automatically true under Condition (i) and also follows from (2.10) by virtue of Condition (ii).

On the other hand, suppose the process does not explode. Then $\phi_t(\lambda) < \infty$ $(t = 0, 1, 2, \cdots)$, which entails $\phi_t(s) < \infty$ for $1 \leqq s \leqq \lambda$, $t = 0, 1, 2, \cdots$.

Assume now that all $\phi_t(s)$ converge over $[\lambda^n, \lambda^{n+1}]$ for some non-negative integer n. Inspection of (2.10) reveals that for all $t = 0, 1, 2, \cdots$ and $s \in [\lambda^n, \lambda^{n+1}]$,

$$\phi_{t+1}(s) = \frac{\psi_t(s)\phi_t(\lambda s)}{\phi_t(\lambda)}. \tag{3.2}$$

Since $\psi_t(s) > 0$, $\phi_t(s)$ is finite for $[\lambda^{n+1}, \lambda^{n+2}]$. Convergence of the $\phi_t(s)$ over all $[1, \infty)$ is immediately implied. Using (3.2) again, the same holds for all $\psi_t(s)$.

Unless otherwise stated, we shall now restrict attention only to lasting processes (i.e., when $\phi_t(s) < \infty$ for $s \geqq 1$). A convenient formulation, aiding further investigation of the process $\{F_t(x)\}$, involves independent random variables (r.v.'s) X_t $(t = 0, 1, 2, \cdots)$, distributed as $F_t(x)$ respectively, called the successive fitness r.v.'s. We are interested in the law of the sequence $\{X_t\}_{t=0}^{\infty}$.

Let us call a process without mutations, i.e., with all $\psi_t(s) = 1$, a *pure selection process.*

Theorem 3.2. The t-generation fitness r.v. X_t may be represented as the sum

$$X_t = Z_t + \sum_{k=0}^{t-1} Y_{kt} \tag{3.3}$$

of $t+1$ independent r.v.'s, Z_t being the t-generation fitness r.v. of a pure selection process starting with a fitness distribution F_0, and $Y_{k\,t}$ standing for the k generation pure selection process starting with a fitness distribution G_{t-k-1}, and the equality is in law.

Proof. By iteration of (2.10) we get

$$Es^{X_t} = \phi_t(s) = \frac{\phi_0(\lambda^t s)}{\phi_0(\lambda^t)} \prod_{k=0}^{t-1} \frac{\psi_{t-k-1}(\lambda^k s)}{\psi_{t-k-1}(\lambda^k)}. \tag{3.4}$$

As a special case, for a pure selection process starting with F_0 (then $\psi_t(s) \equiv 1$) we get

$$Es^{Z_t} = \phi_0(\lambda^t s)/\phi_0(\lambda^t).$$

In the same way, for the k generation pure selection process starting with G_{t-k-1}

$$ES^{Y_{k,t}} = \psi_{t-k-1}(\lambda^k s)/\psi_{t-k-1}(\lambda^k).$$

From (3.4)

$$ES^{X_t} = ES^{Z_t} \prod_{k=0}^{t-1} ES^{Y_{k,t}},$$

and the theorem follows immediately.

In a time-homogeneous process, (3.4) has the form

$$\phi_t(s) = \frac{\phi_0(\lambda^t s)}{\phi_0(\lambda^t)} \prod_{k=0}^{t-1} \frac{\psi(\lambda^k s)}{\psi(\lambda^k)}, \tag{3.5}$$

and (3.3) (Theorem 3.2) becomes

$$X_t = Z_t + \sum_{k=0}^{t-1} Y_k. \tag{3.6}$$

Theorem 3.2 allows us to study a general process of evolution by consideration of the much simpler pure selection process. For this we require the following definition.

Definition. For any distribution $H(x)$, we define the value $\bar{H} = \sup\{x \mid H(x) < 1\}$ as the (upper) *bound* of $H(x)$. The distribution is said to be *bounded* (has bounded support from above) iff $\bar{H} < \infty$.

Lemma A. In a pure selection process $\{H_t(x)\}_{t=0}^{\infty}$

$$\lim_{t\to\infty} H_t(x) = \begin{cases} 0 & \text{if} \quad x < \bar{H}_0, \\ 1 & \text{if} \quad x \geqq \bar{H}_0. \end{cases} \tag{3.7}$$

For the special case where $\bar{H}_0 = \infty$, $\lim_{t\to\infty} H_t(x) = 0$ for all $-\infty < x < \infty$. Furthermore, if Z_t is the t-generation fitness r.v. of the process, then,

$$\lim_{t\to\infty} EZ_t = \bar{H}_0 \tag{3.8}$$

(clearly $\bar{H}_0 = \bar{H}_t$, $t = 0, 1, 2, \cdots$).

Proof. If $x \geqq \bar{H}_0$, then $H_t(x) = 1$ for all t. If $x < \bar{H}_0$, choose $\varepsilon < \bar{H}_0 - x$, so that $1 - H_0(x + \varepsilon) > 0$.

From (3.5):

$$\int_{-\infty}^{\infty} s^x dH_t(x) = \int_{-\infty}^{\infty} s^x \lambda^{tx} dH_0(x) \Big/ \int_{-\infty}^{\infty} \lambda^{tx} dH_0(x),$$

and thus

$$\begin{aligned} H_t(x) &= \int_{-\infty}^{x} \lambda^{tu} dH_0(u) \Big/ \int_{-\infty}^{\infty} \lambda^{tu} dH_0(u) \\ &\leqq \int_{-\infty}^{x} \lambda^{tu} dH_0(u) \Big/ \left\{ \int_{-\infty}^{x} \lambda^{tu} dH_0(u) + \int_{x+\varepsilon}^{\infty} \lambda^{tu} dH_0(u) \right\} \\ &\leqq \lambda^{tx} / \{ \lambda^{tx} + \lambda^{t(x+\varepsilon)} [1 - H_0(x+\varepsilon)] \}, \end{aligned} \tag{3.9}$$

from which $\lim_{t\to\infty} H_t(x) \leqq 0$. The conclusion of (3.8) is also inferred from the left hand side identity of (3.9).

As an immediate result we have the following theorem.

Theorem 3.3. For a time homogeneous process with $\bar{F}_0 < \infty$

$$\lim_{t\to\infty} \{EX_{t+1} - EX_t\} = \bar{G}. \tag{3.10}$$

We see that the rate of evolution tends to the supremum of the offspring-parent difference in fitness.

Proof. From (3.6) we have

$$EX_{t+1} - EX_t = EZ_{t+1} - EZ_t + EY_t.$$

By Lemma A

$$\lim_{t\to\infty} EY_t = \bar{G},$$

and since $\bar{F}_0 < \infty$,

$$EZ_{t+1} - EZ_t = \bar{F}_0 - \bar{F}_0 = 0$$

which completes the proof.

Definition. A time homogeneous process $\{F_t(x)\}_t$ is called *initially regular* if $\bar{F}_0 < \infty$. If, in addition, $\bar{G} < \infty$, the process is called a *regular process.*

It is easy to see that the following statements are true.

(i) In a regular process $\bar{F}_t < \infty$ for all t. In fact

$$\bar{F}_t = \bar{F}_0 + t\bar{G}. \tag{3.11}$$

(ii) A time homogeneous process in which $\bar{F}_t < \infty$ for some t is a regular process.

The main claims of Theorem 3.3 can be stated as follows.

(i) The rate of evolution of an initially regular process tends to a limit (finite or infinite) as $t \to \infty$.

(ii) This limit is independent of both $F_0(x)$ and λ and depends on $G(x)$ only through its upper bound.

(iii) This limit rate of evolution is finite iff the process is regular; i.e., if the fitness in the initial population is bounded from above, and so is the offspring-parent change due to mutation. These assumptions are manifestly plausible for a biological application of the model (see [4]).

Remark. The theorem does not necessarily hold if $\bar{F}_0 = \infty$. Consider, for example, a normal fitness distribution of the initial population

$$\phi_0(s) = e^{\frac{1}{2}(\ln s)^2},$$

then

$$Es^{Z_t} = \phi_0(\lambda^t s) / \phi_0(\lambda^t) = s^{\,t \ln\lambda + \frac{1}{2}\ln s},$$

and $Z_t \sim N(t \ln \lambda, 1)$ with $EZ_t = t \ln \lambda$ for all t.

Unlike the homogeneous case, the limit rate of evolution may not exist in non-homogeneous processes. For the more general case, we are thus interested in the weaker Cesàro average limit $\lim \{EX_t/t\}$. If $\bar{F}_0 < \infty$, then (3.3) and Lemma A show that this limit, if it exists, is also independent of $F_0(x)$. We shall prove its existence and also calculate it in a certain class of semi-Markov processes.

Definition. The process $\{F_t(x)\}$ is said to be semi-Markov if the distribution of its mutation is stochastically varied in time, being randomly equal to one of the n distributions $H_1(x), \cdots, H_n(x)$ according to the Markovian Law

$$P\{G_{t+1}(x) = H_j(x) \mid G_t(x) = H_i(x)\} = a_{ij}, \qquad 1 \leqq i,\ j \leqq n, \tag{3.12}$$

where $\| a_{ij} \| = A$ is an irreducible stochastic matrix.

Theorem 3.4. In an initially regular semi-Markov process with $\bar{F}_0 < \infty$,

$$(3.13) \qquad \lim_{t\to\infty} EX_t/t = \sum_{i=1}^{n} P_i\bar{H}_i, \quad \text{a.s.}$$

where P_i is the ergodic probability $\lim_{t\to\infty} t^{-1}\sum_{k=0}^{t-1} P(G_k = H_i)$.

Proof. For all $1 \leqq i \leqq n$ and $t = 0,1,2,\cdots$, denote by $Y_{i,t}^*$ the t-generation fitness r.v. of a pure selection process starting with H_i. Denote by $\bar{H}$ the right hand side of (3.13).

First, assuming $\bar{H} < \infty$, set $c = \max_{1\leqq i\leqq n}|\bar{H}_i - \bar{H}| < \infty$.

Let $\varepsilon > 0$. By Lemma A, there is a number N such that for all $1 \leqq i \leqq n$

$$(3.14) \qquad t \geqq N \Rightarrow |EY_{i,t}^* - \bar{H}_i| < \tfrac{1}{2}\varepsilon.$$

For $t > N$, let N_t^i be the number of generations up to $t - N + 1$, for which $G_\tau \equiv H_i$. Clearly

$$\sum_{i=1}^{n} N_t^i = t - N,$$

and from (3.14) we get

$$\sum_{i=1}^{n} N_t^i\bar{H}_i - \tfrac{1}{2}\varepsilon(t-N) \leqq \sum_{k=N+1}^{t} EY_{k,t} \leqq \sum_{i=1}^{n} N_t^i\bar{H}_i$$

(here the $Y_{k,t}$ are defined as in Theorem 3.2). For t large enough the ergodic theorem implies that

$$|(t-N)^{-1}N_t^i - P_i| < \delta = \begin{cases} \varepsilon/2cn & \text{if} \quad c > 0, \quad 1 \leqq i \leqq n, \\ 1 & \text{if} \quad c = 0, \quad 1 \leqq i \leqq n. \end{cases}$$

For such a t we thus get

$$\begin{aligned} \bar{H} - \varepsilon &\leqq \sum_{i=1}^{n} P_i\bar{H}_i - \delta cn - \tfrac{1}{2}\varepsilon \leqq (t-N)^{-1}\sum_{i=1}^{n} N_t^i\bar{H}_i - \tfrac{1}{2}\varepsilon \\ &\leqq (t-N)^{-1}\sum_{k=N+1}^{t} EY_{k,t} \leqq (t-N)^{-1}\sum_{i=1}^{n} N_t^i\bar{H}_i \leqq \sum_{i=1}^{n} P_i\bar{H}_i + \delta c \\ &\leqq \bar{H} + \tfrac{1}{2}\varepsilon. \end{aligned}$$

Eventually, since $\bar{F}_0 < \infty$ and $\sup_{k,t} EY_{k,t} \leqq \max_{1\leqq i\leqq n}\bar{H}_i < \infty$, we have

$$\lim_{t\to\infty}\left\{EZ_t/t + t^{-1}\sum_{k=0}^{N} EY_{k,t}\right\} = 0.$$

Hence

$$\lim_{t\to\infty}\frac{EX_t}{t} = \lim_{t\to\infty}\left\{\frac{EZ_t}{t} + \frac{1}{t}\sum_{k=0}^{N} EY_{k,t} + \frac{t-N}{t}\,\frac{1}{t-N}\sum_{k=N+1}^{t-1} EY_{k,t}\right\} = \bar{H}, \text{a.s.}$$

Now, assuming $\bar{H} = \infty$, then $\bar{H}_i = \infty$ for some $1 \leqq i \leqq n$. In this case $EY^*_{i,t} \to \infty$ by Lemma A and again, since the proportion of the $Y^*_{i,t}$ in the sum $\sum_{j=0}^{t-1} y_{j,t}$ tends a.s. to $P_i > 0$, $t^{-1} EX_t \to \infty$ a.s.

Corollary. In a deterministic periodic process, $\lim_{t\to\infty} EX_t/t = n^{-1} \sum_{i=1}^{n} \bar{H}_i$.

Taking into account the slow rate of evolution in nature, Theorem 3.4 indicates the rarity with which the too advantageous mutation appears (see Fisher [10]). Although based on a different approach, this result agrees with Kimura [20] and [21] (see also [23] and [24]).

In cases when the distribution of the mutation may, in itself, be subject to a stabilizing selection (see Kimura [21], [22] and also Eshel [6]), it is of interest to prove the following proposition.

Proposition 3.5. If $\bar{F}_0 < \infty$, $\lim_{t\to\infty} G_t(x) = G(x)$ uniformly and $\bar{G}_t \to \bar{G}$, then $EX_t/t \to \bar{G}$.

Proof. Let us first suppose $\bar{G} < \infty$. Denote $t - k - 1 = n$. For n fixed, since λ^{nx} and $x\lambda^{nx}$ are continuous and bounded over $(-\infty, \bar{G}]$,

$$\lim_{tk\to\infty} EY_{t,t+k+1} = \lim_{t,k\to\infty} \left\{ \int_{-\infty}^{\bar{G}} x\lambda^{nx} dG_k(x) \Big/ \int_{-\infty}^{\bar{G}} \lambda^{nx} dG_k(x) \right\}$$

$$= \int_{-\infty}^{\bar{G}} x\lambda^{nx} dG(x) \Big/ \int_{-\infty}^{\bar{G}} \lambda^{nx} dG(x),$$

and on the other hand, when $t - k \to \infty$

$$\lim_{n\to\infty} \left\{ \int_{-\infty}^{\bar{G}} x\lambda^{nx} dG(x) \Big/ \int_{-\infty}^{\bar{G}} \lambda^{nx} dG(x) \right\} = \bar{G};$$

$$\lim_{t\to\infty} EY_{t,t+k+1} = \bar{G}_k; \quad \lim_{k\to\infty} \bar{G}_k = \bar{G}.$$

Given thus $\varepsilon > 0$, a number N exists such that for t and k with $N \leqq k < t - N$

$$\left| EY_{t,t+k+1} - \bar{G} \right| < \varepsilon.$$

Hence

$$\frac{1}{t} \sum_{k=N}^{t-N} \left| EY_{t,t+k+1} - \bar{G} \right| < \varepsilon.$$

In the case, $k < N$, since $\lim_{t\to\infty} \left| EY_{t,t+k+1} \right| = \left| \bar{G}_k \right| < \infty$, we get

$$\lim_{t\to\infty} \frac{1}{t} \sum_{k=0}^{N-1} \left| EY_{t,t+k+1} - \bar{G} = \right| 0.$$

For $k \geqq t - N$ we have

$$\bar{G} + (\bar{G}_t - \bar{G}) \geqq EY_{t,t+k+1} \geqq EY_{t\,t+k} = \int_{-\infty}^{\infty} x dG_t(x),$$

and

$$\lim_{t\to\infty} \int_{-\infty}^{\infty} x dG_t(x) = \int_{-\infty}^{\infty} x dG(x) > -\infty .$$

But $\lim_{t\to\infty}\{\bar{G}_t - \bar{G}\} = 0$, therefore

$$\lim_{t\to\infty} \frac{1}{t} \sum_{k=t-N}^{t-1} \left| EY_{t,t+k+1} - \bar{G} \right| = 0.$$

We have thus proved

$$\overline{\lim_{t\to\infty}} \frac{1}{t} \sum_{k=0}^{t-1} \left| EY_{t,t+k+1} - \bar{G} \right| \leqq \varepsilon \text{ for all } \varepsilon > 0,$$

so

$$\lim_{t\to\infty} \frac{1}{t} \sum_{k=0}^{t-1} \left| EY_{t,t+k+1} - \bar{G} \right| = 0.$$

We also know that $EZ_t/t \to 0$, so

$$\lim_{t\to\infty} EX_t/t = \lim_{t\to\infty} \left\{ EZ_t/t + \frac{1}{t} \sum_{k=0}^{t-1} EY_{t,t+k+1} \right\} = \bar{G}.$$

Suppose now that $\bar{G} = \infty$. For each real number r such that $G(r) > 0$

$$\begin{aligned} EY_{t,t+k+1} &= \int_{-\infty}^{\infty} x \lambda^{(t-k-1)x} dG_k(x) \Big/ \int_{-\infty}^{\infty} \lambda^{(t-k-1)x} dG_k(x) \\ &\geqq \int_{-\infty}^{r} x \lambda^{(t-k-1)x} dG_k(x) \Big/ \int_{-\infty}^{r} \lambda^{(t-k-1)x} dG_k(x) \end{aligned}$$

and, as $t \to \infty$, by Lemma A,

$$\lim_{t\to\infty} EY_{t,t+k+1} \geqq \mathrm{Min}(r, \bar{G}_k).$$

But $\bar{G}_k \to \infty$ and so $\lim_{t\to\infty} EY_{t,t+k+1} \geqq r$ for all r with $G(r) > 0$. We get $\lim_{t\to\infty} EY_{t,t+k+1} = \infty$ for all k, and by exactly the same method we used before:

$$\lim_{t\to\infty} EX_t/t = \infty .$$

Remarks. (i) The requirement $\bar{F}_0 < \infty$ is not needed for the case $\bar{G} = \infty$.
(ii) The conclusion of Proposition 3.5 may not hold without the condition $\bar{G}_t \to \bar{G}$.

Example. Let us have $X_0 \equiv 0$ and

$$G_t(x) = \begin{cases} 0, & x < 0, \\ 1 - 1/t + 1, & 0 \leqq x < 1, \quad t = 0, 1, 2, \cdots, \\ 1, & 1 \leqq x. \end{cases}$$

In this process

$$\lim_{t\to\infty} G_t(x) = G(x) = \begin{cases} 0, & x < 0, \\ 1, & x \geqq 0, \end{cases}$$

the rate of mutations tends uniformly to 0 as $t \to \infty$; the fitness distributions are bounded and yet the rate of evolution does not tend to $\bar{G} = 0$.

Proof. The mutation g.f.'s are: $\psi_t(s) = 1 + (s-1)/(t+1)$. From (3.4)

$$\phi_t(s) = \prod_{k=0}^{t-1} \frac{1+(k+1)^{-1}(s\lambda^{t-k-1}-1)}{1+(k+1)^{-1}(\lambda^{t-k-1}-1)} = \prod_{k=0}^{t-1} \frac{k+s\lambda^{t-k-1}}{k+\lambda^{t-k-1}},$$

$$EX_t = \sum_{k=0}^{t-1} \frac{\lambda^{t-k-1}}{k+\lambda^{t-k-1}},$$

and so

$$\begin{aligned} EX_{t+1} - EX_t &= \sum_{k=0}^{t-1} \frac{k(\lambda-1)\lambda^{t-k-1}}{(k+\lambda^{t-k})(k+\lambda^{t-k-1})} + \frac{1}{t+1} \\ &\geqq \frac{\lambda-1}{\lambda} \max_{0 \leqq k \leqq t} \frac{k\lambda^{t-k}}{(k+\lambda^{t-k})^2}. \end{aligned} \tag{3.14a}$$

For a given $t \geqq 1$, let $n = n(t)$ be the largest integer for which $n < \lambda^{t-n}$. Clearly $n \geqq 1$ (since $1 \leqq \lambda^{t-1}$) and also $n \leqq t$ (since $x > \lambda^{t-x}$ for all $x \geqq t$). Hence, from (3.14a):

$$EX_{t+1} - EX_t \geqq \frac{\lambda-1}{\lambda} \frac{n\lambda^{t-n}}{(n+\lambda^{\;\;n})^2}.$$

But from the definition of n, we know that $\lambda^{t-n} \geqq n$, and $\lambda^{t-n-1} < n+1$. We thus get

$$EX_{t+1} - EX_t \geqq \frac{\lambda-1}{\lambda} \frac{n^2}{[n+\lambda(n+1)]^2} \geqq \frac{\lambda-1}{\lambda(2\lambda+1)} > 0 \tag{3.15}$$

for all $t \geqq 1$, and

$$\underline{\lim}_{t\to\infty} (EX_{t+1} - EX_t) > 0.$$

This example is of interest by itself since it demonstrates a situation in which the distribution of the mutation tends uniformly to the trivial case of no mutation, and still the rate of evolution does not tend to zero.

4. Mean square and convergence-in-law of time-homogeneous processes

For most biological applications one is interested in relative fitnesses and their fluctuations about the mean, rather than in their absolute values. Thus, in this section we shall study the behavior of the relative fitness distribution.

$$H_t(x) = F_t(x + EX_t). \tag{4.1}$$

As before, this distribution is represented by the law of its relative fitness r.v., U_t defined by

$$U_t = X_t - EX_t = Z_t - EZ_t + \sum_{k=0}^{t-1} (Y_k - EY_k) \tag{4.2}$$

and by its g.f.,

$$\zeta_t(s) = \int_{-\infty}^{\infty} s^x dH_t(x) = s^{-EX_t}\phi_t(s). \tag{4.3}$$

Lemma B. If the rate of evolution is bounded (in particular, if the process is regular) then for all $1 \leqq a < b < \infty$ there is a constant c such that for all $t = 0, 1, 2, \cdots$ and $a \leqq s \leqq b$, $\zeta_t(s) \leqq c$.

Proof. $\zeta_t(s) \leqq 1 + \int_0^\infty s^x dH_t(x)$. The second term increases with s, so it is sufficient to prove equi-boundedness over the intervals $[1, \lambda^n]$ where n is any arbitrary integer.

For $t = 0, 1, 2, \cdots$

$$\phi_t'(s) = s^{EX_t}\zeta_t'(s) + EX_t s^{EX_t - 1}\zeta_t(s)$$

and so

$$\frac{s\zeta_t'(s)}{\zeta_t(s)} = \frac{s\phi_t'(s)}{\phi_t(s)} - EX_t.$$

Consider now a time-truncated process, starting from the tth generation of the original one. For the nth generation g.f. $\phi_{t+n}(s)$ of the truncated process, we get, as a special case of (3.6):

$$\phi_{t+n}(s) = \frac{\phi_t(\lambda^n s)}{\phi_t(\lambda^n)} \prod_{k=0}^{n-1} \frac{\psi(\lambda^k s)}{\psi(\lambda^k)},$$

and so

$$\begin{aligned} EX_{t+n} - EX_t &= \frac{\lambda^n \phi_t'(\lambda^n)}{\phi_t(\lambda^n)} - EX_t + \sum_{k=0}^{n-1} \frac{\lambda^k \psi'(\lambda^k)}{\psi(\lambda^k)} \\ &= \frac{\lambda^n \zeta_t'(\lambda^n)}{\zeta_t(\lambda^n)} + \sum_{k=0}^{n-1} \frac{\lambda^k \psi'(\lambda^k)}{\psi(\lambda^k)}. \end{aligned} \tag{4.4}$$

Let $M = \sup_t (EX_{t+1} - EX_t)$. Having assumed a bounded rate of evolution we know $M < \infty$ and $EX_{t+n} - EX_t \leqq nM$. From (4.4) we get

$$\frac{\lambda^n \zeta_t'(\lambda^n)}{\zeta_t(\lambda^n)} \leqq nM - \sum_{k=0}^{n-1} \frac{\lambda^k \psi'(\lambda^k)}{\psi(\lambda^k)} = c_n < \infty, \text{ say.} \tag{4.5}$$

Employing now the logarithmic convexity of the Laplace transform whenever it is defined on $[0,\infty)$, we infer the convexity of $\ln\zeta_t(\lambda^u)$ for all $u \geqq 0$. Equivalently:

$$\frac{d}{du}\ln\zeta_t(\lambda^u) = \frac{\lambda^u\zeta_t'(\lambda^u)}{\zeta_t(\lambda^u)}\ln\lambda \tag{4.6}$$

is thus monotonically increasing with u. For $0 \leqq u \leqq n$, inserting (4.5) we get:

$$\frac{d}{du}\ln\zeta_t(\lambda^u) \leqq \frac{\lambda^n\zeta_t'(\lambda^n)}{\zeta_t(\lambda^n)}\ln\lambda \leqq c_n\ln\lambda.$$

We know $\ln\zeta_t(\lambda^0) = 0$ and so for $0 \leqq u \leqq n$,

$$\ln\zeta_t(\lambda^n) \leqq uc_n\ln\lambda \leqq nc_n\ln\lambda.$$

For $1 \leqq s \leqq \lambda^n$, we get

$$\zeta_t(s) \leqq \lambda^{nc_n}$$

and this holds for all $t = 0, 1, 2, \cdots$.

Definition. The process $\{F_t(x)\}$ is said to be *converging* if a limit relative fitness distribution $F(x)$ exists such that

$$H_t(x) \to F(x) \qquad \text{in law.} \tag{4.7}$$

If, in addition,

$$\zeta_t(s) \to \zeta(s) = \int_{-\infty}^{\infty} s^x dF(x) < \infty \tag{4.8}$$

over all $[1,\infty)$, the process is said to be *strongly converging*.

Proposition 4.1. A converging process $\{F_t(s)\}$ is strongly converging iff its rate of evolution is bounded. In this case its rate of evolution also has a finite limit.

Proof. (a) If the rate of evolution is bounded, then for all $b > a \geqq 0$ the Laplace transforms $\zeta_t(e^u)$ are uniformly bounded over $[a,b]$ (Lemma B), $H_t(x) \to F(x)$ in law and so

$$\lim_{t\to\infty}\zeta_t(e^u) = \int_{-\infty}^{\infty} e^{ux}dF(x) = \zeta(e^u),$$

ay for all $u \geqq 0$. For $s \geqq 1$

$$\lim_{t\to\infty}\zeta_t(s) = \int_{-\infty}^{\infty} s^x dF(x).$$

(b) Suppose $\lim_{t\to\infty}\zeta_t(s) = \zeta(s) < \infty$ over $[1, \infty)$. From the analyticity of $\zeta_t(s)$ and $\zeta(s)$ we know that $\lim_{t\to\infty}\zeta_t'(s) = \zeta'(s) < \infty$ for all $s > 1$. By virtue of (4.5) we thus get:

$$\text{(4.9)} \qquad \lim_{t\to\infty}\{EX_{t+1} - EX_t\} = \lim_{t\to\infty}\frac{\lambda\zeta_t(\lambda)}{\zeta_t(\lambda)} + \psi'(1) = \frac{\lambda\zeta'(\lambda)}{\zeta(\lambda)} + \psi'(1) < \infty,$$

and we have also proved that the rate of evolution tends to a finite limit.

Let us assume convergence of the pure selection process, that is, convergence in law of $Z_t - EZ_t$. As implied from Lemma A this holds trivially for any initially regular process. Then the process $\{F_t(x)\}$ converges iff the sum $\sum_{k=0}^{\infty}(Y_k - EY_k)$ converges in law (immediately from (3.7)). By virtue of the 3-series theorem, this sum converges if the sum $\sum_{k=0}^{\infty}V(Y_k)$ of the variances converges (see, for example, Chung [2]). Since $V(X_t) = V(Z_t) + \sum_{k=0}^{t}V(Y_k)$, a sufficient condition for $\sum_{k=0}^{\infty}V(Y_k)$ converging, is the convergence of the sequence $\{V(X_t)\}_t$. In an initially regular process (and more generally, if the pure selection variance $V(Z_t)$ converges), this condition is also necessary.

The main theorem of this section is thus as follows.

Theorem 4.2. The variance $\sigma_t^2 = V(X_t)$ of a regular process of evolution tends to a finite limit $\sigma^2 < \infty$ as $t \to \infty$. Furthermore,

$$\text{(4.10)} \qquad \lim_{t\to\infty}H_t(x) = \lim_{t\to\infty}F_t(x - EX_t) = F(x)$$

in law, where $F(x)$ is a distribution function with mean 0 and variance σ^2.

Proof. We know

$$\sigma_t^2 = V(Z_t) + \sum_{k=0}^{t-1} V(Y_k)$$

where $\lim_{t\to\infty}V(Z_t) = 0$. Without loss of generality, we assume $X_0 = 0$ so that $V(Z_t) = 0$ for all t.

In this case, the sequence $\{\sigma_t\}_{t=0}^{\infty}$, being monotonic increasing, either converges or tends to ∞. Let us assume $\sigma_t \to \infty$ and show first that the sum $X_t \sum_{k=0}^{t-1} Y_k$ in law, satisfies the Lindeberg condition, that is, for all $\tau > 0$,

$$\text{(4.10a)} \qquad \lim_{t\to\infty}\frac{1}{\sigma_t^2}\sum_{k=0}^{t-1}\int_{|y-EY_k|>\tau\sigma}(y - EY_k)^2\,dG_k(y) = 0,$$

where $G_k(y)$ is the distribution of y_k, i.e.,

$$\text{(4.11)} \qquad G_k(y) = \frac{1}{\psi(\lambda^k)}\int_{-\infty}^{y}\lambda^{kx}\,dG(x).$$

Since by Lemma A, $\lim_{k\to\infty} EY_k = \bar{G}$, there is a number l_1 such that for $k \geqq l_1$,

$$\bar{G} < EY_k + \tau\sigma_0 \leqq EY_k + \tau\sigma_t \tag{4.12}$$

for all $t(\sigma_t \geqq \sigma_0)$.

But $\psi(\lambda^k) = \int_{-\infty}^{\bar{G}} \lambda^{kx} dG(x)$ and from (4.11) we have $G_k(\bar{G}) = 1$. Hence for all t and $k \geqq l_1$, using (4.12) we get

$$G_k(EY_k + \tau\sigma_t) = 1$$

and

$$\int_{EY_k+\tau\sigma}^{\infty} (y - EY_k)^2 dG_k(y) = 0.$$

For $k \geqq l_1$ and all t we thus have:

$$\begin{aligned} &\int_{|y-EY_k|>\tau\sigma_t} (y - EY_k)^2 dG_k(y) \\ (4.13)\qquad &= \int_{-\infty}^{EX_t-\tau\sigma_t} (y - EY_k)^2 dG_k(y) \leqq \int_{-\infty}^{\bar{G}-\tau\sigma_t} (\bar{G} - y)^2 dG_k(y) \\ &= \frac{1}{\psi(\lambda^k)} \int_{-\infty}^{\bar{G}-\tau\sigma_t} (\bar{G} - y)^2 \lambda^{ky} dG(y). \end{aligned}$$

Having assumed $\sigma_t = \infty$ we get

$$\lim_{t\to\infty} \sup_{y \leqq \bar{G}-\tau\sigma_t} \{(y - \bar{G})^2 \lambda^y\} = \lim_{y\to\infty} \{(y - \bar{G})^2 \lambda^y\} = 0.$$

It is thus possible to choose a value $T > 0$ such that, for all $t > T$,

$$\sup_{y \leqq \bar{G}-\tau\sigma_t} \{(y - \bar{G})^2 \lambda^y\} < 1 \tag{4.14}$$

and

$$\bar{G} - \tau\sigma_t < \bar{G} - 1. \tag{4.15}$$

From (4.14) and (4.15) we get

$$\sup_{y \leqq \bar{G}-\tau\sigma_t} (y - \bar{G})^2 \lambda^{ky} \leqq \sup_{y \leqq \bar{G}-\tau\sigma_t} \lambda^{(k-1)y} < \lambda^{(k-1)(\bar{G}-1)}$$

and so

$$\int_{-\infty}^{\bar{G}-\tau\sigma_t} (y - \bar{G})^2 \lambda^{ky} dG(y) < \lambda^{(k-1)(\bar{G}-1)}. \tag{4.16}$$

As an immediate result from Lemma A we get, for all $\varepsilon > 0$,

$$\lim_{s\to\infty} s^{\bar{G}-\varepsilon}/\psi(s) = 0,$$

and as a special case ($\varepsilon = 1$)

$$\lim_{k\to\infty} \frac{\lambda^{(k-1)(\bar{G}-1)}}{\psi(\lambda^k)} = \lambda^{1-\bar{G}} \lim_{k\to\infty} \frac{\lambda^{k(\bar{G}-1)}}{\psi(\lambda^k)} = 0. \tag{4.17}$$

From (4.13) and (4.17) we thus conclude, for all $t > T$ and $k > 1$,

$$\begin{aligned}\overline{\lim_{k\to\infty}} \int_{|y-EY_k|>\tau\sigma_t} & (y - EY_k)^2 dG_k(y) \\ & \leqq \overline{\lim_{k\to\infty}} \frac{1}{\psi(\lambda^k)} \int_{-\infty}^{\bar{G}-\tau\sigma_t} (\bar{G} - y)^2 \lambda^{ky} dG(y) \\ & \leqq \lim_{k\to\infty} \frac{\lambda^{(k-1)(\bar{G}-1)}}{\psi(\lambda^k)} = 0.\end{aligned}$$

A number l thus exists such that for $k > l$, $t > T$

$$\int_{|y-EY_k|>\tau\sigma_t} (y - EY_k)^2 dG_k(y) < \lambda^{2-\bar{G}-k}. \tag{4.18}$$

Denote

$$C_t = \sum_{k=0}^{l} \int_{|y-EY_k|>\tau\sigma_t} (y - EY_k)^2 dG_k(y).$$

The sequence $\{C_t\}$ is a decreasing sequence, and for $t > T$ (4.18) immediately indicates

$$\sum_{k=0}^{t} \int_{|y-EY_k|>\tau\sigma_t} (y - EY_k)^2 dG_k(y) \leqq C_t + \sum_{k=l}^{t} \lambda^{2-\bar{G}-k} \leqq C_t + \frac{\lambda^{2-\bar{G}}}{\lambda - 1} < \infty.$$

Under our assumption that $\sigma_t \to \infty$, the Lindeberg condition (4.10a) is immediately satisfied and we obtain that

$$U_t/\sigma_t \to N(0,1) \qquad \text{in law.}$$

For $s \geqq 1$,

$$\lim_{t\to\infty} \zeta_t(s^{1/\sigma_t}) = e^{\frac{1}{2}(\ln s)^2}$$

and since all g.f.'s converge on $[1, \infty)$

$$\begin{aligned}&\lim_{t\to\infty} \frac{1}{\sigma_t} s^{1/\sigma_t} \zeta_t'(s^{1/\sigma_t}) = e^{\frac{1}{2}(\ln s)^2} \ln s, \\ &\lim_{t\to\infty} \frac{s^{1/\sigma_t} \zeta_t'(s^{1/\sigma_t})}{\sigma_t \zeta_t(s^{1/\sigma_t})} = \ln s.\end{aligned} \tag{4.19}$$

From (4.6) it follows that $s\zeta_t'(s)/\zeta_t(s)$ is an increasing function of s. For a given $s > 1$ we now choose a number R such that for $t > R$, $\lambda > s^{1/\sigma_t}$ (we use again $\sigma_t \to \infty$) and so

$$\lim_{t\to\infty} \frac{\lambda\zeta_t'(\lambda)}{\sigma_t\zeta_t(\lambda)} \geqq \lim_{t\to\infty} \frac{s^{1/\sigma_t}\zeta_t'(s^{1/\sigma_t})}{\sigma_t\zeta_t(s^{1/\sigma_t})} = \ln s.$$

This may be done for all $s > 1$ and so

$$\lim_{t\to\infty} \frac{\lambda\zeta_t'(\lambda)}{\sigma_t\zeta_t(\lambda)} = \infty.$$

Since $\sigma_t \to \infty$ we get, even more strongly,

$$\lim_{t\to\infty} \lambda\zeta_t'(\lambda)/\zeta_t(\lambda) = \infty. \tag{4.20}$$

But as a special case of (4.4), with $n = 1$

$$EX_{t+1} - EX_t = \frac{\lambda\zeta_t'(\lambda)}{\zeta_t(\lambda)} + \psi'(1),$$

and by (4.20):

$$\lim_{t\to\infty} \{EX_{t+1} - EX_t\} = \infty \tag{4.21}$$

in a contradiction to Theorem (3.3).

This completes the proof of the first section of the theorem:

$$\sum_{k=0}^{\infty} V(Y_k) = \lim_{t\to\infty} \sigma_t = \sigma < \infty.$$

The convergence in law of the sum $\sum_{k=0}^{\infty} (Y_k - EY_k)$ is now implied by virtue of the 3-series theorem. From Lemma A we know $\lim_{t\to\infty}(Z_t - EZ_t) = 0$ and the convergence in law of the r.v.'s

$$U_t = Z_t - EZ_t + \sum_{k=0}^{t-1} (Y_k - EY_k)$$

follows immediately.

As an immediate result of Proposition 4.1 and Theorems 4.2 and 3.3 we have Corollary 4.3.

Corollary 4.3. (i) A regular process is strongly converging since it is converging and has a finite limit rate of evolution.

(ii) A strongly-converging process has a finite limit rate of evolution.

It must be mentioned, however, that not all strongly converging processes are regular (for example, take any process with bounded mutation and initial normal distribution, as previously described).

Corollary 4.4. A time homogeneous process with a bounded rate of evolution is converging (and thus, by Proposition 4.1, it is strongly converging) iff its associated pure selection process $\{Z_t\}_{t=0}^{\infty}$ is converging.

Proof. Since the rate of evolution is bounded, the mutation is bounded and hence the sum $\sum_{k=0}^{\infty} (Y_k - EY_k)$ converges in law by Theorem 4.2. Corollary 4.4 is thus immediately implied by the representation

$$U_t = X_t - EX_t = Z_t - EZ_t + \sum_{k=0}^{t-1} (Y_k - EY_k).$$

From the last two corollaries, together with Theorems 3.3 and 4.2 and Proposition 4.1, we immediately obtain Proposition 4.5.

Proposition 4.5. Under the assumption of initial regularity, i.e., a bounded fitness in the initial population, the following properties are equivalent:

(i) regularity; (ii) convergence; (iii) strong convergence;

(iv) bounded mutation; (v) bounded rate of evolution;

(vi) finite limit rate of evolution.

As we know from Theorem 4.2, a finite limit of the variance is a necessary condition for (i)–(vi). A still unsettled problem is whether it is also a sufficient condition.

Proposition 4.6. Let $\{F_t(x)\}$ be a strongly-converging process with M the limit rate of evolution, $\zeta(s)$ the limit g.f. and $\psi(s)$ the mutation g.f. Then

$$s^M\zeta(s) = \zeta(\lambda s)\psi(s)/\zeta(\lambda). \tag{4.22}$$

Proof.

$$\lim_{t\to\infty} s^{-EX_{t+1}}\phi_{t+1}(s) = \zeta(s).$$

But also

$$\begin{aligned} s^{-EX_{t+1}}\phi_{t+1}(s) &= s^{-EX_{t+1}}\phi_t(\lambda s)\psi(s)/\phi_t(\lambda) \\ &= s^{-(EX_{t+1}-EX_t)}(\lambda s)^{-EX_t}\phi_t(\lambda s)\psi(s)/\lambda^{-EX_t}\phi_t(\lambda), \end{aligned} \tag{4.23}$$

and the limit of this as $t \to \infty$ is

$$s^{-M}\zeta(\lambda s)\psi(s)/\zeta(\lambda).$$

Remark. If the process is regular, (4.22) becomes

$$s^G\zeta(s) = \zeta(\lambda s)\psi(s)/\zeta(x). \tag{4.22$'$}$$

In the general case of a converging rate of evolution we have, as an immediate result of identity (2.4):

$$M = \lim_{t\to\infty} (EX_{t+1} - EX_t) = \bar{G} + \lim_{t\to\infty} (EZ_{t+1} - EZ_t).$$

Notation. (i) R.v.'s X and Y are said to be shifting congruent $(X \sim Y)$ if $X = Y + r$ for some real r. Analagously, for g.f.'s

(4.24) $$\phi \sim \psi \Leftrightarrow \phi(s) = s^r \psi(s).$$

(ii) Any g.f. congruent to a limit g.f. of a strongly converging process (i.e., a limit g.f. converging over $[1, \infty)$) is called a *limit g.f.* If the process is regular, we speak about a *regular limit g.f.*

If $\psi(s)$ is the mutation g.f. of the process, we say that the limit g.f. is generated by $\psi(s)$.

As an immediate result of Proposition 4.6 we obtain Proposition 4.7.

Proposition 4.7. For any limit g.f. $\zeta(s)$, the mutation g.f. $\psi(s)$ by which it is generated is uniquely determined up to a shifting congruence

(4.25) $$\psi(s) \sim \frac{\zeta(\lambda)\zeta(s)}{\zeta(\lambda s)} = R\zeta(s), \qquad \text{say}.$$

The transformation R maps the set of all limit g.f.'s onto the set of all congruence classes of bounded g.f.'s.

The following three propositions indicate that this is a 1–1 mapping, up to a shift.

Proposition 4.8. (i) If $\zeta \sim \zeta_1$ and ζ is a limit g.f., then $R\zeta_1 = R\zeta$, i.e.,

(4.26) $$R(s^r\zeta(s)) = R(\zeta(s)).$$

(ii) If $\zeta = \zeta_1\zeta_2$, ζ_1 and ζ_2 are limit g.f.'s, then $R\zeta = R\zeta_1 R\zeta_2$

Proof. The proof is immediate from (4.25).

Definition. For any g.f. $\psi(s)$ which is converging over $[1, \infty)$, let us define

(4.27) $$T\psi(s) = \prod_{k=0}^{\infty} s^{-\lambda^k\psi'(\lambda^k)/\psi(\lambda^k)} \frac{\psi(\lambda^k s)}{\psi(\lambda^k)}$$

provided the right hand side converges.

Proposition 4.9. (i) $T\psi(s)$ is a probability g.f. which converges for all s in $[1, \infty)$ iff $\psi(s)$ belongs to a r.v. which is bounded from above (henceforth, a *bounded generating function*).

(ii) If $\{F_t(x)\}$ is any converging, initially regular process with a mutation g.f. $\psi(s)$, then $\zeta(s) = T\psi(s)$ is its limit g.f. whenever it converges.

As a special case, $T\psi(s)$ is the limit g.f. of a regular process with a mutation g.f. $\psi(s)$.

Proof. For an initially regular process $\{F_t(x)\}$ we have:

$$\zeta_t(s) = s^{-EZt}\ \frac{\phi_0(\lambda^t s)}{\phi_0(\lambda^t)} \prod_{k=0}^{t-1} s^{-EY_k}\frac{\psi(\lambda^k s)}{\psi(\lambda^k)}$$

where $EY_k = \lambda^k\psi'(\lambda^k)/\psi(\lambda^k)$. Immediately from Lemma A (since $\bar{F}_0 < \infty$) we find that

$$\lim_{t\to\infty} s^{-EZ_t}\frac{\phi_0(\lambda^t s)}{\phi_0(\lambda^t)} = 1$$

for all $s \geqq 1$, and so, whenever the limit g.f. $\zeta(s)$ exists, we have

$$\zeta(s) = \prod_{k=0}^{\infty} s^{-EY_k}\frac{\psi(\lambda^k s)}{\psi(\lambda^k)} = T\psi(s).$$

From Proposition 4.1 we know that $\zeta(s) = T\psi(s)$ converges over $[1, \infty)$ if the rate of evolution is bounded. For an initially regular process, this is the case (Theorem 3.3) iff the mutation r.v. corresponding to $\psi(s)$ is bounded.

By a routine calculation one may prove Proposition 4.10.

Proposition 4.10. For all g.f.'s ψ_1, ψ_2 and a real number r,

$$T(\psi_1\psi_2) = T\psi_1 T\psi_2, \tag{4.28}$$

$$T((\psi(s))^r = (T\psi(s))^r, \tag{4.29}$$

$$\psi_1 \sim \psi_2 \Rightarrow T\psi_1 = T\psi_2, \tag{4.30}$$

whenever these terms are well defined.

Theorem 4.11. The transformations T and R define a 1-1 correspondence (up to a shifting congruence) between the set of all regular limit g.f.'s and that of all bounded g.f.'s. Furthermore, for all bounded g.f. ψ

$$RT\psi \sim \psi, \tag{4.31}$$

and for all regular limit g.f. ζ

$$TR\zeta = \zeta. \tag{4.32}$$

Proof. The proof follows immediately from Corollary 4.7 and Propositions 4.8–4.10. The strict equality in (4.32) is implied by the fact that both sides belong to zero-mean r.v.'s.

5. Relations between limit-distributions of the fitness and time-homogeneous distributions of the mutation

Employing the basic transformations T and R, we now develop criteria to determine whether a given distribution of fitness is, in fact, a stable limit of a time-homogeneous process of evolution, especially whether it is a limit of a regular process. By considering the image RA of a class A of limit distributions, we then attempt to draw some general information about the distribution of the mutation allowing the limit to be in this class. As a special case we concentrated on a general mutation law that allows bounded-from-above fitness-distributions in the limit. Finally, a certain continuity feature of the transformations T and R will be checked in order to apply the theoretical findings of this section to possible statistical data.

5.1. *Basic Criteria.*

Let us denote by Γ the class of bounded g.f.'s, i.e., g.f.'s belonging to r.v.'s which are bounded from above (henceforth *bounded g.f.'s*). By Γ^+ we mean the class of all g.f.'s which are finite on $[1,\infty)$. We further denote by Ω the class of all regular limit g.f.'s and by Ω^+ the class of all limit g.f.'s. Clearly

$$\Omega = T\Gamma \subset \Omega^+ \subset \Gamma^+.$$

Let $\tilde{\phi}$ be the congruence class of a g.f. ϕ, due to shiftings of the r.v. Respectively, for a set A of g.f.'s, let $\tilde{A} = \{\tilde{\phi} \mid \phi \in A\}$ be the corresponding set of the congruence classes.

Applying Propositions 4.8 and 4.10 we define the class transformations $\tilde{T}$ and $\tilde{R}$ by $\tilde{T}\tilde{\psi} = \widetilde{T\psi}$ and $\tilde{R}\tilde{\zeta} = \widetilde{R\zeta}$. Theorem 4.11 indicates

$$\tilde{T}\tilde{R}: \tilde{\Omega}^+ \xrightarrow{\text{onto}} \tilde{\Omega}. \tag{5.1}$$

Furthermore, $\tilde{T}\tilde{R}/\tilde{\Omega}$ is the identity transformation on $\tilde{\Omega}$. Similarly, $\tilde{R}\tilde{T}$ is the identity on $\tilde{\Gamma}$. Using this we have Criterion A.

Criterion A. A converging g.f. ζ is a limit g.f. of a time homogeneous process iff $R\zeta(s)$ is finite for all $s \geqq 1$. Furthermore, in this case $R\zeta$ is a g.f. of a bounded-from-above r.v.

Proof. In a formal way, Criterion A may be written as

$$\tilde{\Omega}^+ = \tilde{R}^{-1}\tilde{\Gamma}^+ = \tilde{R}^{-1}\tilde{\Gamma}. \tag{5.2}$$

Since $\tilde{R}: \tilde{\Omega}^+ \to \tilde{\Gamma} \subseteq \tilde{\Gamma}^+$, we know that $\tilde{\Omega}^+ \subseteq \tilde{R}^{-1}\tilde{\Gamma} \subseteq \tilde{R}^{-1}\tilde{\Gamma}^+$. Assume, on the other hand, $\tilde{R}\tilde{\zeta} \in \tilde{\Gamma}^+$. In order to show $\tilde{\zeta} \in \tilde{\Omega}^+$, let us observe a time-homogeneous process with an initial g.f. $\phi_0(s) = \zeta(s)$ and a mutation g.f. $\psi(s) = R\zeta(s) = \zeta(\lambda)\zeta(s)/\zeta(\lambda s)$. Since both ϕ_0 and ψ are finite on $[1,\infty)$, the process is lasting (Theorem 3.1). Thus from (3.6) it follows that for all $t = 0, 1, 2, \cdots$

$$\begin{aligned}\phi_t(s) &= \frac{\zeta(\lambda s)}{\zeta(\lambda)} \prod_{k=0}^{t-1} \frac{R\zeta(\lambda^k s)}{R\zeta(\lambda^k)} \\ &= \frac{\zeta(\lambda s)}{\zeta(\lambda)} \prod_{k=0}^{t-1} \frac{\zeta(\lambda^k s)\zeta(\lambda^{k+1})\zeta(\lambda)}{\zeta(\lambda^{k+1})\zeta(\lambda^k)\zeta(\lambda)} = \zeta(s).\end{aligned} \tag{5.3}$$

The requirement $\lim_{t\to\infty} \phi_t(s) = \zeta(s)$ is trivially satisfied, the rate of evolution, being identically 0, is indeed bounded, and therefore $\tilde{\zeta} \in \tilde{\Omega}^+$. We have thus proved $\tilde{R}^{-1}\tilde{\Gamma}^+ \subseteq \tilde{\Omega}^+$ and this completes the proof.

Proposition 5.1. A converging g.f. ζ is a regular limit g.f. iff $TR\zeta \in \Gamma^+$.

Proof. Formally, the proposition may be written as:

$$\tilde{\Gamma}^+ = \tilde{T}\tilde{R}\tilde{\Gamma}^+ = \tilde{\Omega}. \tag{5.4}$$

From Proposition 4.3 we know that $TR\zeta$ converges for all $s \geqq 1$ iff $R\zeta \in \Gamma$. As we know from Criterion A, this holds iff $\tilde{\zeta} \in \tilde{\Omega}^+$. Employing (5.1), this implies $\tilde{T}\tilde{R}\tilde{\zeta} \in \tilde{\Omega}$. We have thus proved $\Gamma^+ \subseteq \tilde{T}\tilde{R}\tilde{\Gamma}^+ \subseteq \tilde{\Omega}$. On the other hand, since $\Omega \subset \tilde{\Gamma}^+$ and $\Omega = TR\Omega \subseteq TR\Gamma^+, \Omega \subseteq \Gamma^+ \subseteq TR\Gamma^+$ and (5.4) immediately follows.

As an immediate result of Proposition 5.1 we get Criterion B.

Criterion B. A converging g.f. ζ is a regular limit g.f. iff $TR\zeta \sim \zeta$.

Proof. From (4.32) we already know that if $\tilde{\zeta} \in \tilde{\Omega}$ then $\tilde{T}\tilde{R}\tilde{\zeta} \in \tilde{\Omega}$. If, on the other hand, $\tilde{T}\tilde{R}\tilde{\zeta} = \zeta \in \tilde{\Gamma}^+$, we get $\zeta \in \tilde{\Gamma}^+ = \tilde{T}\tilde{R}\tilde{\Gamma}^+$ and by Proposition 5.1 $\tilde{\zeta} \in \tilde{\Omega}$. Since $\tilde{T}\tilde{R}$ is the identity-transformation on $\tilde{\Omega}$, this completes the proof.

Let us denote by Δ the class of all converging g.f.'s χ with $R\chi \sim 1$. In other words, Δ is the class of all limit g.f.'s generated by the trivial mutation g.f. $\psi(s) \equiv 1$. We call such g.f.'s trivial limit g.f.'s.

Examples. (i) The normal g.f. $\chi(s) = e^{\frac{1}{2}(\ln s)^2}$ is a trivial limit g.f. since

$$R\chi(s) = e^{\frac{1}{2}(\ln s)^2} + \tfrac{1}{2}(\ln\lambda)^2 - \tfrac{1}{2}(\ln\lambda + \ln s)^2 = s^{-\ln\lambda} \sim 1.$$

(ii) The trivial g.f. $\chi(s) \equiv 1$ is, up to a shifting factor, the only trivial limit g.f. which is also a regular limit g.f.

Criterion C. A converging g.f. is a limit g.f. iff it is a product of a regular limit g.f., to be called its *regular component*, and a trivial limit g.f., to be called its *non-regular* component. Futhermore, these components are uniquely determined up to a shift transformation of their r.v.'s.

Proof. (i) Assume $\tilde{\zeta} \in \tilde{\Omega}^+$, then we define $\zeta_1 = TR\zeta$. From Theorem 4.11 we know $\zeta_1 \in \Omega$. For all $s \geqq 1$, $\zeta_1(s) > 0$ and, thus, we may define

$$\chi(s) = \frac{\zeta(s)}{\zeta_1(s)} = \frac{\zeta(s)}{TR\zeta(s)},$$

$$R\chi(s) = \frac{\chi(\lambda)\chi(s)}{\chi(\lambda s)} = \frac{TR\zeta(\lambda s)\zeta(\lambda)\zeta(s)}{\zeta(\lambda s)TR\zeta(\lambda)TR\zeta(s)} = \frac{R\zeta(s)}{R\{TR\zeta(s)\}} \sim 1,$$

and thus $\chi \in \Delta$. Clearly $\zeta = \chi\zeta_1$.

(ii) Let $\zeta = \chi\zeta_1$ where $\zeta_1 \in \Omega$ and $\chi \in \Delta$. The requirement $\chi \in \Delta$ means that a real value r exists such that for all $s \geqq 1$

$$R\chi(s) = \frac{\chi(\lambda)\chi(s)}{\chi(\lambda s)} = s^r \sim 1.$$

As before, we consider an auxiliary process with an initial g.f. $\phi_0(s) = \zeta(s)$ and with a mutation g.f. $\psi(s) = s^{-r}R\zeta_1(s) = s^{-r}\zeta_1(s)\zeta_1(\lambda)/\zeta_1(\lambda s)$.

In such a process:

$$ {}_1(s) = \frac{\zeta(\lambda s)\psi(s)}{\zeta(\lambda)} = s^{-r}\,\frac{\chi(\lambda s)\zeta_1(\lambda s)\zeta_1(\lambda)\zeta_1(s)}{\chi(\lambda)\zeta_1(\lambda)\zeta_1(\lambda s)}$$

$$= s^{-r}\frac{\chi(\lambda s)}{\chi(\lambda)}\zeta_1(s) = \chi(s)\zeta_1(s) = \zeta(s).$$

By iterations we get, for all $t = 0, 1, 2, \cdots;\ \phi_t(s) = \zeta(s)$, and trivially, ζ is a limit g.f.

(iii) To prove uniqueness assume, as before, $\zeta = \chi\zeta_1$, $\tilde{\chi} \in \tilde{\Delta}$, $\tilde{\zeta}_1 \in \tilde{\Omega}$. From Proposition 4.8 we know $R\zeta = R\chi R\zeta_1 \sim R\zeta_1$. From Proposition 4.10 and Theorem 4.11 it thus follows that $TR\zeta = TR\zeta_1 \sim \zeta_1$ and $\chi \sim \zeta/TR\zeta$.

Examples. (i) The negative Poisson g.f. $\zeta(s) = \exp c(s^{-1} - 1)$ is a regular limit g.f.

Proof. By Criterion B:

$$R\zeta(s) = \exp c\left\{\left(\frac{1}{s} - 1\right) + \left(\frac{1}{\lambda} - 1\right) - \left(\frac{1}{\lambda s} - 1\right)\right\} = \exp\left\{c\frac{\lambda - 1}{\lambda}\left(\frac{1}{s} - 1\right)\right\}.$$

This is again a negative Poisson g.f. with a parameter $c(\lambda - 1)\lambda^{-1}$.

$$TR\zeta(s) = \prod_{k=0}^{\infty} s^{c(\lambda-1)\lambda^{-k-1}}\,\frac{\psi(\lambda^k s)}{\psi(\lambda^\lambda)}$$

$$= s^{-c/\lambda}\prod_{k=0}^{\infty}\exp\left\{\frac{c(\lambda - 1)}{\lambda^{k+1}}\left(\frac{1}{s} - 1\right)\right\} \sim \exp c\left(\frac{1}{s} - 1\right) = \zeta(s).$$

(ii) The Poisson g.f. $\zeta(s) = \exp c(s - 1)$ is not a limit g.f. (and clearly not a regular limit g.f.).

Proof. By Criterion A:

$$R\zeta(s) = \exp c(\lambda - 1)(1 - s).$$

Since $1 < R\zeta(0) = \exp c(\lambda - 1) < \infty$, this cannot be a probability g.f. (For all p.g.f.'s $\chi(s)$, $\lim_{s\downarrow 0}\chi(s) = \infty$ if $p(x < 0) > 0$, or $\lim_{s\downarrow 0}\chi(s) = p(x = 0) \leqq 1$ if $p(x < 0) = 0$.)

(iii) $\zeta(s) = \exp\{(\ln s)^2 + s^{-1} - 1\}$ is a limit g.f. but not a regular one.

Proof.

$$\begin{aligned} R\zeta(s) = {} & \exp\left\{(\ln s)^2 + \frac{1}{s} - 1 + (\ln\lambda)^2 + \frac{1}{\lambda} - 1 \right. \\ & \left. - (\ln\lambda s)^2 - \frac{1}{\lambda s} + 1\right\} \\ = {} & s^{-2\ln\lambda}\exp\left\{\frac{\lambda - 1}{\lambda}\left(\frac{1}{s} - 1\right)\right\} \sim \exp\left\{\frac{\lambda - 1}{\lambda}\left(\frac{1}{s} - 1\right)\right\}, \end{aligned}$$

which is a probability g.f. (a negative Poisson g.f.). By Criterion A, $\zeta(s)$ is thus a limit g.f. Yet

$$TR\zeta(s) \sim \exp\left\{\frac{1}{s} - 1\right\} \nsim \zeta(s).$$

By Criterion B, $\zeta(s)$ is not a *regular* limit g.f.

Clearly, we get $\zeta(s) = \chi(s)\zeta_1(s)$ (Criterion C), where

$$\zeta_1(s) \sim TR\zeta(s) = \exp\left\{\frac{1}{s} - 1\right\} \in \Gamma$$

and

$$\chi(s) = \frac{\zeta(s)}{\zeta_1(s)} = \exp(\ln s)^2 \in \Delta.$$

5.2. *Perfect Processes.*

The regularity condition (boundedness of the mutation and of the initial fitness) is equivalent to the boundedness of the relative fitness of each generation. Yet uniform boundedness, as well as boundedness of relative fitness in the limit, is not implied by the regularity conditions alone. Since fitness-boundedness from above has been amply assumed in this work let us introduce the following definition.

Definition. A regular process of evolution is said to be *perfect* if its limit distribution is bounded from above. The g.f. of such a limit distribution is said to be a *perfect limit g.f.*

Denote by Ω^- the class of all perfect limit g.f.'s. From the definition, $\Omega^- = \Omega \cap \Gamma$.

By $\Gamma^- = R\Omega^-$ we denote the class of all mutation g.f.'s which generate perfect processes. Our first objective in this section is to characterize this class; i.e., to characterize a perfect process by its law of mutation.

For this we use the following lemma.

Lemma C. In a regular process of evolution

$$\lim_{t\to\infty} \bar{H}_t = \lim_{t\to\infty} \bar{F}_t - EX_t = \bar{F}. \tag{5.5}$$

Remark. Because $H_t(x) \to F(x)$ in law it clearly follows that

$$\underline{\lim}_{t\to\infty} \bar{H}_t \geqq \bar{F}.$$

Yet, in general, convergence in law alone does not imply:

$$\overline{\lim}_{t\to\infty} \bar{H}_t \geqq \bar{F}.$$

We shall prove the latter for the special case of a time-homogeneous process of evolution.

Proof. From (3.3) it follows that

$$\bar{H}_t = \bar{F}_t - EX_t = \bar{F}_0 + \bar{G}t - EZ_t - \sum_{k=0}^{t-1} Y_k.$$

Having $\lim_{t\to\infty}\{\bar{F}_0 - EZ_t\} = 0$ (Lemma A), it is sufficient to prove

$$\lim_{t\to\infty} \left\{\bar{G}t - \sum_{k=0}^{t-1} EY_k\right\} = \bar{F}. \tag{5.6}$$

For this aim, consider a process $\{F_t^*(x)\}$ with the same law of mutation and with the limit distribution $F(x)$ as an initial fitness distribution. For this new process, let X_t^* and ϕ_t^* be the t-generation fitness r.v. and fitness g.f. respectively. By definition $\phi_0(s) = \zeta(s)$. Furthermore, by employing the identity

$$\frac{\zeta(\lambda s)\psi(s)}{\zeta(\lambda)} = s^{\bar{G}}\zeta(s)$$

and by an iterating use of:

$$\phi_{t+1}^*(s) = \frac{\phi_t^*(\lambda s)\psi(s)}{\phi_t^*(\lambda)},$$

the identity

$$\phi_t^*(s) = s^{t\bar{G}}\zeta(s) \tag{5.7}$$

follows immediately. In terms of r.v.'s this is

$$X_0^* + \bar{G}t = X_t^* = Z_t^* + \sum_{k=0}^{t-1} Y_k$$

where Z_t^* is the t-generation fitness r.v. of the pure selection process, starting with X_0^*.

Since $EX_0^* = 0$ we thus get

$$\bar{G}t - \sum_{k=0}^{t-1} EY_k = EZ_t^*.$$

From Lemma A we know $\lim_{t\to\infty} EZ_t^* = \bar{F}$, and (5.6) follows immediately.

Corollary 5.2. An initially regular process of evolution with a distribution $G(y)$ of the mutations is perfect if and only if

$$\sum_{k=0}^{\infty} (\bar{G} - EY_k) < \infty .$$

Proof. As an immediate consequence of Lemma C,

$$\bar{F} = \lim_{t\to\infty} \bar{H}_t = \lim_{t\to\infty} \left\{ \bar{F}_0 - EZ_t + \bar{G}t - \sum_{k=0}^{t-1} EY_k \right\}$$

$$= \lim_{t\to\infty} (\bar{F} - EZ_t) + \lim_{t\to\infty} \sum_{k=0}^{t-1} (\bar{G} - EY_k) = \sum_{k=0}^{\infty} (\bar{G} - EY_k).$$

Corollary 5.3. A mutation g.f. $\psi \in \Gamma$ generates a perfect process (i.e., $\psi \in \Gamma^-$) iff:

$$T\psi(s) \sim \prod_{k=0}^{\infty} \frac{\psi(\lambda^k s)}{s^{\bar{G}}\psi(\lambda^k)} . \tag{5.8}$$

Furthermore, the right hand side of (5.8) converges for all $s \geqq 1$ to a non-zero value iff $\psi \in \Gamma^-$.

Proof. For all $s \geqq 1$ we clearly have $s^{\bar{G} - EY_k} \geqq 1$ and $\psi(\lambda^k s)/s^{\bar{G}}\psi(\lambda^k s) \leqq 1$. Assume $\psi \in \Gamma^-$, then $\sum_{k=0}^{\infty} (\bar{G} - EY_k) < \infty$, and thus we get

$$T\psi(s) = s^{\sum_{k=0}^{\infty}(\bar{G} - EY_k)} \prod_{k=0}^{\infty} \frac{\psi(\lambda^k s)}{s^{\bar{G}}\psi(\lambda^k)} \sim \prod_{k=0}^{\infty} \frac{\psi(\lambda^k s)}{s^{\bar{G}}\psi(\lambda^k)} .$$

On the other hand, if $\sum_{k=0}^{\infty} (\bar{G} - EY_k) = \infty$, we have

$$\prod_{k=0}^{\infty} \frac{\psi(\lambda^k s)}{s^{\bar{G}}\psi(\lambda^k)} = 0 \nsim T\psi(s).$$

By Corollary 5.2, this completes the proof.

Definition. A bounded distribution $G(x)$ is said to be *jump-bounded* if $P(Y = \bar{G}) > 0$, where Y is a r.v. distributed $\bar{G}(x)$. Respectively, we speak about a *jump-bounded* g.f.

Theorem 5.4 (*The Theorem of Perfect Evolution*). (i) Γ^- is the class of all jump-bounded g.f.'s. In other words, a process of evolution is perfect iff it is regular and there is a positive probability for the maximal mutation $\bar{G}$.

(ii) If Y is the mutation r.v. of a perfect process of evolution, then

$$P(Y = \bar{G}) = \lambda^{-\bar{F}}\zeta(\lambda). \tag{5.9}$$

Proof. For a regular process $\{F_t(x)\}$, define the associated process $\{F_t^*(x)\}$ in the same way as in the proof of Lemma C, i.e., with $F_0^* = F$ and with the original distribution of the mutation. From (5.7) we get, for all real r, $F_0^*(r) = F_1^*(r + \bar{G})$, hence:

$$\begin{aligned} 1 - F(r) &= 1 - F_0^*(r) = 1 - F_1^*(r + \bar{G}) \\ &= \frac{1}{\zeta(\lambda)} \int_r^\infty \lambda^u G(r + \bar{G} - u)dF(u) \\ &= \frac{1}{\zeta(\lambda)} \int_r^\infty \lambda^u [1 - G(r + \bar{G} - u)]dF(u) \\ &= \frac{1}{\zeta(\lambda)} \int_r^\infty \lambda^u P(Y \geqq r + \bar{G} - u)dF(u) \\ &\geqq \frac{\lambda^r}{\zeta(\lambda)} \int_r^\infty P(Y = \bar{G})dF(u) \\ &= \frac{\lambda^r}{\zeta(\lambda)} P(Y = \bar{G})[1 - F(r)]. \end{aligned} \tag{5.10}$$

For all $r < \bar{F}$, $1 - F(r) > 0$, and from (5.10) we obtain,

$$P(Y = \bar{G}) \leqq \lim_{R \to \bar{F}} \lambda^{-r}\zeta(\lambda) = \lambda^{-\bar{F}}\zeta(\lambda). \tag{5.11}$$

If we denote $\lambda^\infty = \infty$ and $1/\infty = 0$, this also includes the non-perfect case

$$\bar{F} = \infty \Rightarrow P(Y = \bar{G}) = 0. \tag{5.11a}$$

If on the other hand, $\bar{F} < \infty$, let us choose $r = \bar{F} - \varepsilon$. We then get

$$\begin{aligned} 1 - F(\bar{F} - \varepsilon) &= \frac{1}{\zeta(\lambda)} \int_{\bar{F}-\varepsilon}^{\bar{F}} \lambda^u P(Y \geqq \bar{F} - \varepsilon + \bar{G} - u)dF(u) \\ &\leqq \frac{\lambda^{\bar{F}}}{\zeta(\lambda)} \int_{\bar{F}-\varepsilon}^{\bar{F}} P(Y \geqq \bar{G} - \varepsilon)dF(u) \\ &= \frac{\lambda^{\bar{F}}}{\zeta(\lambda)} P(Y \geqq \bar{G} - \varepsilon)[1 - F(\bar{F} - \varepsilon)]. \end{aligned} \tag{5.12}$$

Since $1 - F(\bar{F} - \varepsilon) > 0$ for all $\varepsilon > 0$, it follows that

$$P(Y \geqq \bar{G} - \varepsilon) \geqq \lambda^{-\bar{F}} \zeta(\lambda).$$

Thus

$$P(Y = \bar{G}) = \lim_{\varepsilon \downarrow 0} P(Y \geqq \bar{G} - \varepsilon) \geqq \lambda^{-\bar{F}} \zeta(\lambda)$$

and this completes the proof.

For an application of Theorem 5.4 to the situation of mutation-selection balance and accumulation of deleterious mutants, the reader is referred to [4].

5.3. *Continuity of the Transformations. Almost Regular Limit G.F.'s.*

Let $\Phi(n, s)$ be a consistent n-sample estimate of a limit fitness g.f. $\zeta(s)$; i.e., $P\{\lim_{n\to\infty} \Phi(n, s) = \zeta(s)\} = 1$. Naturally, we are interested in the following questions:

(i) is $R\Phi(n, s)$ a consistent estimate of the mutation g.f. $\psi(s) = R\zeta(s)$; or, *vice versa,*

(ii) is $T\psi(n, s)$ a consistent estimate of the limit fitness g.f. when $\psi(n, s)$ is a consistent estimate of the mutation g.f. of the process?

To answer these questions, let us assume the point-convergence weak topology over Γ^+.

Proposition 5.5. R is a continuous mapping of Ω^+ on Γ.

Proof. Assume $\zeta_n \to \zeta$; ζ, $\zeta_n \in \Omega^+$. Having $\zeta_n(\lambda s) \to \zeta(\lambda s) > 0$ for all $s \geqq 1$ we get

$$\lim_{n\to\infty} R\zeta_n(s) = \lim_{n\to\infty} \frac{\zeta_n(\lambda)\zeta_n(s)}{\zeta_n(\lambda s)} = \frac{\zeta(\lambda)\zeta(s)}{\zeta(\lambda s)} = R\zeta(s), \tag{5.14}$$

for all $s \geqq 1$.

Proposition 5.6. T is not a continuous transformation from Γ to Ω^+.

Proof. Let us assume a generalized Poisson distribution of deleterious mutations, each with the same effect $-\varepsilon$ on the fitness:

$$P(Y = -n\varepsilon) = e^{-1/\varepsilon}\varepsilon^{-n}/n!$$

and

$$\psi_\varepsilon(s) = \exp\{1/\varepsilon(s^{-\varepsilon} - 1)\}. \tag{5.15}$$

Since the process is perfect, we obtain ((5.8) with $\bar{G} = 0$)

$$\begin{aligned} T\psi_\varepsilon(s) &= \zeta_\varepsilon(s) \sim \prod_{k=0}^{\infty} \frac{\psi_\varepsilon(\lambda^k s)}{\psi_\varepsilon(\lambda^k)} = \exp\left\{\sum_{k=0}^{\infty} \frac{1}{\varepsilon}\lambda^{-k\varepsilon}(s^{-\varepsilon} - 1)\right\} \\ &= \exp\left\{\frac{\lambda^\varepsilon}{\varepsilon(\lambda^\varepsilon - 1)}(s^{-\varepsilon} - 1)\right\} \sim \exp\left\{\frac{\lambda^\varepsilon}{\varepsilon(\lambda^\varepsilon - 1)}(s^{-\varepsilon} - 1 + \varepsilon \ln s)\right\} \\ &= \zeta_\varepsilon^*(s), \text{ say}. \end{aligned}$$

In fact, we know $\zeta_\varepsilon'(1) = 0$ and it may also be shown that $\zeta_\varepsilon^{*\prime}(1) = 0$. Hence,

$$\zeta_\varepsilon(s) = \zeta_\varepsilon^*(s) = \exp\left\{\frac{\lambda^\varepsilon}{\varepsilon(\lambda^\varepsilon - 1)}(s^{-\varepsilon} - 1 + \varepsilon \ln s)\right\}. \tag{5.16}$$

As $\varepsilon \downarrow 0$ this gives the limit $(\ln s)^2 \exp\{-2\ln\lambda\}$ which is the g.f. of the normal distribution $N(0, 1/\ln\lambda)$.

On the other hand, for all $s \geqq 1$,

$$\lim_{\varepsilon\downarrow 0} \psi_\varepsilon(s) = \lim_{\varepsilon\downarrow 0} \exp\frac{1}{\varepsilon}(s^{-\varepsilon} - 1) = s^\alpha \sim 1$$

and from this, in conjunction with (5.16), we have

$$T(\lim_{\varepsilon\downarrow 0} \psi_\varepsilon(s)) = T(s^\alpha) = T(1) = 1 \nsim \exp\left\{\frac{(\ln s)^2}{2\ln\lambda}\right\} = \lim_{\varepsilon\downarrow 0} T\psi_\varepsilon(s).$$

The last two propositions provide a positive answer to question (i) and a negative answer to question (ii): a consistent estimation of a stable-shape fitness distribution may provide consistent information about the law of the mutation, but not *vice versa.*

As it has appeared in the proof of Proposition (5.6), a non-regular limit g.f. like the normal one (see also an example to Criterion B), may be approached as closely as possible by regular or even by perfect g.f.'s.

Definition. A converging g.f. is said to be *almost regular* if it is in the closure $\mathrm{cl}(\Omega)$ of the regular limit g.f.'s. Similarly, one may speak about *almost perfect g.f.'s.*

We now see that an almost regular g.f. is always a limit g.f., i.e., $\mathrm{cl}(\Omega) \subset \Omega^+$. Further, we prove Proposition 5.7.

Proposition 5.7. The class Ω^+ of limit g.f.'s is closed in the point convergence topology on Γ^+, i.e., $\mathrm{cl}(\Omega) \subset \mathrm{cl}(\Omega^+) = \Omega^+$.

Proof. Let $\zeta \in \mathrm{cl}(\Omega^+)$. For each n there is a $\zeta_n \in \Omega^+$ such that $\lim_{n\to\infty} \zeta_n = \zeta$, so

$$\lim_{n\to\infty} R\zeta_n(s) = \lim_{n\to\infty} \frac{\zeta_n(\lambda)\zeta_n(s)}{\zeta_n(\lambda s)} = \frac{\zeta(\lambda)\zeta(s)}{\zeta(\lambda s)} = R\zeta(s).$$

Clearly, $R\zeta(s)$ is a continuous function over $[1, \infty)$ and $R\zeta_n(s)$ are g.f.'s; thus, $R\zeta(s) = \lim_{n\to\infty} R\zeta_n(s)$ is a g.f., (which converges for all s in $[1, \infty)$). By Criterion 5.1 we get $\zeta \in \Omega^+$.

In conclusion, we suggest that it might be of biological interest to investigate cases where the effect of mutation is changed according to parental type rather than to time. The influence of sex on diploidity on a similar model is studied in a different paper [4].

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