

**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  $\alpha_1$  and  $\alpha_2$  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  $\tau_y$  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  $\{P_x : x \in I\}$  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  $\bar{\beta}_i$ . 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  $\psi$  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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