

**ERGODICITY OF DIFFUSION AND TEMPORAL
 UNIFORMITY OF DIFFUSION APPROXIMATION**

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Abstract

Let $\{X_N(t), t \geq 0\}$, $N = 1, 2, \dots$ be a sequence of continuous-parameter Markov processes, and let $T_N(t)f(x) = E_x[f(X_N(t))]$. Suppose that $\lim_{N \rightarrow \infty} T_N(t)f(x) = T(t)f(x)$, and that convergence is uniform over x and over $t \in [0, K]$ for all $K < \infty$. When is convergence uniform over $t \in [0, \infty)$? Questions of this type are considered under the auxiliary condition that $T(t)f(x)$ converges uniformly over x as $t \rightarrow \infty$. A criterion for such ergodicity is given for semigroups $T(t)$ associated with one-dimensional diffusions. The theory is illustrated by applications to genetic models.

DIFFUSION APPROXIMATION; ERGODIC THEORY; GENETIC MODELS

1. Introduction

The problem treated in this paper is conveniently illustrated within the framework of the Wright–Fisher model for changes in gene frequency in a monoecious diploid population of N individuals (see [2], Section 4.8). Let genotypes A_1A_1 , A_1A_2 and A_2A_2 have fitnesses $1 + s_1$, $1 + s_2$ and 1, respectively, and let α_1 and α_2 be the probabilities of mutation from A_1 to A_2 and from A_2 to A_1 . Suppose that $s_i = \bar{s}_i/N$ and $\alpha_i = \bar{\alpha}_i/N$, where \bar{s}_i and $\bar{\alpha}_i$ are constants, and $\bar{\alpha}_i \geq 0$. The sequence, $\{X_n^N, n \geq 0\}$, of A_1 gene proportions is a Markov process in $I_N = \{j/2N: j = 0, 1, \dots, 2N\}$. Let

$$T_N f(x) = E[f(X_{n+1}^N) | X_n^N = x],$$

$x \in I_N$, be the transition operator of the process, so that

$$T_N^n f(x) = E[f(X_n^N) | X_0^N = x].$$

These operators are defined for real-valued functions on I_N or on any larger set such as $I = [0, 1]$. Let $C(I)$ be the continuous real-valued functions on I .

There is a diffusion, $\{X(t), t \geq 0\}$, in I such that

$$\lim_{N \rightarrow \infty} T_N^n f(x_N) = E[f(X(t)) | X(0) = x] = T(t)f(x)$$

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for all $f \in C(I)$, if $n_N/N \rightarrow t$ and $x_N \rightarrow x$ ([7], Section 18.1). Letting $T_N(t) = T_N^{(Nt)}$, and noting that $T(t)f(x)$ is continuous in (t, x) , it follows that

$$(1) \quad \lim_{N \rightarrow \infty} \sup_{0 \leq t \leq K} \|T_N(t)f - T(t)f\| = 0$$

if $K < \infty$, where $\|g\| = \max_{x \in I_N} |g(x)|$. It is natural to wonder whether $\|T_N(t)f - T(t)f\| \rightarrow 0$ as $N \rightarrow \infty$, uniformly over all $t \geq 0$, i.e.,

$$(2) \quad \lim_{N \rightarrow \infty} \sup_{0 \leq t} \|T_N(t)f - T(t)f\| = 0.$$

This is a prototype of the question considered in this paper.

It follows from a result of Ethier ([1], Corollary 4.2) that (2) holds for all $f \in C(I)$ when there is no selection ($\bar{s}_1 = \bar{s}_2 = 0$). Ethier's result does not apply to models with selection. In Section 4 we shall show that (2) is also valid for the Wright–Fisher model with selection as well as mutation. Moreover this result extends to the non-Markovian gene frequency processes that arise in Moran's models for dioecious populations.

Our theory is not, however, limited to genetic models. Theorem 1 of the next section applies to discrete- or continuous-time Markov processes with arbitrary state space for which (1) holds and $T(t)f(x) \rightarrow T(\infty)f(x)$ uniformly over x as $t \rightarrow \infty$. According to the theorem, (2) is valid if and only if the same condition holds with $T(\infty)f$ in place of f . This is clearly the case if $T(\infty)f$ is constant, but the criterion is also satisfied in certain cases with non-constant $T(\infty)f$, such as the Wright–Fisher model with $\bar{\alpha}_1 = \bar{\alpha}_2 = 0$. Theorem 2 is an analogous limit theorem for non-Markovian processes, under the assumption that $T(\infty)f$ is constant.

Since Theorems 1 and 2 presuppose uniform convergence of $T(t)f$ as $t \rightarrow \infty$, application of these theorems requires appropriate ergodic theorems. Section 3 considers the ergodic theory of semigroups $T(t)$ corresponding to diffusions on real intervals. Theorem 3 shows that the required uniform convergence obtains if f is bounded and continuous and if there are no natural boundaries.

2. A limit theorem

Let (S, \mathcal{F}) be a measurable space, let S_N be a subset of S , and let $\mathcal{F}_N = \mathcal{F} \cap S_N$. Let $B(S)$ and $B(S_N)$ be the bounded \mathcal{F} - and \mathcal{F}_N -measurable real-valued functions on S and S_N , respectively. For $f \in B(S_N)$, let

$$\|f\| = \sup_{x \in S_N} |f(x)|.$$

We use the same notation for the supremum norm on $B(S)$. Let $\{T(t), t \geq 0\}$ be a semigroup of (linear) contractions on $B(S)$, i.e., $T(s)T(t) = T(s+t)$ and $\|T(t)f\| \leq \|f\|$. In order to treat continuous- and discrete-parameter semigroups

simultaneously, $\{T_N(t), t \geq 0\}$ may be either a semigroup of contractions on $B(S_N)$, or a family of operators derived from a contraction T_N in the following way: $T_N(t) = T_N^n$, where $n = [t/h_N]$ and h_N is a sequence of positive numbers with limit 0. In the latter case, $T_N(s)T_N(t) = T_N(s+t)$ whenever s or t is a multiple of h_N . (In our genetic example, $h_N = N^{-1}$.) For $f \in B(S)$ and $K < \infty$, let

$$r_N(f, K) = \sup_{0 \leq t \leq K} \|T_N(t)f - T(t)f\|$$

and

$$r_N(f, \infty) = \sup_{0 \leq t} \|T_N(t)f - T(t)f\|.$$

The notation $T_N(t)f$ is shorthand for $T_N(t)f_N$, where f_N is the restriction of f to S_N .

Theorem 1. Suppose that $f \in B(S)$ has the following properties:

$$(3) \quad \lim_{t \rightarrow \infty} \|T(t)f - T(\infty)f\| = 0$$

for some $T(\infty)f \in B(S)$, and

$$(4) \quad \lim_{N \rightarrow \infty} r_N(f, K) = 0$$

for all $K < \infty$. Then

$$(5) \quad \lim_{N \rightarrow \infty} r_N(f, \infty) = 0$$

if and only if

$$(6) \quad \lim_{N \rightarrow \infty} r_N(T(\infty)f, \infty) = 0.$$

Kurtz [4] has given useful criteria for (4) in terms of the generator, A_N , of $T_N(t)$. Kurtz's results are formulated in a more general setting, to which Theorem 1 is easily extended.

Proof. Let K be positive, and, in the discrete case, let K be an integer multiple of h_N . If $u = t - K > 0$,

$$\begin{aligned} T_N(t)f - T(t)f &= T_N(u)T_N(K)f - T(u)T(K)f \\ &= T_N(u)(T_N(K)f - T(K)f) \\ &\quad + T_N(u)(T(K)f - T(\infty)f) \\ &\quad + (T_N(u)T(\infty)f - T(u)T(\infty)f) \\ &\quad + T(u)(T(\infty)f - T(K)f). \end{aligned}$$

Thus

$$\|T_N(t)f - T(t)f\| \leq r_N(f, K) + r_N(T(\infty)f, \infty) + 2\|T(K)f - T(\infty)f\|$$

for $t > K$. But this inequality holds trivially for $t \leq K$, so

$$r_N(f, \infty) \leq r_N(f, K) + r_N(T(\infty)f, \infty) + 2\|T(K)f - T(\infty)f\|.$$

It follows immediately that (3), (4), and (6) imply (5). A similar argument, which we omit, shows that (3) and (5) imply (6).

Note that $T(t)T(\infty)f = T(\infty)f$, so

$$r_N(T(\infty)f, \infty) = \sup_{0 \leq t} \|T_N(t)T(\infty)f - T(\infty)f\|.$$

Thus (6) says that $T(\infty)f$ is asymptotically invariant for $T_N(t)$. Condition (6) is certainly satisfied if $T_N(t)T(\infty)f = T(\infty)f$ for all N and t , e.g., if $T(\infty)f$ is a constant function and $T_N(t)$ is conservative ($T_N(t)1 = 1$). More generally, (6) holds if there is a sequence $g_N \in B(S_N)$ such that $T_N(t)g_N = g_N$ for all N and t , and $\|g_N - T(\infty)f\| \rightarrow 0$ as $N \rightarrow \infty$. Indeed, if $T_N(t)g_N = g_N$, then

$$T_N(t)T(\infty)f - T(\infty)f = T_N(t)(T(\infty)f - g_N) + (g_N - T(\infty)f),$$

so

$$r_N(T(\infty)f, \infty) \leq 2\|g_N - T(\infty)f\|.$$

We now give a limit theorem for non-Markovian processes that is analogous to a special case of Theorem 1. For each $N \geq 1$, let $\{X_N(t), t \geq 0\}$ be a continuous-parameter stochastic process in S_N . The process may, for example, arise from a discrete-parameter process $\{X_n^N, n \geq 0\}$ in the usual way: $X_N(t) = X_n^N$, $n = [t/h_N]$. Let $\{T(t), t \geq 0\}$ be a semigroup of positive ($T(t)f \geq 0$ if $f \geq 0$) conservative linear operators on $B(S)$. For $f \in B(S)$ and $K < \infty$, let

$$\rho_N(f, K) = \sup_{\substack{0 \leq s \\ 0 \leq t \leq K}} |E[f(X_N(t+s))] - E[T(t)f(X_N(s))]|$$

and let $\rho_N(f, \infty)$ be defined analogously.

Theorem 2. If (3) holds, $T(\infty)f$ is constant, and $\lim_{N \rightarrow \infty} \rho_N(f, K) = 0$ for $K < \infty$, then $\lim_{N \rightarrow \infty} \rho_N(f, \infty) = 0$.

The straightforward proof is omitted.

3. Ergodic theory for diffusions

In many applications, the limiting semigroup $T(t)$ corresponds to a one-dimensional diffusion. In this section we give a criterion for (3) to hold for such a

semigroup. The ergodic theory of these semigroups is well developed (see [6]). The only novelty of our work is consideration of uniformity of convergence.

Let I be a real interval, let $d_0 = \inf I$ and $d_1 = \sup I$, and let $\{P_x: x \in I\}$ be a family of probabilities on $\Omega = C([0, \infty))$ that constitutes a regular diffusion in the sense of Freedman [3]. Let S and m be, respectively, the scale function and speed measure of the process. These can be used to classify d_i as a regular, exit, entrance or natural boundary (see Mandl [5], pp. 24–25). If $d_i \in I$, it may also be classified as absorbing or instantaneous (see Freedman [3], p. 107). For $\omega \in \Omega$, let $X(t) = X(t, \omega) = \omega(t)$, and let

$$T(t)f(x) = E_x[f(X(t))] = \int_{\Omega} f(\omega(t))P_x(d\omega)$$

for $f \in B(I)$. Finally, let $BC(I)$ be the bounded continuous real-valued functions on I .

Theorem 3. *If there are no natural boundaries, then (3) holds for all $f \in BC(I)$. If neither boundary is absorbing, then*

$$T(\infty)f = \int_I f(x)m(dx)/m(I).$$

If d_i is absorbing but the other boundary is not, then $T(\infty)f = f(d_i)$. Finally, if both boundaries are absorbing, then

$$T(\infty)f(x) = f(d_1)\psi(x) + f(d_0)(1 - \psi(x)),$$

where $\psi(x) = (S(x) - S(d_0))/(S(d_1) - S(d_0))$.

Proof. Suppose, first, that there are no absorbing (or natural) boundaries. Then $m(I) < \infty$. Also, $E_x[\tau_y] < \infty$ for all $x, y \in I$, where τ_y is the time at which $X(t)$ first reaches y , so the proof of Theorem 3.2 of Maruyama and Tanaka [6] applies, and we conclude that $T(t)f(x) \rightarrow T(\infty)f$ as $t \rightarrow \infty$ for all $x \in I$ and $f \in BC(I)$. (It is not difficult to show that Maruyama's and Tanaka's expression for the limiting distribution is equivalent to $m(I)^{-1}m$.) Thus it remains only to show that convergence is uniform. Let $d \in I$, let $\tau = \tau_d$, and assume, without loss of generality, that $T(\infty)f = 0$. Then, for $0 < s < t$,

$$\begin{aligned} T(t)f(x) &= E_x[f(X(t)), \tau \leq s] + E_x[f(X(t)), \tau > s] \\ &= E_x[T(t - \tau)f(d), \tau \leq s] + E_x[f(X(t)), \tau > s]. \end{aligned}$$

Hence

$$\|T(t)f\| \leq \sup_{K \geq t-s} |T(K)f(d)| + \|f\| \sup_{x \in I} P_x\{\tau > s\}.$$

It is not difficult to show that $\sup_{x \in I} P_x\{\tau > s\} \rightarrow 0$ as $s \rightarrow \infty$, and (3) follows. The

other cases in Theorem 3, involving absorbing boundaries, can be treated by analogous and equally simple arguments, which we omit.

The assumption that $\{P_t : x \in I\}$ is regular implies that $d_i \notin I$ if d_i is an entrance boundary. It is sometimes convenient to close the state space, I , by adjoining entrance boundaries, and Theorem 3 applies equally well to the extended semigroup thus obtained.

4. Applications

We have already seen that (4) holds for $f \in C(I)$ in the Wright–Fisher model, regardless of the values of $\bar{\alpha}_i$ and $\bar{\delta}_j$. We now show that (5) is also valid. The limiting diffusion never has natural boundaries; i is an exit (hence absorbing) boundary if $\bar{\alpha}_i = 0$, and i is entrance or regular (and instantaneous) if $\bar{\alpha}_i > 0$. Thus (3) holds by Theorem 3. If $\bar{\alpha}_1 > 0$ or $\bar{\alpha}_2 > 0$, then $T(\infty)f$ is constant, and (6) is satisfied. Thus (5) follows from Theorem 1. Suppose now that $\bar{\alpha}_1 = \bar{\alpha}_2 = 0$, so that both boundaries are absorbing for the limiting diffusion. We also have $\alpha_1 = \alpha_2 = 0$, so 0 and 1 are absorbing for X_N^N . Let $\varphi_N(x)$ be the probability of absorption at 1, starting at x , and let

$$g_N(x) = T_N(\infty)f(x) = f(1)\varphi_N(x) + f(0)(1 - \varphi_N(x)).$$

Then $T_N g_N = g_N$. Also, $\|\varphi_N - \psi\| \rightarrow 0$ as $N \rightarrow \infty$ ([7], p. 260), so $\|g_N - T(\infty)f\| \rightarrow 0$ as $N \rightarrow \infty$ (see Theorem 3 for ψ and $T(\infty)f$). As observed following the proof of Theorem 1, these conditions imply (6). Hence Theorem 1 yields (5).

It can be shown that Theorem 2 applies to the two genetic models of Moran considered in [8]. The conclusion is that $\lim_{N \rightarrow \infty} \rho_N(f, \infty) = 0$ for $f \in C([0,1])$ if $\max\{\bar{\alpha}_1, \bar{\alpha}_2\} > 0$ or if $\bar{\alpha}_1 = \bar{\alpha}_2 = 0$ and $f(0) = f(1)$. Nothing need be assumed about the distribution of $X^N(0)$. We omit details.

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