EIGENVALUE INEQUALITIES FOR RANDOM EVOLUTIONS: ORIGINS AND OPEN PROBLEMS

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This paper has three parts. The first give an expository review of a model from stochastic population biology. This model leads to eigenvalue inequalities for random evolutions. The second gives a proof by Charles M. Newman of one of these inequalities. The third gives conjectures and questions. Some of these have been previously stated; most are new.

1. Introduction. The growth of a population in a random environment can be modeled in a simple way by a stochastic process called a random evolution. Bounds on the growth rate of a population in a random environment can be expressed in terms of certain eigenvalues. The first purpose of this paper is to describe informally how a population can be modelled by a random evolution and why eigenvalue inequalities arise naturally (section 2). The main inequalities to be discussed have been proved by Cohen, Friedland, Kato and Kelly (1982). I shall henceforth refer to this paper as CFKK. The second purpose of this paper is to give a proof (section 3) of one of these inequalities that was discovered by Charles M. Newman of the University of Arizona during my talk at the symposium on Inequalities in Statistics and Probability. The third purpose of this paper is to state conjectures, open problems and questions concerning further inequalities (section 4).

2. Populations in Random Environments and Eigenvalue Inequalities. Suppose one has a vat of bacteria sitting in a laboratory. Suppose the number of bacteria is large enough so that there is no discomfort in taking $N(t)$, the number of bacteria at (real scalar) time t, to be a real variable rather than strictly integer valued. Suppose also that the number of bacteria is small compared to the number of bacteria that the nutrient medium in the vat can support, or that the medium is continuously refreshed. If the division cycles of the bacteria are unsynchronized, then the simplest model of the population is to suppose that the number of fissions that occur per unit time is directly proportional to the number of bacteria in the vat. Thus, for some real constant b,

$$dN(t) / dt = bN(t) \text{ for } t \geqslant 0, N(0) = N_0.$$

It is well known, even among biologists, that the solution of this equation is

$$N(t) = N_0 e^{bt}.$$

In this deterministic model, the long-run growth rate b may be computed from an observed trajectory $N(t)$ of the size of the population from the formula

$$\lim_{t \to \infty} t^{-1} \log N(t) = b.$$

The left side of this equation is referred to as a Liapunov characteristic number of the process.

If one interprets the growth rate b as a stochastic process that is degenerate at a single fixed value for all time t, one can take averages wherever one wishes in the Liapunov characteristic number, i.e.,

$$t^{-1} E \log N(t) = t^{-1} \log E N(t),$$

because both sides are equal with probability 1 to b. However, if b is a stochastic process that is not degenerate, the above equality must be replaced by

$$t^{-1} E \log N(t) \leqslant t^{-1} \log E N(t)$$

because of Jensen's inequality and the concavity of log.

Now suppose that the conditions of our vat of bacteria are not perfectly uniform in time, but fluctuate randomly because of changes in the outside weather, in the voltages of the power lines that drive the vat's heating bath and mixers, and in other factors affecting the growth rate of the bacteria. Let us model these fluctuations by supposing that

$$dN(t) / dt = b(t)N(t) \text{ for } t \geqslant 0, N(0) = N_0,$$

where $b(t)$ is a real-valued functional of an n-state $(1 < n < \infty)$ continuous-time homogeneous irreducible Markov process $V(t)$. This means that the sample paths of $b(t)$ are piecewise constant, and each piece is constant at one of n real numbers $b_1, \ldots, b_n$. The Markov chain $V(t)$ on the state space $\{1, \ldots, n\}$ may be thought of as determining the subscript i of the growth rate b_i that is current at time t according to

$$b(t) = b_{V(t)}, \text{ with } b(0) = b_1.$$

Given that the Markov chain $V(t)$ starts in state 1, the subsequent behavior is determined by the intensity matrix $\mathbf{Q}$ according to

$$P[V(t + s) = j \mid V(t) = i] = (e^{\mathbf{Q}s})_{ij} \text{ for } s \geqslant 0, t \geqslant 0.$$

Recall that the intensity matrix $\mathbf{Q}$ is essentially nonnegative, i.e., $q_{ij} \geqslant 0$ if $i \neq j$, with the additional condition that $\Sigma_{j=1}^n q_{ij} = 0, i = 1, 2 \ldots, n$.

The process $N(t)$ is called a random evolution. It is a special case of the random evolutions studied by Griego and Hersh (1971), reviewed by Hersh (1974) and inspired by Kac (1957).

Since $V(t)$ and $b(t)$ are piecewise constant, a graph of a sample path of $\log N(t)$ as a function of t is piecewise linear, increasing when $b(t) > 0$, constant when $b(t) = 0$, and declining when $b(t) < 0$.

If $g_j(t)$ is the occupancy time in state j up to time t, i.e., the sum of the lengths of the time intervals up to time t such that $V(t) = j$, then an explicit formula for the random evolution $N(t)$ is

$$N(t) = N_0 \exp(\Sigma_{j=1}^n b_j g_j(t)).$$

This formula is obvious because, as long as $V(t) = j$, $N(t)$ grows exponentially at rate b_j as if $b(t)$ were fixed at b_j.

The formula makes it easy to compute one of the plausible measures of the long-run growth rate. First, since $\mathbf{Q}$ is irreducible (meaning that every growth rate is accessible from every other growth rate), there is an invariant or equilibrium probability vector π with positive elements $\pi_i, i = 1, 2, \ldots, n$, such that

$$\pi^T \mathbf{Q} = 0$$

and such that

$$g_j(t) / t \to \pi_j \text{ with probability 1, for } j = 1, \ldots, n.$$

Then using the above formula for $N(t)$ gives

$$\lim_{t\to\infty} t^{-1} E \log N(t) = \lim_{t\to\infty} t^{-1} E(\Sigma_{j=1}^n b_j g_j(t)) = \Sigma_{j=1}^n b_j \pi_j.$$

In words, the mean of the growth rates of population size (averaged over sample paths) equals the mean growth rate (averaged over the growth rates of any single sample path).

The second plausible measure of the long-run growth rate, namely the growth rate of mean population size, is given by a Feynman-Kac formula for this random evolution (Cohen, 1979a) as

$$(2.1) \qquad \lim_{t\to\infty} t^{-1} \log E N(t) = \log r(e^{\mathbf{Q+B}}),$$

where r is the spectral radius, or maximum of the moduli of the eigenvalues, and $\mathbf{B}$ is the $n \times n$ diagonal matrix with jth diagonal element equal to b_j.

Whereas the mean of the growth rates of population size depends on the intensity matrix $\mathbf{Q}$ only through its leading left eigenvector π^T, and is therefore the same for any intensity matrix with the same π^T, the growth rate of mean population size depends on all of $\mathbf{Q}$.

While it is plausible to suppose that the bacteria grow in continuous time, it is equally plausible to suppose that a biologist observes them at discrete time intervals. Suppose he or she observes once a day the conditions (temperature, light, nutrient concentration) affecting bacterial growth and infers or records a time series $b(0)$, $b(1)$, $b(2)$, ... of instantaneous growth rates. Suppose the observer models $N^D(t)$ the number of bacteria (D for "discrete") by

$$N^D(t + 1) = N_D(t)e^{b(t)}, t = 0, 1, 2, \ldots, N^D(0) = N_0.$$
$$P[b(t + 1) = b_j | b(t) = b_i] = (e^{\mathbf{Q}})_{ij} \equiv p_{ij}, b(0) = b_1.$$

According to the first of these equations, if the observer sees growth rate $b(t)$ at the epoch of observation on day t, he supposes that this growth rate will continue without variation until the epoch of observation on the next day. Since he has no information to tell him otherwise, this seems a reasonable first approximation. According to the second of these equations, he takes the transition probability p_{ij} from growth rate b_i to growth rate b_j to be just the transition probability that would be estimated from any long sample path of $V(t)$ by sampling at unit intervals.

The biologist's purpose in constructing this discrete approximation $N^D(t)$ to the random evolution $N(t)$ is to estimate the growth rates of $N(t)$. If he computes $\lim t^{-1} E \log N^D(t)$ and $\lim t^{-1} \log E N^D(t)$, how will these rates relate to the corresponding rates for $N(t)$?

For the average growth rate of population size, it follows from the explicit formula

$$N^D(t) = N_0 \exp(\Sigma_{j=1}^n b_j g_j^D(t))$$

and the fact that

$$g_j^D(t) / t \to \pi_j \quad with probability \ 1, j = 1, \ldots, n,$$

where $g_j^D(t)$ is the discrete occupancy time of state j prior to time t (= number of days from 0 up to and including $t-1$ such that $V(.) = j$) that

$$\lim_{t\to\infty} t^{-1} E \log N^D(t) = \Sigma_{j=1}^n b_j \pi_j$$

$$= \lim_{t\to\infty} t^{-1} E \log N(t).$$

Thus the discrete model for $N^D(t)$ give exactly the average growth rate of the continuous time random evolution $N(t)$.

What about the second measure, the growth rate of average population size? An elementary computation shows that

$$E N^D(t) = e^{b(0)} \times \text{first row sum of } (e^{\mathbf{Q}} e^{\mathbf{B}})^t.$$

Because $\mathbf{Q}$ is irreducible, $e^{\mathbf{Q}}$ is (elementwise) positive, so that by the Perron-Frobenius theorem

$$(2.2) \qquad \lim_{t \to \infty} t^{-1} \log E N^D(t) = \log r(e^{\mathbf{Q}} e^{\mathbf{B}}).$$

After publishing this formula (Cohen, 1979b, p. 249), I discovered that it was known to LeBras (1974). I have recently learned from a secondary source (Iosifescu, 1980, pp. 162–163) that the formula should be credited to papers by O. Onicescu and G. Mihoc published during World War II.

The growth rate (2.2) of mean population size in the discrete model is an upper bound on the growth rate (2.1) of mean population size in the random evolution. More precisely, Theorem 2 of CFKK (p. 64) states: If $\mathbf{A}$ and $\mathbf{B}$ are two real $n \times n$ matrices, all $a_{ij} \geq 0$ if $i \neq j$, and all $b_{ij} = 0$ if $i \neq j$, then

$$(2.3) \qquad r(e^{\mathbf{A} + \mathbf{B}}) \leq r(e^{\mathbf{A}} e^{\mathbf{B}}).$$

Moreover, this inequality is strict if $\mathbf{A}$ is irreducible and at least two diagonal elements of $\mathbf{B}$ are distinct. The next section gives a proof of the weak inequality.

Before giving that proof, let me informally show how (2.2) can be used to derive (2.1). (This does not pretend to be a rigorous proof.) We construct a sequence of discrete approximations $N_1^D(t) = N^D(t)$, $N_2^D(t)$, $N_3^D(t)$, ... In the kth approximation a unit interval of time is divided into k equal subintervals. The growth rate $b(t)$ is constrained to be constant on each subinterval but is permitted to change, with transition probability matrix $e^{\mathbf{Q}/k}$, from one subinterval to the next. Within each subinterval of length $1/k$, the long-run growth rate of mean population size, from (2.2), is $\log r(e^{\mathbf{Q}/k} e^{\mathbf{B}/k})$. Therefore, in one unit of time, which is k subintervals of length $1/k$, the growth rate of mean population size is

$$k \log r(e^{\mathbf{Q}/k} e^{\mathbf{B}/k}) = \log r^k(e^{\mathbf{Q}/k} e^{\mathbf{B}/k}) = \log r([e^{\mathbf{Q}/k} e^{\mathbf{B}/k}]^k).$$

But for any two $n \times n$ matrices $\mathbf{A}$ and $\mathbf{B}$, there is a formula attributed to Sophus Lie (can anyone tell me the original source?)

$$\lim_{k \to \infty} (e^{\mathbf{A}/k} e^{\mathbf{B}/k})^k = e^{\mathbf{A} + \mathbf{B}}.$$

If you accept that

$$\lim_{k \to \infty} \lim t^{-1} \log E N_k^D(t) = \lim t^{-1} \log E N(t),$$

so that the growth rate of mean population size in the discrete approximations approaches that of the continuous-time random evolution, then the two preceding formulas and an exchange of limits combine to yield the Feynman-Kac formula (2.1).

If the Markov chain $V(t)$ is reversible, CFKK proved (p. 62) that many more eigenvalue inequalities hold. For example, if the eigenvalues $\lambda_1, \ldots, \lambda_n$ of an arbitrary $n \times n$ complex matrix M are ordered so that $|\lambda_1| \geq |\lambda_2| \geq \ldots \geq |\lambda_n|$, and if

$$\varphi_k = \Sigma_{i=1}^k |\lambda_i|, k = 1, \ldots, n,$$

then for any reversible intensity matrix $\mathbf{Q}$, any diagonal real matrix $\mathbf{B}$ and $k = 1, \ldots, n$,

$$\varphi_k(e^{\mathbf{Q} + \mathbf{B}}) \leq \varphi_k(e^{\mathbf{Q}} e^{\mathbf{B}}).$$

The random evolution described here has also been found useful by economists to whom

I have suggested it as a model of price inflation in random (political, social and economic) environments. In this application, $N(t)$ is an index of price, $b(t)$ the instantaneous rate of inflation, and one of the interesting questions is: given $0 < N_1 < N_2$ and $t_1 < t_2$ and $N(t_1) < N_1$, what is the probability that $N(t) < N_2$ for all $t_1 \leqslant t \leqslant t_2$? Another question is: given $N(t_1) = N_1$, what is the distribution of the first time $t_2 > t_1$ such that $N(t_2) = N_2 > N_1$?

I hope it will both aid and promote people's interest in studying discrete and continuous random evolutions to observe that these random evolutions are special multiplicative functionals of Markov chains and processes. Markov's first paper in 1906 on these chains (again according to Iosifescu [1980]) aimed for a central limit theorem for additive functionals of a chain. Since then, many publications, scattered and apparently overlapping, have dealt with various functionals of Markov chains and processes. Among them are Doeblin (1937), Frechet (1952), Blanc-Lapierre and Fortet (1953 [1965]), Volkov (1958), Kemeny and Snell (1960 [1976]), Meyer (1962), Keilson and Wishart (1964, 1967) Fukushima and Hitsuda (1967), Pinsky (1968), Keilson and Rao (1970), Kertz (1974), O'Brien (1974), Ellis (1974), Serfozo (1975), Çinlar (1975), Keepler (1976), Wolfson (1977), Katz (1977), Durrett and Resnick (1978), Dagsvik (1978), primary papers cited in Iosifescu (1980), Friedland (1981) and Siegrist (1981). This work needs coherent synthesis.

3. Newman's Proof. After my lecture at the Nebraska Conference on Inequalities, Charles M. Newman presented me with a proof of (2.3). I give this proof with his kind permission.

LEMMA 1. *Let* **A** *and* **B** *be two real* $n \times n$ *matrices with* $a_{ij} \geqslant 0$ *if* $i \neq j$, *and* $b_{ij} = 0$ *if* $i \neq j$. *Then for any positive integer* m, *any real* x_i, $i = 1, \ldots, m$, *and* $a > 0$,

$$F(x_1, \ldots, x_m) = Tr(e^{a\mathbf{A}}e^{x_1\mathbf{B}}e^{a\mathbf{A}}e^{x_2\mathbf{B}}\ldots e^{a\mathbf{A}}e^{x_m\mathbf{B}})$$

is minimized on $\{x_i \geqslant 0, \Sigma x_i = ma\}$ *at* $x_i = a$ *for all* i.

Proof. We may express **A** as $\mathbf{A} = \mathbf{Q} + \mathbf{D}$ where **Q** is an intensity matrix and **D** is diagonal real. Let $V(t)$ be the Markov process determined by **Q** with an initial distribution that is uniform on the states $\{1, \ldots, n\}$ and conditioned so that $V(0) = V(T)$ where $T = am$. Thinking of $a = T/m$ as a discrete timestep for observing $V(t)$, we have by the Feynman-Kac formula that

$$KF(x_1, \ldots, x_m) = E\exp\{\int_0^T d_{V(t)}dt + \Sigma_{j=1}^m x_j b_{V(ja)}\}$$

where $d_j = \mathbf{D}_{jj}$ and $b_j = \mathbf{B}_{jj}$ and $K = [Tr(e^{T\mathbf{Q}})]^{-1}$.

To see that F is a convex function of $(x_1, \ldots, x_m)$ it suffices to show that the matrix with (i,j)th element equal to $\partial^2 F/\partial x_i\partial x_j$ is positive semi-definite.

If $c_1, \ldots, c_m$ are any m complex numbers it follows that

$$K\Sigma_{i,j}\bar{c}_i\{\partial^2 F/\partial x_i\partial x_j\}c_j = E(|\Sigma_j c_j b_{V(ja)}|^2 \exp[\Sigma_h x_h b_{V(ha)} + \int_0^T d_{V(t)}dt]) \geqslant 0.$$

Thus F is convex in $(x_1, \ldots, x_m)$.

On $\{x_1 \geqslant 0, \Sigma x_i = ma\}$, write $x_m = ma - \Sigma_{i=1}^{m-1} x_i$ so that $x_1, \ldots, x_{m-1}$ are independent. To prove Lemma 1, it suffices to show that

$$\partial F/\partial x_j = 0 \quad \text{at} \quad (x_1, \ldots, x_m) = (a, a, \ldots, a).$$

But because x_m depends on all x_j, $1 \leqslant j \leqslant m-1$, we find

$$\partial F/\partial x_j = Tr(e^{a\mathbf{A}}e^{x_1\mathbf{B}}\ldots e^{a\mathbf{A}}\mathbf{B}e^{x_j\mathbf{B}}\ldots e^{a\mathbf{A}}e^{x_m\mathbf{B}})$$
$$- Tr(e^{a\mathbf{A}}e^{x_1\mathbf{B}}\ldots e^{a\mathbf{A}}e^{x_j\mathbf{B}}\ldots e^{a\mathbf{A}}e^{x_m\mathbf{B}}\mathbf{B}).$$

When $(x_1, \ldots, x_{m-1}) = (a, \ldots, a)$ the two Trace terms are equal and $\partial F/\partial x_j = 0$. □

LEMMA 2. *For all* $N = 1, 2, \ldots,$

$$Tr([e^A e^B]^N) \geqslant Tr(e^{(A+B)N}).$$

Proof. Choosing $a = 1/K$, $m = KN$ as before, let $x_j = 0$ for all j that are not exactly divisible by K and let $x_j = 1$ if K divides j exactly. In this case,

$$F(x_1, \ldots, x_m) = Tr([e^A e^B]^N).$$

On the other hand

$$F(a, \ldots, a) = Tr([e^{aA} e^{aB}]^m) = Tr([e^{A/K} e^{B/K}]^{KN})$$

and Lemma 1 asserts that

$$Tr([e^A e^B]^N) \geqslant Tr([e^{A/K} e^{B/K}]^{KN})$$

Hold N fixed and let $K \to \infty$, using Sophus Lie's formula.   □

Proof of (2.3). For any nonnegative $n \times n$ matrix $\mathbf{M}$,

$$r(\mathbf{M}) = \lim_{N \to \infty} [Tr(\mathbf{M}^N)]^{1/N}.$$

Apply this to the inequality of Lemma 2, using $\mathbf{M} = e^A e^B$ on the left and $\mathbf{M} = e^{A+B}$ on the right.   □

The central idea in this proof of (2.3) is to use the Feynman-Kac formula. It seems to be harder to find a proof of the strict inequality in (2.3).

4. Open Problems.   The concluding section is devoted to conjectures and open problems.

The first three conjectures, taken from CFKK (pp. 92–93), arose in attempts to find proofs of (2.3) and related results.

CONJECTURE 1.   *Let* $\mathbf{A}$ *be an* $n \times n$ *essentially nonnegative matrix,* $\mathbf{B}$ *an* $n \times n$ *real diagonal matrix. Then* $F(t) = \log r(e^{At} e^{Bt})$ *is convex in the real variable* t. *If, in addition,* $\mathbf{A}$ *is irreducible and* $\mathbf{B}$ *is not a scalar matrix, then* $F(t)$ *is strictly convex in* t.

The conjecture is proved only for 2×2 matrices. I have checked it numerically with examples of 3×3 matrices, including matrices $\mathbf{A}$ with real and complex spectra. For $n \times n$ matrices, it is not hard to show that $F(t) + F(-t) \geqslant 0 = 2F(0)$. If r is replaced by Tr, then $F(t)$ is not convex in t for some 3×3 matrices $\mathbf{A}$ with complex spectra. If the stated conjecture is true, it provides another proof of both the weak and strict inequality (2.3) via Theorem 5 of CFKK (p. 78).

CONJECTURE 2.   *Let* $\mathbf{A}_1, \ldots, \mathbf{A}_k$ *be nonnegative irreducible* $n \times n$ *matrices with positive diagonal elements, for some positive integer* k. *Let* $\mathbf{D}_1, \ldots, \mathbf{D}_k$ *be real diagonal* $n \times n$ *matrices with zero trace. Then*

$$f(\mathbf{D}_1, \ldots, \mathbf{D}_k) = \log r(\mathbf{A}_1 e^{\mathbf{D}_1} \ldots \mathbf{A}_k e^{\mathbf{D}_k})$$

is a strictly convex function of $(\mathbf{D}_1, \ldots, \mathbf{D}_k)$.

If true, this conjecture would provide sufficient conditions for strict inequality in a generalization (Theorem 3 of CFKK, pp. 71–72) of (2.3).

CONJECTURE 3.   *Let* $\mathbf{A}$ *and* $\mathbf{B}$ *be* $n \times n$ *Hermitian matrices and* $a_i \geqslant 0$, $b_i \geqslant 0$, $i = 1, \ldots, n$. *Let* $a = \Sigma_i a_i$, $b = \Sigma_i b_i$. *Then*

$$\| e^{a_1 \mathbf{A}} e^{b_1 \mathbf{B}} \ldots e^{a_k \mathbf{A}} e^{b_k \mathbf{B}} \| \leqslant r(e^{2a\mathbf{A}} e^{2b\mathbf{B}})^{1/2},$$
$$r(e^{a_1 \mathbf{A}} e^{b_1 \mathbf{B}} \ldots e^{a_k \mathbf{A}} e^{b_k \mathbf{B}}) \leqslant r(e^{a\mathbf{A}} e^{b\mathbf{B}}).$$

The first of these inequalities is known to be true if, for some nonnegative scalar c, and

$i = 1, \ldots, k$, we have $b_i = ca_i$. The second inequality is known to be true when the same conditions hold and in addition max $a_i \leqslant a/2$.

Instead of the initial condition $P[V(0) = i] = 1$ assumed in section 2, assume that $P[V(0) = i] = \pi_i \geqslant 0$, $i = 1, \ldots, n$, where $\pi = (\pi_i)$ is an equilibrium probability row vector of Q, i.e. $\pi^T Q = 0$, $\Sigma_i \pi_i = 1$. Denote the expectations of $N(t)$ and $N^D(t)$ under these initial conditions by $E_\pi N(t)$ and $E_\pi N^D(t)$. Let 1 be the n-vector with all elements equal to 1. It is known (CFKK, p. 76) that, for integral times t,

$$E_\pi N(t) = \pi^T e^{(Q+B)t} 1 \leqslant E_\pi N^D(t) = \pi^T (e^Q e^B)^t 1,$$

with strict inequality if $t \geqslant 1$, Q is irreducible and at least two diagonal elements of B are distinct.

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What about higher moments of $N(t)$ and $N^D(t)$? For simplicity, take Q to be irreducible and $N_0 = 1$. Then $\pi > 0$ elementwise. For any real c,

$$E_\pi N^c(t) = E \exp[\Sigma_j b_j g_j(t)]c = E \exp[\Sigma_j (cb_j)g_j(t)] = \pi^T e^{(Q+cB)T} 1, \ t \geqslant 0,$$

and similarly

$$E_\pi[N^D(t)]^c = \pi^T (e^Q e^{cB})^t 1, \ t = 0, 1, 2, \ldots$$

Since Var $N(t) \geqslant 0$ and Var $N^D(t) \geqslant 0$, with both inequalities strict provided $t > 0$ and at least two diagonal elements of B are distinct, we have

$$\pi^T e^{(Q+2B)t} 1 \geqslant (\pi^T e^{(Q+B)t} 1)^2, \ t \geqslant 0,$$

$$\pi^T (e^Q e^{2B})^t 1 \geqslant (\pi^T (e^Q e^B)^t 1)^2, \ t = 0, 1, 2, \ldots,$$

with strict inequalities under the conditions stated.

More generally, I can prove that if A is an essentially nonnegative $n \times n$ matrix, B is a diagonal real $n \times n$ matrix, and x and y are nonnegative n-vectors $(1 < n < \infty)$, then

$$(x^T e^{(A+2B)t} y)(x^T e^{At} y) \geqslant (x^T e^{(A+B)t} y)^2, \ t \geqslant 0,$$

$$(x^T [e^A e^{2B}]^t y)(x^T e^{At} y) \geqslant (x^T [e^A e^B]^t y)^2, \ t = 0, 1, 2, \ldots,$$

with strict inequality if $t > 0$, A is irreducible, $x > 0$, $y > 0$, and at least two diagonal elements of B are distinct. Also,

$$r(e^{A+2B})r(e^A) \geqslant r^2(e^{A+B}),$$

$$r(e^A e^{2B})r(e^A) \geqslant r^2(e^A e^B).$$

If A is irreducible and at least two diagonal elements of B are distinct, the preceding inequalities are strict. The preceding inequalities hold if r is replaced throughout by Tr.

CONJECTURE 4. *Let A be an essentially nonnegative matrix and B a diagonal real matrix. Then*

(4.1) $$r(e^{2B} e^A)r(e^A) - r^2(e^B e^A) \geqslant r(e^{2B+A})r(e^A) - r^2(e^{B+A}),$$

If $u \geqslant 0$, $v \geqslant 0$ are n-vectors such that

(4.2) $$u^T e^A = u^T r(e^A),$$

(4.3) $$e^A v = r(e^A)v,$$

then for positive integers θ,

(4.4)
$$[\mathbf{u}^T(e^{2\mathbf{B}}e^{\mathbf{A}})^\theta\mathbf{v}][\mathbf{u}^Te^{\mathbf{A}\theta}\mathbf{v}] - [\mathbf{u}^T(e^{\mathbf{B}}e^{\mathbf{A}})^\theta\mathbf{v}]^2$$
$$\geq [\mathbf{u}^Te^{(2\mathbf{B}+\mathbf{A})\theta}\mathbf{v}][\mathbf{u}^Te^{\mathbf{A}\theta}\mathbf{v}] - [\mathbf{u}^Te^{(\mathbf{B}+\mathbf{A})\theta}\mathbf{v}]^2.$$

*When **A** is irreducible and **B** is not a scalar matrix (i.e. at least two diagonal elements of **B** are distinct), both inequalities are strict.*

If either (4.2) or (4.3) fails to hold, then the conjectured inequality (4.4) need not hold. For example, let

$$\mathbf{A} = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, \mathbf{B} = \begin{pmatrix} 1 & 0 \\ 0 & 0 \end{pmatrix}$$
$$\mathbf{u} = \begin{pmatrix} 1 \\ 0 \end{pmatrix}, \mathbf{v} = \begin{pmatrix} 1 \\ 1 \end{pmatrix}$$

so that (4.3) holds but (4.2) fails. Then with $\theta = 1$, the left member of (4.4) is 0 while the right member is approximately 18.6917.

If **A** and **B** are complex Hermitian matrices, (4.1) need not hold. Numerous numerical examples have failed to falsify Conjecture 4. Conjecture 4 implies that

$$\mathrm{Var}\, N(t) \leq \mathrm{Var}\, N^D(t), t = 0, 1, 2, \dots ,$$

and gives (potentially) sufficient conditions for strict inequality.

CONJECTURE 5. *Under the assumptions of Conjecture 4, for every nonnegative integer k,*

$$r^k(e^{\mathbf{A}}e^{2\mathbf{B}})r^k(e^{\mathbf{A}}) - r^{2k}(e^{\mathbf{A}}e^{\mathbf{B}}) \geq r^k(e^{\mathbf{A}/2}e^{\mathbf{B}}e^{\mathbf{A}/2}e^{\mathbf{B}})r^k(e^{\mathbf{A}}) - r^{4k}(e^{\mathbf{A}/2}e^{\mathbf{B}/2}),$$

with strict inequality under the additional conditions given in Conjecture 4.

The use of Lie's formula shows that Conjecture 5 implies (4.1). For

$$r(e^{\mathbf{A}+2\mathbf{B}})r(e^{\mathbf{A}}) - r^2(e^{\mathbf{A}+\mathbf{B}})$$
$$= \lim_{k\to\infty}[r^{2^k}(e^{\mathbf{A}/2^k}e^{2\mathbf{B}/2^k})r^{2^k}(e^{\mathbf{A}/2^k}) - r^{2^{k+1}}(e^{\mathbf{A}/2^k}e^{\mathbf{B}/2^k})]$$

and (4.1) would hold if the sequence in brackets on the right were a decreasing function of k. The left side of (4.1) is the case when $k = 0$.

CONJECTURE 6. *Let **E** and **F** be $n \times n$ nonnegative matrices (elementwise), **F** diagonal. Then for every nonnegative integer k, the function*

$$H(t) = r^k(\mathbf{E}^2\mathbf{F}^{2(1+t)})r^k(\mathbf{E}^2\mathbf{F}^{2(1-t)}) - r^{2k}(\mathbf{EF}^{1+t})r^{2k}(\mathbf{EF}^{1-t})$$

*is convex in t on $[-1, +1]$. If **E** > 0 elementwise and all diagonal elements of **F** are positive and at least two of them are distinct, then $H(t)$ is strictly convex.*

I claim Conjecture 6 implies Conjecture 5. For

$$H(1) = r^k(\mathbf{E}^2\mathbf{F}^4)r^k(\mathbf{E}^2) - r^{2k}(\mathbf{EF}^2)r^{2k}(\mathbf{E})$$
$$= H(-1)$$

and by convexity $(H(1) + H(-1))/2 = H(1) \geq H(0)$. Thus

$$r^k(\mathbf{E}^2\mathbf{F}^4)r^k(\mathbf{E}^2) - r^{2k}(\mathbf{EF}^2)r^{2k}(\mathbf{E}) \geq r^{2k}(\mathbf{E}^2\mathbf{F}^2) - r^{4k}(\mathbf{EF}).$$

Letting $\mathbf{E} = e^{\mathbf{A}/2}$, $\mathbf{F} = e^{\mathbf{B}/2}$ and rearranging terms gives

$$r^k(e^{\mathbf{A}}e^{2\mathbf{B}})r^k(e^{\mathbf{A}}) - r^{2k}(e^{\mathbf{A}}e^{\mathbf{B}}) \geq r^{2k}(e^{\mathbf{A}/2}e^{\mathbf{B}})r^{2k}(e^{\mathbf{A}/2}) - r^{4k}(e^{\mathbf{A}/2}e^{\mathbf{B}/2})$$

which is equivalent to Conjecture 5.

The illustrative inequalities in section 2 for a random evolution driven by a reversible Markov chain are special cases of Corollary 4 of CFKK (p. 62), which states: If $\mathbf{A} = \mathbf{DSD}^{-1}$ where **S** is symmetric and **D** is diagonal nonsingular, **B** is diagonal real, and φ is a real-val-

ued continuous function of the eigenvalues of its matrix argument, finite when all elements of its argument are finite, such that

$$(4.5) \qquad \varphi([MM^*]^k) \geq |\varphi(M^{2k})|, \, k = 1, 2, \ldots ,$$

for every $n \times n$ complex matrix M, then

$$(4.6) \qquad \varphi(e^A e^B) \geq \varphi(e^{A+B}).$$

Does this result have a converse? If true, Conjecture 7 would provide a new characterization of reversibility.

CONJECTURE 7. *Let A be an essentially nonnegative matrix such that (4.6) holds for every diagonal real matrix B and every φ, as just described, that satisfies (4.5). Then there exists a symmetric matrix S and a diagonal nonsingular matrix D such that*

$$A = DSD^{-1}$$

So far in this paper, I have considered only the case where $N(t)$ is a real scalar. However, if the vat of bacteria contains more than one species of bacteria, or more than one genotype of the same species, or subgroups of a species differentiated by physical or biochemical markers, it is natural to try to model the simultaneous evolution of all distinguishable types.

Consider the following k-dimensional random evolution, where k is a fixed positive integer greater than 1. Let $B_1, \ldots, B_n$ be $k \times k$ real matrices and (as before) $V(t)$ a homogeneous continuous-time irreducible Markov process on the state space $\{1, \ldots, n\}$, with $V(0) = 1$, and with intensity matrix Q. Let $N(t)$ be a k-vector that evolves according to

$$dN(t)/dt = B_{V(t)}N(t) \text{ for } t \geq 0, N(0) = N_0.$$

For biological applications, the vector $N(t)$ of number of individuals of each type is required to be nonnegative. Given $N_0 \geq 0$, a condition sufficient to guarantee that, for all $t \geq 0$, $N(t) \geq 0$ is that each B_j is essentially nonnegative, i.e., every off-diagonal element of B_j is nonnegative, $j = 1, \ldots, n$. I henceforth assume that every B_j is essentially nonnegative.

This assumption makes the model more relevant to biological situations where an increase in the number of one type of bacteria leads to an increase (or no decrease) in the number of other types, as when types correspond to genotypes. It makes the model less relevant to biological situations where the types are different species, some of which consume other species.

Under these assumptions, I can prove that, if $\|.\|$ is any vector norm,

$$\lim t^{-1} \log \| E N(t) \| = \log r(e^{A+B}),$$

where A and B are both $(kn) \times (kn)$ matrices defined by

$$A = Q \otimes I_k, \, I_k = k \times k \text{ identity matrix}$$
$$B = \text{diag}(B_1, \ldots, B_n).$$

The same norm applied to matrices means the matrix norm induced by the chosen vector norm. It is easy to show that

$$\lim t^{-t} E \log \| N(t) \| \leq \Sigma_{i=1}^n \pi_i \| B_i \|.$$

QUESTION 1. *Is there a simple exact expression for $\lim t^{-1} E \log \| N(t) \|$ (analogous to that in the one-dimensional case)?*

As in the one-dimensional case, it is natural to suppose that a biologist who observed

this k-dimensional random evolution would construct a discrete-time approximation $N^D(t)$ according to

$$N^D(t+1) = \exp(B_{V(t)})N^D(t), t = 0, 1, \ldots, N^D(0) = N_0.$$

$$P[B_{V(t+1)} = B_j | B_{V(t)} = B_i] = (e^Q)_{ij} = p_{ij}, B_{V(0)} = B_1.$$

Thus $N^D(t)$ is determined by a Markovian product of random nonnegative matrices according to

$$N^D(t) = \exp(B_{V(t-1)})\exp(B_{V(t-2)}) \ldots \exp(B_{V(0)})N_0.$$

It follows from Furstenberg and Kesten (1960) that $\lim t^{-1} \log \|N^D(t)\|$ exists and equals $\lim t^{-1} E \log \|N^D(t)\|$ with probability 1.

QUESTION 2. *Is there a simple exact expression for $\lim t^{-1} E \log \|N^D(t)\|$?*

QUESTION 3. *What is the relation between $\lim t^{-1} E \log \|N(t)\|$ and $\lim t^{-1} E \log \|N^D(t)\|$?*

It is easy to show that

$$\lim t^{-1} \log \|E N^D(t)\| = \log r(e^A e^B),$$

where A and B are the $(kn) \times (kn)$ matrices defined above. This follows from a formula for $E N^D(t)$ that I published (Cohen, 1977) without knowing that it had been previously derived in a never-published (so far as I know) report of Bharucha (1960). The above formula is a Feynman-Kac formula for products of random matrices. The expression $\log r(e^{A+B})$ for the continuous-time random evolution may be derived by constructing a sequence of approximations to $N(t)$ using ever finer subdivisions of time, as in the one-dimensional case.

What is the relation between $\lim t^{-1} \log \|E N(t)\|$ and $\lim t^{-1} \log \|E N^D(t)\|$? The following conjecture would cover the special case when all the B_j matrices commute with one another.

CONJECTURE 8. *If n essentially nonnegative $k \times k$ matrices B_j satisfy*

$$B_i B_j = B_j B_i, \quad i, j = 1, \ldots, n,$$

then

$$r(e^{A+B}) \leq r(e^A e^B),$$

where R is any essentially nonnegative $n \times n$ matrix and

$$A = R \otimes I_k,$$

$$B = \text{diag}(B_1, \ldots, B_n).$$

If R and B_i, $i = 1, \ldots, n$ are all irreducible, then the inequality is strict.

The conjectured inequality need not hold if the assumed commutativity is not true. For example, if

$$R = \begin{pmatrix} 1 & 1 \\ 1 & 1 \end{pmatrix}, B_1 = \begin{pmatrix} 1 & 1 \\ 2 & 1 \end{pmatrix}, B_2 = \begin{pmatrix} 1 & 2 \\ 1 & 1 \end{pmatrix}.$$

then $B_1 B_2 \neq B_2 B_1$ and

$$r(\exp[R \otimes I_2 + \text{diag}(B_1, B_2)]) = 85.583$$
$$> r(\exp[R \otimes I_2]\exp[\text{diag}(B_1, B_2)]) = 84.671$$

(These numerical computations, and other tests of conjectures, were performed on the MATLAB system of Moler [1981] as implemented on SCORE in the Stanford University Computer Science Department.)

A sufficient condition for Conjecture 8 is:

CONJECTURE 9. *If* **R** *is an elementwise nonnegative* $n \times n$ *matrix and* $\mathbf{B}_i$, $i = 1, \dots ,$
n *are commuting (elementwise) nonnegative* $k \times k$ *matrices, then*

$$r(\mathbf{A}^2\mathbf{B}^2) \geqslant r^2(\mathbf{AB})$$

where **A** *and* **B** *are defined in Conjecture 8. If* **R** *and all* $\mathbf{B}_i$ *are (elementwise) positive,*
then the inequality is strict.

The counterexample to Conjecture 8 without commutativity also shows that Conjecture
9 fails without commutivity. In this case

$$\mathbf{A}^2\mathbf{B}^2 = \begin{pmatrix} 6 & 4 & 6 & 8 \\ 8 & 6 & 4 & 6 \\ 6 & 4 & 6 & 8 \\ 8 & 6 & 4 & 6 \end{pmatrix}, \mathbf{AB} = \begin{pmatrix} 1 & 1 & 1 & 2 \\ 2 & 1 & 1 & 1 \\ 1 & 1 & 1 & 2 \\ 2 & 1 & 1 & 1 \end{pmatrix}.$$

Since all row sums of $\mathbf{A}^2\mathbf{B}^2$ are 24, $r(\mathbf{A}^2\mathbf{B}^2) = 24$. Since all row sums of $\mathbf{AB}$ are 5, $r(\mathbf{AB})$
$= 5$. Thus $r(\mathbf{A}^2\mathbf{B}^2) < r^2(\mathbf{AB})$, contrary to the desired inequality.

So far we have considered two measures of the long-run growth rate of the k-dimensional
random evolution $N(t)$ in continuous time, namely $\lim t^{-1} E \log \|N(t)\|$ and $\lim t^{-1} \log \|E$
$N(t)\|$ (with corresponding measures for the discrete-time approximation $N^D(t)$). Another
plausible measure is $\lim t^{-1} \log E \|N(t)\|$. By the triangle inequality for norms,

$$\lim t^{-1} \log \|E N(t)\| \leqslant \lim t^{-1} \log E \|N(t)\|.$$

I claim that this inequality is in fact an equality for any vector norm. For any real or complex
k-vector x, the vector norm defined by

$$\|x\|_1 = \Sigma_j |x_j|$$

is the Hölder p-norm for $p = 1$. By construction, $N(t) \geqslant 0$. So $\|N(t)\|_1 = \Sigma_j N_j(t)$ and $\|E$
$N(t)\|_1 = \Sigma_j[EN(t)]_j = \Sigma_j E[N(t)]_j = E \Sigma_j N_j(t) = E \|N(t)\|_1$. For any other vector norm $\|.\|$,
there exist constants c and c_1 depending on $\|.\|$, such that for all x, $\|x\| \leqslant c_1\|x\|_1$ and $\|x\|_1$
$\leqslant c\|x\|$ (see e.g. Lancaster, 1977, pp. 199, 204). Therefore

$$\begin{aligned}
\lim t^{-1} \log E \|N(t)\| &\leqslant \lim t^{-1} \log c_1 E \|N(t)\|_1 \\
&= \lim t^{-1} \log E \|N(t)\|_1 \\
&= \lim t^{-1} \log \|EN(t)\|_1 \\
&\leqslant \lim t^{-1} \log c \|EN(t)\| \\
&= \lim t^{-1} \log \|EN(t)\|.
\end{aligned}$$

Combining this with the reverse inequality previously established shows that

$$\lim t^{-1} \log \|E N(t)\| = \lim t^{-1} \log E \|N(t)\|.$$

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