

## EVOLUTION IN DIPLOID POPULATIONS WITH CONTINUITY OF GAMETIC TYPES

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### Abstract

This work studies the long-term effects of mutation and selection pressures on a diploid population embracing many genetic types. A number of results previously established for the simpler asexual case (see [4]) are extended to the cases of random mating and complete inbreeding (Theorem 1), and then, under particular conditions, to certain circumstances of mixed random mating and inbreeding (Theorem 3 and Corollary 1). Several implications for sex and diploidy are drawn from Theorem 2 and its corollaries. Further biological interpretations of these findings, especially of Theorem 2, are given in [3].

HAPLOID; DIPLOID; SEX; INBREEDING; RANDOM MATING; HETEROZYGOTE; MUTATION SELECTION; RATE OF EVOLUTION; DISTRIBUTION OF FITNESS; DISTRIBUTION OF MUTATION; ASYMPTOTIC DISTRIBUTION OF FITNESS; MONOTONE LIKELIHOOD RATIO; PÓLYA FUNCTIONS; TOTALLY POSITIVE FUNCTIONS; STATISTIC ORDERING OF FITNESS

### 1. The general model for a diploid-sexual population

In [4] we analyzed some long-term effects of mutation and selection on a multitype haploid population. The type of each individual in such a population is characterized by multiple factors inherited from a single parent of the previous generation. For the mathematical analysis, each type in the haploid population has been identified with a point of a Euclidean space  $E$ , the identification scaling the properties of the type in accordance with  $n$  quantitative features in which we are interested.

For the analysis of the corresponding *diploid* model we now consider an infinite population in which the type of each individual is determined by two parental *gametes*. Each gamete is transmitted by a distinct parent of the previous generation. We associate each type in the diploid population with a pair  $(x_1, x_2)$ , where  $x_1, x_2 \in E$  represent its two constituent gametes. Analogously to the haploid case the distribution  $F_t(x)$  describes the cumulative frequency distribution of gametes of type less than or equal to  $x$  in the population at generation  $t$ . Before we can study the composition of types in the

diploid population, however, we must have further information about the manner in which the gametes are paired. Thus we must know the conditional distributions  $F_t(x|u)$  of gametes  $x$  that are paired with any given gamete  $u \in E$ .

From generation  $t$  to generation  $t+1$ , selection, mutation, and mating act in the following manner.

(a) A function  $\gamma(x_1, x_2)$  defined for  $x_1, x_2 \in E$  (the *viability function*), determines, up to a normalizing factor, the frequency of survivors among all individuals of type  $(x_1, x_2)$ . Obviously, the survival probability of any specific gamete  $x$  depends on the other gamete with which it is paired. The frequency of survivors of *all* gametes  $x$  is thus proportional to

$$\int_E \gamma(u, x) dF_t(u|x)$$

and the distribution of the gamete types existing *after selection* is

$$(1.1) \quad F_t^*(x) = \frac{\int_{v \leq x} \int_E \gamma(u, v) dF_t(u|v) dF_t(v)}{\int_E \int_E \gamma(u, v) dF_t(u|v) dF_t(v)},$$

where  $v = (v_1, v_2, \dots, v_n) \leq (x_1, x_2, \dots, x_n) = x$  signifies  $v_i \leq x_i$ ,  $i = 1, 2, \dots, n$ .

(b) Mutation operates independently on gametes in the same manner as in the haploid model; i.e., within one generation, any given gamete  $x \in E$  may change into a gamete  $u$  with a probability  $dG(u-x)$ . The distribution  $G(u)$  is called the *mutation distribution*.

The distribution of the gametes after selection and mutation is thus

$$(1.2) \quad F_{t+1}(x) = \int_E G(x-u) dF_t^*(u).$$

(c) Reproduction through mating rearranges pairing of gametes and thus affects the conditional distributions  $F_t(x|u)$ . It does not affect, however, the gametic distribution  $F_t(x)$  in the entire population.

In this study we concentrate on mating systems that are equivalent to a partial inbreeding with random mating. More specifically, we assume a value  $0 \leq p \leq 1$ , namely the *rate of inbreeding*, such that in each generation a frequency  $p$  of the gametes of any type is paired with gametes of their own kind, resulting in homozygotes  $(x, x)$ , while the rest of the gametes are paired randomly. As a special case, for  $p = 0$  and  $p = 1$  we have random mating and complete selfing, respectively.

Since we are dealing with an infinite number of gamete types, we assume that, with probability one, any two randomly paired gametes are different

and thus constitute a *heterozygote*  $(x_1, x_2)$ , where  $x_1 \neq x_2$ . In this case, the conditional distributions are uniquely determined by the gametic distribution. More specifically, under the assumption of random mating we get  $F_t(x|u) = F_t(x)$  for all  $u \in E$ , whereas in the more general mixed system we have

$$(1.3) \quad F_t(x|u) = \begin{cases} (1-p)F_t(x) + p & \text{if } x \geq u, \\ (1-p)F_t(x) & \text{otherwise.} \end{cases}$$

As in the haploid case, we further restrict ourselves to the single-parameter property of *fitness*. In order to assign a natural "fitness value" to a gamete  $x$ , we consider the viability of the homozygote  $(x, x)$  that is created by a pair of such identical gametes. And as in the haploid case, it proves convenient to define the *gametic fitness* of  $x$  as a logarithmic function of the viability of the type  $(x, x)$ . Here, by the definition of  $x$ , the viability of the homozygote  $(x, x)$  is given by

$$(1.4) \quad \gamma(x, x) = \lambda^x,$$

where  $\lambda > 1$  is a fixed real number, the *standard malthusian coefficient* (see [3]). The viability of the heterozygotic  $(x_1, x_2)$  ( $x_1 \neq x_2$ ) is determined by the composition of its gametes, and also by its heterozygotic character, which constantly shifts it from the average of its gametic viabilities:

$$(1.5) \quad \gamma(x_1, x_2) = \theta \lambda^{\frac{1}{2}(x_1 + x_2)}.$$

Here  $\theta > 0$  is the heterozygosity-effect (usually, in nature,  $\theta > 1$ ).

Applying identities (1.1)–(1.5) we see that for any given initial distribution  $F_0(x)$  and a mutation distribution  $G(x)$ , the process is uniquely determined by the two parameters  $\theta$  and  $p$ . By virtue of (1.3), the process may be completely described through the sequence  $\{F_t^{p, \theta}(x)\}_t$  of the gametic distributions.

For further investigation of the process, it is useful to introduce the generating functions

$$(1.6) \quad \phi_t^{p, \theta}(s) = \int_{-\infty}^{\infty} s^x dF_t^{p, \theta}(x)$$

and

$$(1.7) \quad \psi(s) = \int_{-\infty}^{\infty} s^x dG(x).$$

The convergence of the integrals for any  $s \geq 1$  is immediate from the spectrum-boundedness of their probability measures. This is implied by our restriction to viability fitnesses. We obtain

$$\begin{aligned} \int_{-\infty}^{\infty} \gamma(u, x) dF_t^{p, \theta}(u|x) &= p\lambda^x + (1-p)\theta \int_{-\infty}^{\infty} \lambda^{\frac{1}{2}(u+x)} dF_t^{p, \theta}(u) \\ &= p\lambda^x + (1-p)\theta \lambda^{\frac{1}{2}x} \phi_t^{p, \theta}(\lambda^{\frac{1}{2}}). \end{aligned}$$

Inserting this into (1.1) and (1.2) we get

$$(1.8) \quad F_{t+1}^{p,\theta}(x) = \frac{p \int_{-\infty}^{\infty} \lambda^u G(x-u) dF_t^{p,\theta}(u) + (1-p)\theta \phi_t^{p,\theta}(\lambda^{\frac{1}{2}}) \int_{-\infty}^{\infty} \lambda^{\frac{1}{2}u} G(x-u) dF_t^{p,\theta}(u)}{p\phi_t^{p,\theta}(\lambda) + (1-p)\theta [\phi_t^{p,\theta}(\lambda^{\frac{1}{2}})]^2}.$$

Equivalently,

$$(1.9) \quad \phi_{t+1}^{p,\theta}(s) = \psi(s) \frac{p\phi_t^{p,\theta}(\lambda s) + (1-p)\theta \phi_t^{p,\theta}(\lambda^{\frac{1}{2}}) \phi_t^{p,\theta}(\lambda^{\frac{1}{2}}s)}{p\phi_t^{p,\theta}(\lambda) + (1-p)\theta [\phi_t^{p,\theta}(\lambda^{\frac{1}{2}})]^2}$$

with  $\phi_0^{p,\theta}(s) = \phi_0(s)$  for all  $p$  and  $\theta$ . Now, set

$$(1.10) \quad q = \frac{p}{p + (1-p)\theta}$$

and

$$(1.11) \quad F_t^{p,\theta}(x) = F_t^q(x), \quad t = 0, 1, 2, \dots$$

Expression (1.9) can then be written

$$(1.12) \quad \phi_{t+1}^q(s) = \psi(s) \frac{q\phi_t^q(\lambda s) + (1-q)\phi_t^q(\lambda^{\frac{1}{2}})\phi_t^q(\lambda^{\frac{1}{2}}s)}{q\phi_t^q(\lambda) + (1-q)[\phi_t^q(\lambda^{\frac{1}{2}})]^2}$$

with  $\phi_0^q(s) = \phi_0(s)$  for all  $q$ . The process is thus determined by a single parameter  $q$ , to be called *the diploidity parameter*. (1.10) makes it clear that  $0 \leq q \leq 1$ , where the extreme values are obtained for the extreme values of the inbreeding rate  $p$ . Furthermore, for any given  $\theta > 0$ ,  $q$  is a monotonically increasing function of  $p$ , and the effect of the inbreeding coefficient on the process may be studied through the effect of the parameter  $q$ .

For the special case of complete inbreeding ( $p = 1$  and thus  $q = 1$ ), (1.12) becomes

$$(1.13) \quad \phi_{t+1}^1(s) = \psi(s) \frac{\phi_t^1(\lambda s)}{\phi_t^1(\lambda)}.$$

For the complete random-mating case ( $p = 0$  and thus  $q = 0$ ) we obtain

$$(1.14) \quad \phi_{t+1}^0(s) = \psi(s) \frac{\phi_t^0(\lambda^{\frac{1}{2}}s)}{\phi_t^0(\lambda^{\frac{1}{2}})}.$$

Since for the asexual process it has already been proved that the generating function  $\phi_{t+1}(s)$  of generation  $t+1$  is given by

$$(1.15) \quad \phi_{t+1}(s) = \psi(s) \frac{\phi_t(\lambda s)}{\phi_t(\lambda)}$$

(see [4]), we obtain, as an immediate result:

**Theorem 1.** (a) *A diploid process with complete inbreeding is equivalent in law to an asexual process with the same initial distribution, the same mutation law, and the same malthusian parameter.*

(b) *A diploid process with completely random mating is equivalent in law to an asexual process with the same initial distributions, but with a lower malthusian parameter  $\lambda^{\frac{1}{2}}$ .*

The proof of the theorem is immediate from (1.13), (1.14), and (1.15). Its first part is quite expected. The second part is, however, more interesting, since it extends all qualitative results of the asexual model to the frequently treated case of a diploid random-mating population. More specifically, in a way consistent with [4], denote by  $EX_t^q = \int_{-\infty}^{\infty} x dF_t^q(x)$  the average fitness in the population of generation  $t$  of the process  $\{F_t^q(x)\}_{t=0}^{\infty}$ , and let  $\bar{G} = \sup\{x \mid G(x) < 1\}$  stand for the maximal mutation. The value  $EX_{t+1}^q - EX_t^q$ , measuring the average change in fitness from generation  $t$  to generation  $t+1$ , is called the *rate of evolution* in generation  $t$ . As has been proved for the asexual model with bounded initial fitness and bounded mutation:

(1) The rate of evolution in a random-mating diploid process tends to a finite limit. This limit is equal to the maximal mutation, independent either of  $\lambda$  or of  $F$ ,

$$(1.16) \quad \lim_{t \rightarrow \infty} \{EX_{t+1}^0 - EX_t^0\} = \bar{G}.$$

(2) The centered distribution  $F_t^0(x - EX_t^0)$  of relative fitnesses tends by law to a limit distribution  $F^0(x)$  with a finite variance.

(3) The limit-fitness distribution  $F^0(x)$  has a bounded support if and only if  $G(x)$  has a "jump" in  $\bar{G}$ , i.e., if there is a positive probability of the maximal mutation. In this case the process is said to be *perfect*.

## 2. Processes with partial inbreeding and random mating

Systems of partial inbreeding and random mating were first treated (though in a different context) by Wright [13], [14]. Further discussions of their mathematical implications or biological applications are given by Hayman [7], Bennet and Binet [1], and Karlin [8]. Mathematical methods similar to those employed in this section were first offered and used by Karlin and Rubin [10]. A more general treatment of the concepts used here may be found in Karlin [9]. The reader is also referred to Karlin and Studden [11] for properties of general convexity that are relevant to the ordering concept, and to Lehman [12] for statistical applications of the concept of monotone likelihood ratio.

To study the effect of inbreeding on the diploid process of evolution, we shall be interested in the families  $\{F_t^q(x)\}_{0 \leq q \leq 1}$  for any fixed  $t = 0, 1, 2, \dots$ . We shall begin by introducing some useful concepts and properties from the theory of total positivity. For the sake of simplicity, since for  $t = 0, 1, 2, \dots$ , the distributions of the family  $\{F_t^q(x)\}_{0 \leq q \leq 1}$  are mutually absolutely continuous (immediate from (1.9)), we restrict the discussion to mutually absolutely continuous families.

(a) A function  $K(q, x)$  is said to be *totally positive of order 2* (TP2) if for all measures  $\sigma$  and a monotonically increasing function  $r(x)$  for which the integral  $\int_{-\infty}^{\infty} r(x)K(q, x)\sigma(dx)$  converges, this integral defines an increasing function of  $q$  (see [9]).

(b) A family of mutually absolutely continuous distributions is said to have an *increasing monotone likelihood ratio* (IMLR) if a TP2 function  $K(q, x)$  and a measure  $\sigma$  exist such that, for all  $q \in Q$  and almost all  $x < \infty$ ,

$$(2.1) \quad F_q(x) = \int_{-\infty}^x K(q, x)\sigma(dx).$$

For  $q_1 < q_2$  we then denote  $F_{q_1} < F_{q_2}$ , say  $F_{q_1}$  is smaller than  $F_{q_2}$  by a *monotone likelihood ratio* (MLR). Further, where two r.v.'s  $X_1, X_2$  are distributed  $F_1, F_2$  with generating functions  $\phi_1, \phi_2$ , respectively, and where  $F_1 < F_2$ , then it is convenient to make  $\phi_1 < \phi_2$  and  $X_1 < X_2$  ( $X_1$  is smaller than  $X_2$  by an MLR). Equivalently:

(b<sub>1</sub>) The family  $\{F_q\}_{q \in Q}$  is IMLR if for all increasing functions  $r(x)$  the integral  $\int_{-\infty}^{\infty} r(x)dF_q(x)$  assumes a monotonically increasing function of  $q$ , wherever it converges (see, for example, [10]).

(b<sub>2</sub>) Where  $F_1$  and  $F_2$  are mutually absolutely continuous distributions,  $F_1 < F_2$ , if the Radon-Nikodim derivative

$$\frac{\partial F_2(x)}{\partial F_1(x)} = \lim_{\varepsilon \rightarrow 0} \frac{F_2(x + \varepsilon) - F_2(x)}{F_1(x + \varepsilon) - F_1(x)}$$

is monotonically increasing on the common support. (Since  $F_2 < F_1$ ,  $\partial F_2 / \partial F_1$  exists a.e. and  $F_1(x) = \int_{-\infty}^x [\partial F_2(u) / \partial F_1(u)] dF_1(u)$  a.e.)

(c) A distribution  $F(x)$  is said to have an order-2 Pólya density if  $F(x) = \int_{-\infty}^x f(u)\mu(du)$  and  $f(x-y)$  is a TP2 function a.e. in the  $F$ -measure. Equivalently:

(c<sub>1</sub>) The function  $f(x)$  is an order-2 Pólya density if  $f(u+\lambda)/f(u)$  is monotonically decreasing a.e. for all  $\lambda > 0$ .

(c<sub>2</sub>) A r.v.  $X$  is said to have an order-2 Pólya density if  $X + \lambda < X$  for all fixed numbers  $\lambda > 0$ .

The proofs are immediate from the definitions. The normal, binomial, Poisson, exponential, geometric,  $\gamma$ ,  $\beta$ , rectangular, and triangular distributions are all of an order-2 Pólya density.

(d) For an order-2 Pólya density, a r.v.  $U$  and any two r.v.'s  $X$  and  $Y$  that are independent of it, it is not difficult to prove

$$(2.2) \quad X + U \succ Y + U$$

(see [6]).

The following properties are more specific, but will be readily proved from (a)–(d):

(e) Let  $F \succ H$  ( $F$ ,  $H$  are mutually absolutely continuous distributions),  $\lambda > \theta > 0$ , and

$$F_1(x) = \int_{-\infty}^x \lambda^u dF(u) / \int_{-\infty}^{\infty} \lambda^u dF(u);$$

$$H_1(x) = \int_{-\infty}^x \theta^u dH(u) / \int_{-\infty}^{\infty} \theta^u dH(u).$$

Then  $F_1 \succ H_1$ .

*Proof.* For almost any  $x$  on the common support

$$\frac{\partial F_1(x)}{\partial H_1(x)} = c \lim_{\varepsilon \rightarrow 0} \frac{\int_x^{x+\varepsilon} \lambda^u dF(u)}{\int_x^{x+\varepsilon} \theta^u dH(u)} = c \left( \frac{\lambda}{\theta} \right)^x \frac{\partial F(x)}{\partial H(x)}$$

which is an increasing function a.e.

(f) If  $\phi_q(s)$  ( $q \in Q$ ) are generating functions of an IMLR family  $\{F_q(x)\}_{q \in Q}$ , and if  $\lambda(q)$  is an increasing function over  $Q$ , then  $\phi_q[\lambda(q)s]/\phi_q[\lambda(q)]$  ( $q \in Q$ ) are again generating functions of an IMLR family.

*Proof.*  $\phi_q(\lambda(q)s)/\phi_q(\lambda(q))$  is the generating function of the distribution

$$F_q^*(x) = \frac{\int_{-\infty}^x [\lambda(q)]^u dF_q(u)}{\int_{-\infty}^{\infty} [\lambda(q)]^u dF_q(u)},$$

and the IMLR property of the family  $\{F_q^*(x)\}_{q \in Q}$  follows immediately from (e).

(g) If  $F \succ H$ ,  $G \succ H$ ,  $0 \leq p \leq 1$ , then  $pF + (1-p)G \succ H$ .

*Proof.* For any increasing function  $r(x)$ ,

$$\int r(x) d\{pF(x) + (1-p)G(x)\} = p \int r(x) dF(x) + (1-p) \int r(x) dG(x)$$

$$> \int r(x) dH(x),$$

provided the integrals converge.

Using the above properties, we shall now prove the following theorem.

**Theorem 2.** Consider a family  $\{\{F_t^q(x)\}_{t=0}^\infty\}_{0 \leq q \leq 1}$  of diploid processes of evolution, determined by the same initial distribution  $F_0(x)$  and the same mutation distribution  $G(y)$  and differing only in their heterozygotic parameter  $q$ . Let the distribution  $G(y)$  have a Pólya density of order 2. Then in any given generation  $t = 0, 1, 2, \dots$ , the family  $\{F_t^q(x)\}_{0 \leq q \leq 1}$  is increasing by a monotone likelihood ratio (IMLR). In other words, a TP2 kernel  $K(q, x)$  exists such that

$$(2.3) \quad F_t^q(x) = \int_{-\infty}^x K(q, u) dF_t^{(0)}(u)$$

for all  $0 \leq q \leq 1$ ;  $-\infty < x < \infty$ .

*Proof.* The theorem is trivially correct for  $t = 0$ . Assume now that it is correct for a given  $t$ . We denote

$$H_t^q(x) = \frac{\int_{-\infty}^x \lambda^{\frac{1}{2}u} dF_t^q(u)}{\int_{-\infty}^\infty \lambda^{\frac{1}{2}u} dF_t^q(u)}.$$

From property (e) above we know that  $\{H_t^q\}_{0 \leq q \leq 1}$  is IMLR. Since  $\lambda^{\frac{1}{2}} > 1$ , (e) also implies that, for all  $0 \leq q \leq 1$ ,  $H_t^q > F_t^q$ . Hence, by virtue of property (g), we obtain, for all  $0 \leq q_1 \leq q_2 \leq 1$ ,

$$(1 - q_2)F_t^{q_2} + q_2 H_t^{q_2} > (1 - q_1)F_t^{q_2} + q_1 H_t^{q_2} > (1 - q_1)F_t^{q_1} + q_1 H_t^{q_1}.$$

The family  $\{(1 - q)F_t^q + qH_t^q\}_{0 \leq q \leq 1}$  is thus IMLR. The generating functions of this family are

$$\begin{aligned} \chi_t^q(s) &= \int_{-\infty}^\infty s^x d[(1 - q)F_t^q(x) + qH_t^q(x)] \\ &= (1 - q)\phi_t^q(s) + q \frac{\phi_t^q(\lambda^{\frac{1}{2}}s)}{\phi_t^q(\lambda^{\frac{1}{2}})} \end{aligned}$$

Property (f) thus implies that the functions  $\chi_t^q(\lambda^{\frac{1}{2}}s)/\chi_t^q(\lambda^{\frac{1}{2}})$  are again generating functions of an IMLR family of distributions, and it follows immediately from (d) that so are the functions

$$\psi(s) \frac{\chi_t^q(\lambda^{\frac{1}{2}}s)}{\chi_t^q(\lambda^{\frac{1}{2}})} = \psi(s) \frac{(1 - q)\phi_t^q(\lambda^{\frac{1}{2}}s)\phi_t^q(\lambda^{\frac{1}{2}}) + q\phi_t^q(\lambda s)}{(1 - q)[\phi_t^q(\lambda^{\frac{1}{2}})]^2 + q\phi_t^q(\lambda)}.$$

But by (1.12) these are simply  $\phi_{t+1}^q(s)$ .

**Corollary 1.** For all increasing functions  $r(x)$  and all  $t = 0, 1, 2, \dots$ ,  $E[r(x_t^q)]$  is an increasing function of  $q$ , whenever it is defined.

*Remark.* Since  $X$  was defined as a *specific* increasing function of the gametic viability (the logarithmic function), Corollary 1 states very generally that, at any given generation, the expected value of any increasing function of the viability is increasing with  $q$ , and thus with the inbreeding parameter  $p$ . For a discussion of the significance of this result for the evolution of sex, see [3].

**Corollary 2.** For all  $0 \leq q \leq 1$ ,

$$(2.4) \quad \lim_{t \rightarrow \infty} \frac{EX_t^q}{t} = \bar{G}.$$

*Proof.* As a special case of Corollary 1, we have  $EX_t^0 \leq EX_t^q \leq EX_t^1$ . From Theorem 1, we know that

$$\lim_{t \rightarrow \infty} \frac{EX_t^q}{t} = \lim_{t \rightarrow \infty} \frac{EX_t^1}{t} = \bar{G},$$

and (2.4) immediately follows.

**Theorem 3.** In a perfect diploid process of evolution (i.e., a process in which the probability of the maximal mutation is strictly positive), the variance  $v(X_t^q)$  is uniformly bounded for all  $q$ .

*Proof.* It is not difficult to establish that if  $G(x)$  has a jump at  $x = \bar{G}$  then

$$\sum_{k=0}^{\infty} \left\{ \bar{G} - \lambda^k \frac{\psi'(\lambda^k)}{\psi(\lambda)} \right\} < \infty \quad \text{for all } \lambda > 1.$$

Also, if  $F_0$  is the upper bound of the support of  $F_0(x)$ , then

$$\lim_{k \rightarrow \infty} \lambda^k \frac{\phi'_0(\lambda^k)}{\phi_0(\lambda^k)} = F_0 < \infty$$

(see [4] for proof). From (1.13) and (1.14) it is not difficult to obtain

$$EX_t^1 = \lambda^t \frac{\phi'_0(\lambda^t)}{\phi_0(\lambda^t)} + \sum_{k=0}^{t-1} \lambda^k \frac{\psi'(\lambda^k)}{\psi(\lambda^k)}$$

and

$$EX_t^0 = \lambda^{\frac{1}{2}t} \frac{\phi'_0(\lambda^{\frac{1}{2}t})}{\phi_0(\lambda^{\frac{1}{2}t})} + \sum_{k=0}^{t-1} \lambda^k \frac{\psi'(\lambda^{\frac{1}{2}k})}{\psi(\lambda^{\frac{1}{2}k})}.$$

From this and Theorem 1, we obtain

$$\begin{aligned}
 0 \leq EX_t^1 - EX_t^0 &= \lambda^t \frac{\phi'_0(\lambda)}{\phi_0(\lambda)} - \lambda^{\frac{1}{2}t} \frac{\phi'_0(\lambda^{\frac{1}{2}})}{\phi_0(\lambda^{\frac{1}{2}})} \\
 &+ \sum_{k=0}^{t-1} \left\{ \lambda^k \frac{\psi'(\lambda^k)}{\psi(\lambda^k)} - \lambda^{\frac{1}{2}k} \frac{\psi'(\lambda^{\frac{1}{2}k})}{\psi(\lambda^{\frac{1}{2}k})} \right\} \\
 (2.5) \quad &\leq C^* + \sum_{k=0}^{\infty} \left\{ \bar{G} - \lambda^{\frac{1}{2}k} \frac{\psi'(\lambda^{\frac{1}{2}k})}{\psi(\lambda^{\frac{1}{2}k})} \right\} \leq C < \infty,
 \end{aligned}$$

where  $C^*$  and  $C$  are constants, independent of  $t$ . Using the inequality  $EX_t^0 \leq EX_t^q \leq EX_t^1$ , we now get

$$\begin{aligned}
 \text{var}(X_t^q) &= \int_{-\infty}^{\infty} (x - EX_t^q)^2 dF_t^q(x) \\
 (2.6) \quad &\leq \int_{-\infty}^{EX_t^q} (x - EX_t^1)^2 dF_t^q(x) + \int_{EX_t^q}^{\infty} (x - EX_t^0)^2 dF_t^q(x).
 \end{aligned}$$

Denote

$$r(x) = \begin{cases} 0, & x < EX_t^q, \\ (x - EX_t^0)^2, & x \geq EX_t^q. \end{cases}$$

Since this is an increasing function of  $x$ , Corollary 1 implies that

$$\begin{aligned}
 \int_{EX_t^q}^{\infty} (x - EX_t^0)^2 dF_t^q(x) &= \int_{-\infty}^{\infty} r(x) dF_t^q(x) \leq \int_{-\infty}^{\infty} r(x) dF_t^1(x) \\
 (2.7) \quad &= \int_{EX_t^q}^{\infty} (x - EX_t^0)^2 dF_t^1(x) \leq \int_{-\infty}^{\infty} (x - EX_t^0)^2 dF_t^1(x) \\
 &= C^2 + \text{var}(X_t^1).
 \end{aligned}$$

In the same way,

$$(2.8) \quad \int_{-\infty}^{EX_t^q} (x - EX_t^1)^2 dF_t^q(x) \leq C^2 + \text{var}(X_t^0).$$

But we know from Theorem 1 that

$$\lim_{t \rightarrow \infty} \text{var}(X_t^0) = \sigma_0^2 < \infty; \quad \lim_{t \rightarrow \infty} \text{var}(X_t^1) = \sigma_1^2 < \infty,$$

and from (2.6)-(2.8), we have

$$\text{var}(X_t^q) \leq 2C^2 + \sigma_0^2 + \sigma_1^2 < \infty.$$

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