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# Total variation approximation for quasi-equilibrium distributions, II

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#### Abstract

Quasi-stationary distributions have been used in biology to describe the steady state behaviour of Markovian population models which, while eventually certain to become extinct, nevertheless maintain an apparent stochastic equilibrium for long periods. However, they have substantial drawbacks; a Markov process may not possess any, or may have several, and their probabilities can be very difficult to determine. Here, we consider conditions under which an apparent stochastic equilibrium distribution can be identified and computed, irrespective of whether a quasi-stationary distribution exists, or is unique; we call it a quasi-equilibrium distribution. The results are applied to multi-dimensional Markov population processes. © 2012 Elsevier B.V. All rights reserved.

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# 1. Introduction

The following Markovian birth and death process X in continuous time can be used to model a rather general population growth process. X(t) represents the number of individuals at time tin a population in a fixed region of area A, and its evolution is governed by the transition rates

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$$q_{i,i+1} = i\beta(i/A), \qquad q_{i,i-1} = i\delta(i/A), \quad i \ge 1;$$
  

$$q_{ij} = 0 \quad \text{otherwise},$$
(1.1)

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where  $\beta(x)$  and  $\delta(x)$  are the *per capita* rates of birth and mortality at population density x = i/A. For instance, the stochastic version of the logistic growth model of Verhulst [23] falls into the above framework, with  $\beta(x) = b$  constant in time, and with  $\delta(x) = d + cx$ , linearly increasing in x. Verhulst [23] was the first to propose a mathematical model for the evolution of a population that exhibits a non-zero equilibrium, something not allowed for in the Malthusian law of exponential growth. However, if the set of states  $\mathbb{N}$  is a communicating class and  $\inf_{x>0} \delta(x) > 0$ , the stochastic model does not have a non-zero equilibrium distribution, even if  $\beta(0) > \delta(0)$  and  $\lim_{x\to\infty} (\beta(x) - \delta(x)) < 0$ , since  $\mathbb{N}$  is then transient, and eventual absorption in 0 is certain. This appears to be a significant drawback for the application of the model in practice, but closer analysis reveals that the process can nonetheless exhibit apparent equilibrium behaviour over very long periods of time, with extinction occurring as the result of some 'exceptional' event.

Darroch and Seneta [7], building on the work of Yaglom [24] in the context of branching processes, introduced the concept of a quasi-stationary distribution, in an attempt to describe such long term behaviour in a transient Markov chain, prior to eventual absorption. However, for chains with countably infinite state space, Seneta and Vere-Jones [21] showed that the quasi-stationary distribution need neither exist nor be unique. Furthermore, even when there is a unique quasi-stationary distribution, its calculation may pose substantial problems. This apparently makes the quasi-stationary distribution unsatisfactory for typical biological applications. In an earlier paper [3], we were nonetheless able to give conditions under which the quasi-stationary distribution indeed represents the apparent equilibrium of a continuous time Markov chain X, prior to absorption. Under these conditions, which can be simply expressed in terms of the properties of the chain, there is a unique quasi-stationary distribution, and it can be approximated to a specified accuracy by the equilibrium distribution of a positively recurrent 'returned process'  $X^{\mu}$ , which is typically much easier to compute.

Because the conditions given in [3] imply that the chain X has a unique quasi-stationary distribution, its results shed no light on what happens in the unsatisfactory situations in which there are many quasi-stationary distributions, or in which there are none. For instance, a model for the evolution of a population commonly used in ecology has a *per capita* death rate  $\delta(x) = d$  that remains constant as x increases, and a birth rate that declines exponentially,  $\beta(x) = be^{-\alpha x}$  for some  $\alpha > 0$  [16]. Although this model also gives rise to apparently stable equilibrium behaviour for long periods of time, it follows from [22] that the process actually has infinitely many possible quasi-stationary distributions. In such cases, there is no obvious candidate distribution for describing its quasi-equilibrium.

In this paper, we are concerned with describing the long term behaviour of models, such as that above, in which the quasi-stationary distribution need neither exist nor be unique. We introduce a new set of conditions, complementary to those in [3], which are satisfied in many biologically plausible models. Under these conditions, we show that the 'return' distribution can be used as a good approximation to the distribution that is observed in quasi-equilibrium, and hence that it provides a more robust approximation than the quasi-stationary distribution, in that the latter can only be used in rather restricted circumstances. Furthermore, the 'returned' process has a proper long term limiting distribution, which can be much easier to determine than a quasi-stationary distribution, making it a much more practical alternative.

Denoting the state space of X by  $C \cup \{0\}$ , where 0 is the cemetery state and C is irreducible, the returned process  $X^{\mu}$  is also Markov. It evolves like X, except when it reaches the state 0. Whenever it does, instead of being absorbed in 0, it is instantaneously returned to C according to the 'return' probability distribution  $\mu$ ; hence each  $X^{\mu}$  is a recurrent process. Under our conditions, the returned processes for a wide class of return distributions all have very similar equilibrium distributions, and the distribution of X(t), given any reasonable fixed initial state, is also similar to them for long periods of time. Thus, for computational and practical purposes, the situation is satisfactorily resolved. Any member  $\mu$  of the class of 'good' return distributions can be chosen, and the equilibrium distribution of  $X^{\mu}$  then serves as a quasi-equilibrium approximation to  $\mathcal{L}(X(t))$  in the appropriate range of t.

The main results, Theorems 2.3 and 2.4, are proved in Section 2. In Section 3, as an illustration, we discuss the application of the theorems to birth and death processes. These processes have been widely studied, because of their relatively simple structure, and allow our results to be easily interpreted. Our theorems are however equally applicable to processes with more complicated structure, and we illustrate their application to Markov population processes in several dimensions in Section 4. There are many different multi-dimensional evanescent population processes that are density dependent and satisfy the local irreducibility and persistence conditions used there. These include models of chemical processes [11], competition [2,17], epidemics and rumours [5], metapopulations [19], networks [20,13], viral replication and growth [1,6] and genetics [15]. Theorem 4.1 complements the usual Gaussian approximation for these models, by showing that the equilibrium distribution  $\tilde{\pi}_N^{\delta_s}$  of an 'accelerated return process' is a very good approximation in total variation to the law of the process, at any time in a range bounded below by a suitable power of N and above by a quantity growing exponentially with N.

### 2. The return approximation

Assume that X is a stable, conservative and non-explosive pure jump Markov process on a countable state space, consisting of a single transient class C together with a cemetery state 0. For any probability distribution  $\mu$  on C, define the modified process  $X^{\mu}$  with state space C to have exactly the same behaviour as X while in C, but, on reaching 0, to be instantly returned to C according to the distribution  $\mu$ . Thus, if Q denotes the infinitesimal matrix associated with X, and  $Q^{\mu}$  that belonging to  $X^{\mu}$ , we have

$$q_{ij}^{\mu} = q_{ij} + q_{i0}\mu_j \quad \text{for } i, j \in C.$$
(2.1)

In this section, under a rather simple set of conditions, we show that the *stationary* distribution  $\pi^{\mu}$  of  $X^{\mu}$  is little influenced by the choice of  $\mu$ , for  $\mu$  in a large class  $\mathcal{M}$  of distributions. We give a bound, uniform for all  $\mu, \nu \in \mathcal{M}$ , on the total variation distance

$$d_{\mathrm{TV}}(\pi^{\nu}, \pi^{\mu}) := \sup_{A \in C} |\pi^{\nu}\{A\} - \pi^{\mu}\{A\}| = \frac{1}{2} \sum_{k \in C} |\pi^{\nu}(k) - \pi^{\mu}(k)|$$

between  $\pi^{\nu}$  and  $\pi^{\mu}$ , that is expressed in terms of hitting probabilities and mean hitting times for the process X. The bound is such that it can be expected to be small in circumstances in which the process X typically spends a long time in C in apparent equilibrium, before being absorbed in 0 as a result of an 'exceptional' event.

Define

$$\tau_A := \inf\{t > 0: X(t) \in A, X(s) \notin A \text{ for some } s < t\},$$

$$(2.2)$$

with the infimum over the empty set being taken to be  $\infty$ , noting that  $\tau_A > 0$  a.s. even when  $X(0) \in A$ . Our basic conditions can then be expressed as follows.

**Condition B.** There exists  $s \in C$  such that, defining

$$p_k := \mathbb{P}_k[X_{\tau_{\{s,0\}}} = s]; \qquad T_k := \mathbb{E}_k[\tau_{\{s,0\}}],$$

we have

(i) 
$$\inf_{k \in C} p_k = p > 0;$$
  
(ii)  $T_k < \infty$  for all  $k \in C$ .

Here,  $\mathbb{P}_k$  and  $\mathbb{E}_k$  refer to the distribution of *X* conditional on *X*(0) = *k*.

Condition B(i) can be expected to be satisfied in reasonable generality, and is the same as Condition A(i) in [3]. Condition B(ii) substantially relaxes Condition A(ii) in [3], which stipulated that  $T_k \leq T < \infty$ , *uniformly* for all  $k \in C$ . If X is typically to spend a long time in apparent equilibrium before being absorbed in 0, it will be necessary for  $1 - p_s$ , the probability that an excursion from s lands in 0, to be small.

We first note that

$$T_s = \sum_{k \in C} T_{sk} < \infty,$$

where

$$T_{sk} := \int_0^\infty \mathbb{P}_s[\{\tau_{\{s,0\}} > t\} \cap \{X(t) = k\}] dt$$

is the expected amount of time spent in k before first returning to  $\{s, 0\}$ , starting in s. Hence, for any  $\zeta > 0$ , we can pick  $C_{\zeta} \subset C$  such that

$$\sum_{k \notin C_{\zeta}} T_{sk} \le \zeta (1 - p_s) T_s;$$
(2.3)

we do so in such a way that  $s \in C_{\zeta}$ , and that  $T_{\zeta}^+ := \sup_{k \in C_{\zeta}} T_k$  is as small as possible. We then define the process  $X_{\zeta}$  to be the same as X, except that any excursions outside  $C_{\zeta}$  take zero time to complete. This process  $X_{\zeta}$  now satisfies Condition A of [3], so that the results of [3] can be applied to it. Finally, we extend the results for  $X_{\zeta}$  to the process X. To accomplish this programme, we need some preparatory results.

**Lemma 2.1.** Define  $\mu(T) := \sum_{k \in C} \mu(k)T_k$ . Then, under Condition B,

(i) 
$$\mu(T) \leq \mathbb{E}^{\mu} \tau_{\{s\}}^{\mu} \leq \mu(T)/p$$
;  
(ii)  $\mathbb{E}_{k} \tau_{\{s\}}^{\mu} \leq T_{k} + (1 - p_{k})\mu(T)/p, \quad k \in C$ ;  
(iii)  $\mathbb{E}_{s} \tau_{\{s\}}^{\mu} < \infty \quad \text{if and only if} \quad \mu(T) < \infty$ ,

where  $\tau_A^{\mu}$  is defined similarly to  $\tau_A$ , but with the process  $X^{\mu}$  in place of X, and  $\mathbb{E}^{\mu}$  denotes expectation under the initial distribution  $\mu$ .

**Proof.** The proof is based on the equation

$$\tau_{\{s\}}^{\mu} = \tau_{\{s,0\}}^{\mu} + \tau_{\{s\}}^{\mu,1}, \tag{2.4}$$

in which  $\tau_{\{s\}}^{\mu,1}$  is the time that elapses after  $\tau_{\{s,0\}}^{\mu}$  until  $X^{\mu}$  first reaches *s*, zero if  $X^{\mu}(\tau_{\{s,0\}}) = s$ . Taking expectations with respect to  $\mathbb{P}^{\mu}$ , this yields

$$\mathbb{E}^{\mu}\tau^{\mu}_{\{s\}} = \sum_{k \in C} \mu(k) \{ T_k + (1 - p_k) \mathbb{E}^{\mu}\tau^{\mu, 1}_{\{s\}} \},\$$

from which it follows that

$$\mu(T) \le \mathbb{E}^{\mu} \tau^{\mu}_{\{s\}} \le \mu(T) + (1-p) \mathbb{E}^{\mu} \tau^{\mu}_{\{s\}}$$

and Part (i) is proved. Part (ii) follows by taking expectations in (2.4) with respect to  $\mathbb{P}_k$ , which also gives

$$\mathbb{E}_{k}\tau^{\mu}_{\{s\}} \geq (1-p_{k})\mathbb{E}^{\mu}\tau^{\mu}_{\{s\}} \geq (1-p_{k})\mu(T).$$

Part (iii) follows from these considerations, taking k = s.  $\Box$ 

We now define

 $\mathcal{M}_M := \{ \mu \in \mathcal{PM}(C) \colon \mu(T) \leq MT_s \},\$ 

for any M > 0. The next lemma bounds the equilibrium probability that  $X^{\mu} \notin C_{\zeta}$ , for any  $\mu \in \mathcal{M}_M$ .

**Lemma 2.2.** Under Condition B, for any  $\mu \in \mathcal{M}_M$ , we have

$$\pi^{\mu}(C_{\zeta}^{c}) \leq (1-p_{s})\{\zeta + M/p\} \implies \varepsilon(\zeta, M).$$

Proof. By a standard renewal argument,

$$\pi^{\mu}(A)\mathbb{E}_{s}\tau^{\mu}_{\{s\}} = \sum_{k \in A} \mathbb{E}_{s} \left\{ \int_{0}^{\infty} I[\tau^{\mu}_{\{s\}} > t] I[X(t) = k] dt \right\}$$
$$\leq \sum_{k \in A} T_{sk} + (1 - p_{s})\mathbb{E}^{\mu}\tau^{\mu}_{\{s\}}.$$

It thus follows from (2.3), (2.4) and Lemma 2.1(i) that

$$\pi^{\mu}(C_{\zeta}^{c})T_{s} \leq \pi^{\mu}(C_{\zeta}^{c})\mathbb{E}_{s}\tau_{\{s\}}^{\mu} \leq (1-p_{s})(\zeta T_{s}+\mu(T)/p),$$

and the lemma follows.  $\Box$ 

In what follows, we assume that  $M \ge 1$ , ensuring that the distribution  $\delta_s$  that puts probability 1 on the state *s* itself belongs to  $\mathcal{M}_M$ .

We now return to the pure jump Markov process  $X_{\zeta}$ , which has the same jump chain as X, and the same jump rates  $q_k$  for all  $k \in C_{\zeta}$ , but with  $q_k = \infty$  for  $k \notin C_{\zeta}$ . We also define its returned processes  $X_{\zeta}^{\mu}$  in the same way as for X, but with the new jump rates. We then define

$$T_{s}^{(\zeta)} := \sum_{k \in C_{\zeta}} T_{sk} \ge T_{s} \{1 - \zeta(1 - p_{s})\},$$
(2.5)

the mean time for  $X_{\zeta}$  to return to the set {0, s}, starting from s, the last inequality following from (2.3).

**Theorem 2.3.** Suppose that Condition B holds, and that  $M \ge 1$ . Then, for any  $\mu \in \mathcal{M}_M$ ,

$$d_{\mathrm{TV}}(\pi^{\mu}, \pi^{\delta_s}) \leq 2(1 - p_s) \left( \frac{T_{\zeta}^+}{pT_s} + \zeta + \frac{M}{p} \right).$$

**Proof.** We begin by considering the process  $X_{\zeta}^{\mu}$  for any  $\mu \in \mathcal{M}_M$ , noting that, for any  $k \in C_{\zeta}$ , its equilibrium distribution  $\pi_{\zeta}^{\mu}$  satisfies

$$\pi_{\zeta}^{\mu}(k) = \pi^{\mu}(k) / \pi^{\mu}(C_{\zeta}).$$
(2.6)

Now the process  $X_{\zeta}$  satisfies Condition A of [3], and hence, from (2.13) of [3],

$$d_{\rm TV}(\pi_{\zeta}^{\mu}, \pi_{\zeta}^{\delta_s}) \le 2(T_{\zeta}^+/p) \sum_{k \in C_{\zeta}} \pi_{\zeta}^{\delta_s}(k) q_{k0}.$$
(2.7)

Then, by a renewal argument, letting  $N_k(t)$  denote the number of visits of  $X^{\delta_s}$  to k in [0, t], we have

$$\sum_{k \in C} \pi^{\delta_s}(k) q_{k0} = \lim_{t \to \infty} t^{-1} N_0(t)$$
$$= \lim_{t \to \infty} \{t^{-1} N_s(t)\} \lim_{t \to \infty} \{N_0(t)/N_s(t)\} = T_s^{-1}(1-p_s).$$
(2.8)

It now follows from (2.6)–(2.8) that

$$d_{\rm TV}(\pi_{\zeta}^{\mu},\pi_{\zeta}^{\delta_s}) \le 2(T_{\zeta}^{+}/p)T_s^{-1}(1-p_s)/\pi^{\delta_s}(C_{\zeta}).$$

Hence

$$\begin{split} d_{\mathrm{TV}}(\pi^{\mu}, \pi^{\delta_{s}}) &= \frac{1}{2} \sum_{k \in C_{\zeta}} |\pi^{\mu}_{\zeta}(k) \pi^{\mu}(C_{\zeta}) - \pi^{\delta_{s}}_{\zeta}(k) \pi^{\delta_{s}}(C_{\zeta})| + \frac{1}{2} \sum_{k \notin C_{\zeta}} |\pi^{\mu}(k) - \pi^{\delta_{s}}(k)| \\ &\leq \pi^{\delta_{s}}(C_{\zeta}) d_{\mathrm{TV}}(\pi^{\mu}_{\zeta}, \pi^{\delta_{s}}_{\zeta}) + \frac{1}{2} |\pi^{\delta_{s}}(C_{\zeta}) - \pi^{\mu}(C_{\zeta})| \\ &\quad + \frac{1}{2} (\pi^{\mu}(C^{c}_{\zeta}) + \pi^{\delta_{s}}(C^{c}_{\zeta})) \\ &\leq 2(T^{+}_{\zeta}/p) T^{-1}_{s}(1 - p_{s}) + 2\varepsilon(\zeta, M), \end{split}$$

this last from Lemma 2.2; as before,  $\delta_s \in \mathcal{M}_M$ , because  $M \ge 1$ .  $\Box$ 

**Remark.** Of course, for the theorem to imply that  $\pi^{\mu}$  and  $\pi^{\delta_s}$  are close, one needs  $(1 - p_s)$  to be very small, which has already been noted as a necessary condition for long time stability. One also needs  $\frac{T_{\zeta}^+}{pT_s} + \zeta + \frac{M}{p}$  not to be too large. The smaller  $\zeta$  is chosen, the larger is the value of  $T_{\zeta}^+$ , so that, in specific models, there is an optimum choice of  $\zeta$ , limiting the accuracy of approximation that can be demonstrated by this method.

We now turn our attention to the distribution of X(t) for fixed values of t, starting from any particular state in  $C_{\zeta}$ , and compare it to  $\pi^{\delta_s}$ . We begin by taking the initial state of X to be s, and remark later that this restriction makes little difference, provided that s is hit at least once. To state the theorem, we define

 $r_{\zeta} := \mathbb{P}_{s}[X \text{ does not leave } C_{\zeta} \text{ or hit } 0 \text{ before returning to } s].$ 

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Since  $\lim_{\zeta \to 0} r_{\zeta} = p_s$ , the quantity  $1 - r_{\zeta}$  can be made as close as desired to  $1 - p_s$  by decreasing  $\zeta$ , but at the cost of increasing  $T_{\zeta}^+$  at the same time. A crude bound for  $1 - r_{\zeta}$  in terms of  $1 - p_s$  comes from observing that

$$\sum_{k \notin C_{\zeta}} T_{sk} \geq (1 - r_{\zeta})/q^{(\zeta)},$$

where  $q^{(\zeta)} := \sup_{k \in J_{\zeta}} q_k$  and

$$J_{\zeta} := \{k \notin C_{\zeta} \colon q_{kj} > 0 \text{ for some } j \in C_{\zeta}\};$$

from (2.3), this gives

$$(1-r_{\zeta}) \leq \zeta q^{(\zeta)} T_s (1-p_s).$$

**Theorem 2.4.** Suppose that Condition B holds, and let  $B_{\zeta} := T_{\zeta}^+ q_s/p$ . If  $\varepsilon(\zeta, 1) \le 1/2$ , then there is a universal constant D such that, for all  $t \ge 16T_{\zeta}^+/p$ ,

$$d_{\mathrm{TV}}(\mathcal{L}_{s}(X(t)), \pi^{\delta_{s}}) \leq (1 - r_{\zeta})(2t/T_{s} + \zeta + 1/p) + DB_{\zeta}\sqrt{\frac{T_{\zeta}^{+}}{pt}} + (2/e)^{pt/16T_{\zeta}^{+}}$$
  
=:  $\eta_{\zeta}(t)$ .

**Remark.** Hence, informally, if  $(1 - r_{\zeta})B_{\zeta}^2 T_{\zeta}^+/(pT_s) \ll 1$  and  $(1 - r_{\zeta}) \ll 1$ , the distribution  $\mathcal{L}_s(X(t))$  is close to  $\pi^{\delta_s}$  for all times *t* such that

$$B_{\zeta}^2 T_{\zeta}^+ / p \ll t \ll T_s / (1 - r_{\zeta})$$

note that  $B_{\zeta} \ge 1$ , so that then  $t \gg T_{\zeta}^+/p$  also.

**Proof.** The argument is based on coupling two copies  $X_{\zeta}^{(1)}$  and  $X_{\zeta}^{(2)}$  of the return process  $X_{\zeta}^{\delta_s}$ , with  $X_{\zeta}^{(1)}$  in equilibrium and with  $X_{\zeta}^{(2)}$  starting in *s*, by the method used in [3], Theorem 2.5. The coupling is achieved by forcing  $X_{\zeta}^{(1)}$  to follow the same sequence of states as  $X_{\zeta}^{(2)}$  after the first time that it hits *s*, and to have identical residence times in all states other than *s*; the careful matching of the exponentially distributed residence times of the two processes in *s* is all that is used to achieve the coupling. Now the argument leading to (2.18) of [3] shows that  $X_{\zeta}^{(1)}$  and  $X_{\zeta}^{(2)}$  can be jointly defined in such a way that, if  $t \ge 16T_{\zeta}^+/p$ , the event  $\Delta_{\zeta t}$  that they have coupled by *t* is such that

$$\mathbb{P}[\Delta_{\zeta t}^c] \le 4c_G B_\zeta \sqrt{\frac{T_\zeta^+}{pt}} + (2/e)^{pt/16T_\zeta^+}$$

for a universal constant  $c_G$ , not depending on  $\zeta$ . Now, because  $X_{\zeta}^{(1)}$  is in equilibrium,

$$\mathbb{P}[X_{\zeta}^{(1)} \text{ hits } \{0\} \cup C_{\zeta}^{c} \text{ before } t] \leq t \sum_{k \in C_{\zeta}} \pi_{\zeta}^{\delta_{s}}(k) \sum_{l \in \{0\} \cup C_{\zeta}^{c}} q_{kl},$$

and the double sum is bounded by  $(1 - r_{\zeta})/T_s^{(\zeta)}$ , as in the argument leading to (2.8). If  $X_{\zeta}^{(1)}$  does not hit  $\{0\} \cup C_{\zeta}^c$  before *t*, and if  $\Delta_{\zeta t}$  holds, then  $X_{\zeta}^{(2)}$  also avoids  $\{0\} \cup C_{\zeta}^c$  up to time *t*, in which

case it is indistinguishable from an X-process, starting in s. It thus follows that

$$d_{\rm TV}(\pi_{\zeta}^{\delta_s}, \mathcal{L}_s(X(t))) \le (1 - r_{\zeta})(t/T_s^{(\zeta)}) + DB_{\zeta} \sqrt{\frac{T_{\zeta}^+}{pt}} + (2/e)^{pt/16T_{\zeta}^+},$$
(2.9)

with  $D := 4c_G$ . To complete the proof, it now merely remains to note that  $d_{\text{TV}}(\pi_{\zeta}^{\delta_s}, \pi^{\delta_s}) = \pi^{\delta_s}(C_{\zeta}^c)$ , and to use Lemma 2.2; note that  $(1 - p_s) \ge (1 - r_{\zeta})$ , and that  $T_s^{(\zeta)} \ge T_s/2$ , from (2.5), if  $\varepsilon(\zeta, 1) \le 1/2$ .  $\Box$ 

**Remark.** Denoting by  $A_{\zeta}$  the event that X hits s before  $\{0\} \cup C_{\zeta}^{c}$ , the same argument can be used to show that  $d_{\text{TV}}(\mathcal{L}_{k}(X(t) \mid A_{\zeta}), \mathcal{L}_{s}(X(t)))$  is at most  $\eta_{\zeta}(t)$  for any  $k \in C_{\zeta}$ , under the conditions of Theorem 2.4. Hence, conditional on the event that X hits s before reaching  $\{0\} \cup C_{\zeta}^{c}$ , the distribution of X(t) starting from any  $k \in C_{\zeta}$  is also close to  $\pi^{\delta_{s}}$  for all times t such that

$$B_{\zeta}^2 T_{\zeta}^+ / p \ll t \ll T_s / (1 - r_{\zeta}),$$

provided that  $(1 - r_{\zeta})B_{\zeta}^2 T_{\zeta}^+/(pT_s) \ll 1$ . Thus the return distribution  $\pi^{\delta_s}$  is then indeed an appropriate long time approximation to the distribution of X in C, for times  $t \ll T_s/(1 - r_{\zeta})$ , and  $\pi^{\delta_s}$  can be replaced by  $\pi^{\mu}$  for any  $\mu$  such that  $\mu(T) < \infty$ , with extra error at most that given by the bound in Theorem 2.3, with  $\mu(T)/T_s$  for M.

The emphasis until now has been on approximating  $\mathcal{L}(X(t))$  by  $\pi^{\delta_s}$ . However, there are times when this approximation may also not be useful. Examples of this are processes in which a set  $C_{\zeta}$  can be found that has the properties that  $T_s^{(\zeta)}$  and  $T_{\zeta}^+$  are only moderately large and  $(1 - r_{\zeta})$ is tiny, but for which (2.3) is *not* satisfied. Such is the case if there are states  $k \notin C_{\zeta}$  such that  $T_k$  is extremely large; for instance, if the equilibrium around s is metastable,  $T_s$  itself may be enormously larger than  $T_s^{(\zeta)}$ . Here, nonetheless, the intermediate bound (2.9) shows that  $\pi_{\zeta}^{\delta_s}$  acts as a good approximation for very long periods, even though  $\pi^{\delta_s}$  may be very different.

In practice, computing  $\pi_{\zeta}^{\delta_s}$  may be complicated by having to cope with the detail of the return distribution from  $C_{\zeta}^c$ , which should not really be relevant here. The final approximation is therefore phrased instead in terms of the accelerated return process  $\widetilde{X}_{C'}^{\delta_s}$ , for some  $C' \subset C$  containing *s* but not 0, which is returned to *s* at each time of leaving *C'*. Here, the set *C'* may reasonably be chosen to be finite, in which case computing the equilibrium distribution  $\widetilde{\pi}_{C'}^{\delta_s}$  of the accelerated return process becomes relatively easy. We now define  $\widetilde{T}_{k,C'} := \mathbb{E}_k[\widetilde{\tau}_{\{s\}}^{\delta_s}]$ , where  $\widetilde{\tau}_{\delta_s}^{\delta_s}$  is defined as in (2.2), but with the process  $\widetilde{X}_{C'}^{\delta_s}$  in place of *X*; and we set  $\widetilde{T}_{C'}^+ := \sup_{k \in C'} \widetilde{T}_{k,C'}$  and  $\widetilde{r}_{C'} := \mathbb{P}_s[\widetilde{\tau}_{C\setminus C'}^{\delta_s} = \widetilde{\tau}_{\{s\}}^{\delta_s}]$ .

**Theorem 2.5.** Suppose that Condition B (ii) holds, and let  $B_{C'} := \widetilde{T}_{C'}^+ q_s$ . Then

$$d_{\text{TV}}(\tilde{\pi}_{C'}^{\delta_s}, \mathcal{L}_s(X(t))) \le (1 - \tilde{r}_{C'})(t/\tilde{T}_{s,C'}) + DB_{C'}\sqrt{\frac{\tilde{T}_{C'}^+}{t}} + (2/e)^{t/16\tilde{T}_{C'}^+},$$

for all  $t \ge 16\widetilde{T}_{C'}^+$ , with D the same constant as in Theorem 2.4.

**Proof.** The argument runs exactly as in the proof of (2.9), but with the process  $\widetilde{X}_{C'}^{\delta_s}$  instead of  $X_{\zeta}^{\delta_s}$ . Since this process has no absorbing state 0, *p* can be replaced by 1 in the bound.

Theorem 2.5 is very much in line with the main message of the paper. The difference between Condition A of [3] and Condition B of this paper largely concerns properties of the process starting from states that it rarely ever reaches, and such differences should not prevent effective approximation of the distribution of the process, at least for long periods of time. The essential difference between the situation in which Condition A is satisfied and that in which it is not is that, when it is not satisfied, the approximating distribution need not be a quasi-stationary distribution of the process, or even one of its return distributions, but instead a return distribution associated with the process restricted to a truncated state space. We consider an example of this in Section 4.

# 3. Birth and death processes

Let X be a birth and death process with birth rates  $b_j \ge 0, 1 \le j < \infty$ , with  $b_0 = 0$ , and with strictly positive death rates  $d_j, j \ge 0$ . Define  $\alpha_1 = 1$  and

$$\alpha_j = \frac{b_1 \cdots b_{j-1}}{d_2 \cdots d_j}, \quad j \ge 1;$$

then set

$$S_r^m := \sum_{l=r}^m \frac{1}{\alpha_l d_l}.$$

In order to use the theorems of the previous section, we need to find expressions for the quantities p,  $p_s$ ,  $T_{sk}$ ,  $T_s$ ,  $T_{\zeta}^+$  and  $r_{\zeta}$  that appear there. These can be derived using hitting probabilities, which can be simply expressed using the  $\alpha_j$  and the  $S_r^m$ . First, for any j < m < l, we have

$$\mathbb{P}_m[X \text{ hits } l \text{ before } j] = S_{j+1}^m / S_{j+1}^l.$$
(3.1)

A first consequence is that

$$1 - p_s = \frac{d_s}{b_s + d_s} \left( 1 - \frac{S_1^{s-1}}{S_1^s} \right) = \frac{1}{\alpha_s (b_s + d_s) S_1^s};$$
(3.2)

$$p = p_1 = \frac{1}{d_1 S_1^s}.$$
(3.3)

Next, if  $i \notin \{0, s\}$ , write  $u_{ki} := \mathbb{P}_k[\tau_{\{i\}} < \tau_{\{s,0\}}], k \neq i$ , and  $u_{ii} = 1$ : then we have

$$u_{ki} = \begin{cases} 0 & \text{if } k < s < i \text{ or } i < s < k; \\ 1 & \text{if } s < i \le k; \\ S_{s+1}^k/S_{s+1}^i & \text{if } s < k \le i; \\ S_1^k/S_1^i & \text{if } 0 < k \le i < s; \\ S_{k+1}^s/S_{i+1}^s & \text{if } 0 < i \le k < s, \end{cases}$$

$$(3.4)$$

from which it follows that, for such *i*,

$$1 - \mathbb{P}_{i}[\tau_{\{i\}} < \tau_{\{s,0\}}] = \begin{cases} \frac{1}{\alpha_{i}(b_{i} + d_{i})} \left\{ \frac{1}{S_{i+1}^{s}} + \frac{1}{S_{1}^{i}} \right\} & \text{if } 0 < i < s; \\ \frac{1}{\alpha_{i}(b_{i} + d_{i})S_{s+1}^{i}} & \text{if } i > s. \end{cases}$$
(3.5)

Also, for  $i \notin \{s, 0\}$  and  $k \neq s$ , we have

$$T_{ki} := \int_0^\infty \mathbb{P}_k[\{\tau_{\{s,0\}} > t\} \cap \{X(t) = i\}] dt$$
  
=  $\frac{u_{ki}}{b_i + d_i} \frac{1}{1 - \mathbb{P}_i[\tau_{\{i\}} < \tau_{\{s,0\}}]},$  (3.6)

with  $T_{ks} = T_{k0} = 0$ , and then  $T_{ss} = 1/(b_s + d_s)$  and

$$T_{si} = \begin{cases} \frac{d_s T_{s-1,i}}{b_s + d_s} & \text{if } 0 < i < s; \\ \frac{b_s T_{s+1,i}}{b_s + d_s} & \text{if } i > s. \end{cases}$$
(3.7)

These in turn give

$$T_{k} = \sum_{i \ge 1} T_{ki} = \begin{cases} \frac{1}{S_{1}^{s}} \sum_{i=1}^{s-1} \alpha_{i} S_{1}^{i \land k} S_{(i \lor k)+1}^{s} & \text{if } 0 < k < s; \\ \sum_{i \ge s+1}^{s} \alpha_{i} S_{s+1}^{i \land k} & \text{if } k > s, \end{cases}$$
(3.8)

and

$$T_s = (b_s T_{s+1} + d_s T_{s-1} + 1)/(b_s + d_s) = \frac{1}{\alpha_s (b_s + d_s)} \sum_{i \ge 1} \alpha_i S_1^{i \land s} / S_1^s.$$
(3.9)

Now, choosing any value of s > 0, the formulae (3.7), (3.2) and (3.9) can be used for any  $\zeta$  to determine a suitable set  $C_{\zeta} := \{1, 2, ..., a_{\zeta}\}$  so that (2.3) is satisfied, and (3.8) enables both  $T_{\zeta}^+$  and  $\mu(T)$  to be determined. Furthermore, it follows from (3.5) with  $a_{\zeta}$  for s and with s for i that

$$1 - r_{\zeta} = \frac{1}{\alpha_s (b_s + d_s)} \left\{ \frac{1}{S_{s+1}^{a_{\zeta}}} + \frac{1}{S_1^s} \right\}.$$
(3.10)

Thus, and from (3.3), all the ingredients for the bounds in Theorems 2.3 and 2.4 are available, recalling also, for the calculation of  $B_{\zeta}$ , that  $q_s = b_s + d_s$ .

For example, take the birth and death process given in (1.1) with A large,  $\delta(x) = d$  constant, and with  $\beta(\cdot)$  given by the Ricker choice  $\beta(x) = be^{-\alpha x}$ ; thus  $b_j = jbe^{-\alpha j/A}$  and  $d_j = jd$ . If b > d, the deterministic equilibrium, in which the birth and death rates are equal, is given by  $x = \frac{1}{\alpha} \log(b/d) =: c > 0$ , suggesting the choice of  $s := s(A) := \lfloor Ac \rfloor$ . This gives

$$\alpha_{j} \sim j^{-1} (b/d)^{j} e^{-\alpha j (j+1)/2A}; \qquad \alpha_{s} \approx s^{-1} (b/d)^{s/2}; \alpha_{j}/\{s\alpha_{s}\} \approx j^{-1} e^{-\alpha j/2A} e^{-\alpha (j-s)^{2}/2A};$$
(3.11)

note that  $\alpha_s$  is exponentially large in A. Thus, immediately,  $S_1^s \ge 1/d$ , and  $S_{s+1}^a \ge 1/d$  if a > 2(s(A) + 1). Hence  $1 - p_s = O\{(b/d)^{-s/2}\}$  from (3.2), and  $1 - r_{\zeta} = O\{(b/d)^{-s/2}\}$  also if  $a_{\zeta} \ge 2(s(A)+1)$ , from (3.10). Furthermore,  $S_1^s$  is uniformly bounded in A, so that p is uniformly bounded below, by (3.3).

To choose the set  $C_{\zeta} := \{1, 2, ..., a_{\zeta}\}$ , note that, from (3.4)–(3.7) and (3.11),

$$T_{si} \leq \frac{\alpha_i}{\alpha_s(b_s + d_s)} = O\left(i^{-1}e^{-\alpha(i-s)^2/2A}\right)$$

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for all *i*, and

$$T_s \ge rac{1}{lpha_s(b_s+d_s)}\sum_{i\ge s}lpha_i symp A^{-1/2}$$

Hence, from (2.3), the choice  $a_{\zeta} = \lceil 2(s+1) \rceil$  corresponds to a value of  $\zeta \leq 1$ . For the corresponding value of  $T_{\zeta}^+$ , it is necessary to bound the expressions for  $T_k$ , which is in detail tedious; however, it is not difficult to deduce that  $T_k = O(\log A \vee \log k)$ , so that  $T_{\zeta}^+ = O(\log A)$ . From Theorem 2.4, it now follows that  $\mathcal{L}_s(X(t))$  is close to  $\pi^{\delta_s}$  for all times t such that

$$A^{2}(\log A)^{3} \ll t \ll A^{-1/2}e^{A\alpha c^{2}/2}$$

Furthermore,  $\mu(T) = O(\log A)$  for all return distributions concentrated on sets of the form  $\{1, 2, \ldots, A^m\}$  for any fixed exponent *m*, and Theorem 2.3 thus shows that the corresponding equilibrium distributions  $\pi^{\mu}$  are all exponentially close to  $\pi^{\delta_s}$  as  $A \to \infty$ —indeed,  $\mu$  would have to have extraordinarily long tails for anything else to be the case. Hence the fact that this process has infinitely many quasi-stationary distributions should not be interpreted as showing any kind of practical instability, at least for large A: there is an effective long time stable distribution, and it is extremely close to  $\pi^{\delta_s}$ .

Rather similar analyses could be undertaken for a variety of other well-known models. An analogue of the Beverton and Holt [4] model would have  $\beta(x) = b/(1 + x/m)$  for b > d and m > 0, that of Hassell [8] would have  $\beta(x) = b/(1 + x/m)^c$ , and that of Maynard-Smith and Slatkin [12] would have  $\beta(x) = b/(1 + (x/m)^c)$ . The qualitative conclusions would be entirely similar.

## 4. Markov population processes

In this section, we consider Markov population processes  $X_N := (X_N(t), t \ge 0), N \ge 1$ , taking values in  $\mathbb{Z}^d_+$ , for some  $d \ge 1$ . In many applications, the components represent the numbers of individuals of a particular type or species, with a total of *d* types possible. The process evolves as a Markov process with state-dependent transitions

$$X \to X + J$$
 at rate  $N\alpha_J(N^{-1}X), \quad X \in \mathbb{Z}^d_+, \ J \in \mathcal{J},$  (4.1)

where  $\mathcal{J} \subset \mathbb{Z}^d$  is a fixed finite set, and we define  $J_* := \max_{j \in \mathcal{J}} |J|$ . Density dependence is reflected in the fact that the arguments of the functions  $\alpha_J$  are counts normalised by the 'typical size' *N*. The functions  $\alpha_J : \mathbb{Z}_+ \to \mathbb{R}_+$  are assumed to be twice continuously differentiable on  $\mathbb{R}^d_+$ , and to be such as to ensure that  $X_N$  is *locally irreducible*; that is, the number of steps required to get from any state  $X \neq 0$  to any of its lattice neighbours  $X + e^{(j)}$ ,  $1 \le j \le d$ , with positive probability, is uniformly bounded.

Such processes satisfy a law of large numbers [9], expressed in terms of the system of *deterministic equations* 

$$\frac{d\xi}{dt} = \sum_{J \in \mathcal{J}} J \alpha_J(\xi) \implies F(\xi), \quad \xi \in \mathbb{R}^d;$$
(4.2)

here,  $\xi(t)$  approximates  $x_N(t) := N^{-1}X_N(t)$ , and the quantity F represents the infinitesimal average drift of the components of the random process. We now suppose that F(c) = 0 for some  $c \in \mathbb{R}^d$  with  $c_j > 0, 1 \le j \le d$ , and that all the eigenvalues of the matrix of derivatives

DF(c) =: A have negative real parts. In this case, c is a locally stable equilibrium of the deterministic system (4.2), and, if  $X_N$  is started with  $N^{-1}X_N(0)$  close to c, the law of large numbers implies that  $x_N(t)$  remains close to c, in the sense that

$$\sup_{0 \le t \le T} |x_N(t) - c| \to_d 0, \tag{4.3}$$

for any finite T > 0. The central limit theorem in [10] also shows that

$$N^{1/2}(x_N(\cdot) - c) \Rightarrow x \quad \text{in } D[0, T], \tag{4.4}$$

for any T > 0, where x is a Gaussian process whose stationary distribution has zero mean and covariance matrix  $\Sigma$  satisfying

$$A\Sigma + \Sigma A^T + \sigma^2(c) = 0, \tag{4.5}$$

where  $\sigma^2(x) := \sum_{J \in \mathcal{J}} J J^T \alpha_J(x)$ . Here, we complement this approximation, by using Theorem 2.5 to show that the distribution of  $X_N(t)$  is close in total variation, for time periods that become extremely long as N increases, to the equilibrium distribution  $\tilde{\pi}_N^{\delta_s}$  of a truncated process  $\tilde{X}_N$ , which is returned to a specified state  $s := s_N$  near Nc whenever it leaves a neighbourhood C'(N) of Nc. Of course, this distribution, appropriately centred and normalised, converges to  $MVN_d(0, \Sigma)$  as  $N \to \infty$ .

In order to prove such a result, we need to define the neighbourhood C'(N), and to show that the quantities  $(1 - \tilde{r}_{C'(N)})$ ,  $1/\tilde{T}_{C'(N)}$  and  $\tilde{T}^+_{C'(N)}$  appearing in Theorem 2.5 can be suitably bounded. The inequality

$$1/\widetilde{T}_{C'(N)} \le q_{s_N} = N \sum_{J \in \mathcal{J}} \alpha_J(N^{-1}s_N)$$
(4.6)

is immediate. For the remaining bounds, we use Lyapunov–Foster–Tweedie methods [14]. We write  $y := N^{1/2}(x - c)$  and  $r_y^2 := y^T V y$ , where the positive definite symmetric matrix V is to be chosen later, and we first consider the process  $y_N(\cdot) := N^{1/2}(x_N(\cdot) - c)$  stopped when  $|r_{y_N(t)}| \ge c_0 N^{1/2}$ , for  $c_0$  also to be chosen later. Then, for y such that  $|r_y| < c_0 N^{1/2}$ , the generator  $\mathcal{A}$  of the Markov process acting on a real function g(y) takes the form

$$(\mathcal{A}g)(y) = \sum_{J \in \mathcal{J}} N\alpha_J (c + N^{-1/2}y) \{ g(y + N^{-1/2}J) - g(y) \}.$$
(4.7)

Using Taylor's expansion on g, for  $|r| < c_0 N^{1/2}$ , we have

$$\left| (\mathcal{A}g)(y) - \sum_{J \in \mathcal{J}} N \alpha_J (c + N^{-1/2} y) \left\{ N^{-1/2} J^T Dg(y) + \frac{1}{2} N^{-1} D^2 g(y) [J^{(2)}] \right\} \right|$$
  
$$\leq N^{-1/2} \eta_3(y; g),$$
(4.8)

where

$$\eta_3(y;g) := \sum_{J \in \mathcal{J}} \alpha_J^{*0} J_*^3 \sup_{|u| \le N^{-1/2} J_*} \|D^3 g(y+u)\|,$$

and  $\alpha_J^{*0} := \sup_{x:(x-c)^T V(x-c) \le c_0^2} \alpha_J(x)$ . Similarly, expanding  $\alpha_J$ , we obtain

$$N^{1/2} \sum_{J \in \mathcal{J}} \alpha_J (c + N^{-1/2} y) J^T Dg(y) - y^T A^T Dg(y) \bigg| \le N^{-1/2} \eta_1(y; g),$$
(4.9)

where we have used the facts that  $\sum_{J \in \mathcal{J}} J \alpha_J(c) = F(c) = 0$  and that  $\sum_{J \in \mathcal{J}} D \alpha_J(c) J^T = A^T$ , and where

$$\eta_1(y;g) \coloneqq \|Dg(y)\|J_* \sum_{J \in \mathcal{J}} \alpha_J^{*2} |y|^2,$$

and  $\alpha_J^{*2} := \sup_{x:(x-c)^T V(x-c) \le c_0^2} \|D^2 \alpha_J(x)\|$ ; and then

$$\left| \sum_{J \in \mathcal{J}} \{ \alpha_J(c + N^{-1/2}y) - \alpha_J(c) \} D^2 g(y)[J, J] \right| \le N^{-1/2} \eta_2(y; g),$$
(4.10)

with

$$\eta_2(y;g) \coloneqq \|D^2g(y)\|J_*^2 \sum_{J \in \mathcal{J}} \alpha_J^{*1}|y|,$$

and  $\alpha_J^{*1} := \sup_{x:(x-c)^T V(x-c) \le c_0^2} \|D\alpha_J(x)\|$ . Thus, if one ignores the error terms, the generator acts on *g* as that of a multivariate Ornstein–Uhlenbeck process,

$$(\mathcal{A}g)(y) \approx y^T A^T Dg(y) + \frac{1}{2} \operatorname{tr} \{ \sigma(c) D^2 g(y) \sigma(c) \},$$
(4.11)

with drift matrix A and infinitesimal covariance matrix  $\sigma^2(c)$ .

We now consider the generator acting on functions g of the form  $g(y) = F_{\varepsilon}(r_y)$ , where  $F_{\varepsilon}(r) := \int_{\varepsilon}^{r} f(t) dt$ , and the function f is non-negative. This gives

$$Dg(y) = f(r_y)r_y^{-1}Vy; \quad D^2g(y) = r_y^{-1}f(r_y)V + \{f'(r_y) - r_y^{-1}f(r_y)\}r_y^{-2}Vy(Vy)^T.$$

Thus the first term in the approximation (4.11) to A yields

$$y^{T}A^{T}Dg(y) = f(r_{y})r_{y}^{-1}y^{T}A^{T}Vy = \frac{1}{2}f(r_{y})r_{y}^{-1}y^{T}\{A^{T}V + VA\}y.$$

In order to choose functions g such that  $g(y_N(t))$  is a super-martingale, we would like this expression to be negative, which will be the case if V is chosen in such a way that the symmetric matrix  $(A^T V + VA)$  is negative definite. One way of doing so here is to take  $V := \Sigma^{-1}$ , where  $\Sigma$  is as in (4.5), in which case

$$A^{T}V + VA = \Sigma^{-1} \{ \Sigma A^{T} + A\Sigma \} \Sigma^{-1} = -\Sigma^{-1} \sigma^{2}(c) \Sigma^{-1}$$

is immediately negative definite. The remaining term in (4.11) then gives

$$\frac{1}{2} \operatorname{tr} \{ \sigma(c) D^2 g(y) \sigma(c) \} 
= \frac{1}{2} r_y^{-1} f(r_y) \operatorname{tr} \{ \sigma(c) V \sigma(c) \} + \frac{1}{2} \{ f'(r_y) - r_y^{-1} f(r_y) \} r_y^{-2} \operatorname{tr} \{ \sigma(c) V y(V y)^T \sigma(c) \} 
= \frac{1}{2} r_y^{-1} f(r_y) \operatorname{tr} \{ \tilde{\sigma}^2 \} + \frac{1}{2} \{ f'(r_y) - r_y^{-1} f(r_y) \} R(y),$$

where  $\tilde{\sigma}^2 := \Sigma^{-1/2} \sigma^2(c) \Sigma^{-1/2}$  is positive definite, and

$$R(y) \coloneqq \frac{(\Sigma^{-1/2}y)^T \tilde{\sigma}^2 \Sigma^{-1/2} y}{y^T \Sigma^{-1} y}$$

is bounded between its smallest and largest eigenvalues  $\gamma$  and  $\Gamma$ .

We begin by taking  $f(r) := r^{-m} e^{\beta r^2}$ , for *m* and  $\beta$  to be chosen suitably. Then (4.11) gives the main part of  $(\mathcal{A}g)(y)$  as

$$\frac{1}{2}e^{\beta r_y^2}r_y^{-m+1}\left\{-r_y^{-2}y^T \Sigma^{-1/2}\tilde{\sigma}^2 \Sigma^{-1/2}y + r_y^{-2}\operatorname{tr}\{\tilde{\sigma}^2\} + \{2\beta - r_y^{-2}(m+1)\}R(y)\right\}$$
  
$$\leq -\frac{1}{2}e^{\beta r_y^2}r_y^{-m+1}\left\{(\gamma - 2\beta) + r_y^{-2}((m+1)\gamma - \operatorname{tr}\{\tilde{\sigma}^2\})\right\}$$
  
$$=: -G(r_y).$$

say. We now choose  $\beta$  and *m* such that  $2\beta < \gamma$  and  $(m + 1)\gamma > \text{tr} \{\tilde{\sigma}^2\}$ .

For the remainders, we note first, for  $\eta_3$ , that there exist constants  $c_-$ ,  $c_+$  and K such that

$$\sup_{|u| \le N^{-1/2} J_*} \|D^3 g(y+u)\| \le K \|D^3 g(y)\| \quad \text{for } c_- N^{-1/2} \le \|y\| \le c_+ N^{1/2}$$

and that  $||D^3g(y)|| \leq C_3 r_y^{-m-2} \exp(\beta r_y^2) \{1 + r_y^4\}$  for some  $C_3$ . Thus, for all values of y such that  $N^{-1/2}c_3 \leq r_y \leq c'_3 N^{1/2}$ , for suitable  $c_3, c'_3$ , where we also choose  $c'_3 \leq c_0$ , it follows that  $\eta_3(y;g) \leq G(r_y)/6$ . Similar considerations for  $\eta_1(y;g)$  and  $\eta_2(y;g)$  show that, possibly increasing  $c_3$  and decreasing  $c'_3$ , the inequality

$$\eta_1(y; g) + \eta_2(y; g) + \eta_3(y; g) \le \frac{1}{2}G(r_y)$$

holds for all  $y \in B(N^{-1/2}c_3, N^{1/2}c'_3)$ , where

$$B(\rho, R) := \{ y \colon \rho \le r_y \le R \}.$$

Hence, for such y, we always have

$$(\mathcal{A}g)(y) \leq -\frac{1}{2}G(r_y) < 0.$$

Thus the quantity  $F_{\varepsilon}(y_N(t \wedge \hat{\tau}_{\rho,R}))$  is a non-negative super-martingale, for any  $N^{-1/2}c_3 \leq \rho < R \leq N^{1/2}c'_3$  and any  $0 < \varepsilon \leq \rho$ , where

$$\hat{\tau}_{\rho,R} := \inf_{t \ge 0} \{ y_N(t) \notin B(\rho, R) \}.$$

Defining  $p(\rho, R; r) := \mathbb{P}[y_N(\hat{\tau}_{\rho,R}) \in B(0, \rho) | r_{y_N(0)} = r]$ , it thus follows easily from the optional stopping theorem that

$$1 - p(\rho, R; r) \le F_{\rho}(r) / F_{\rho}(R) \le \frac{4\beta R^{m+1}}{(m-1)\rho^{m-1}} e^{\beta(r^2 - R^2)},$$
(4.12)

for  $\rho$ , R such that  $N^{-1/2}c_3 \leq \rho < R \leq N^{1/2}c_3'$  and  $2\beta R(R - \rho) \geq 1$ , with the last condition ensuring that a simple lower bound for  $F_{\rho}(R)$  is valid. So take

$$C'(N) := \{X : N^{-1/2}(X - Nc) \in B(0, N^{1/2}c'_3)\},$$
(4.13)

and let  $s_N \in \mathbb{Z}_+^d$  be the closest lattice point to Nc. Any path of  $y_N$  starting in  $B(0, N^{-1/2}c_3)$  has positive probability of hitting  $N^{-1/2}(s_N - Nc)$  by taking the most direct path from  $y_N(0)$  to  $N^{-1/2}(s_N - Nc)$ , and this probability is uniformly bounded away from 0, by the local irreducibility assumption on  $X_N$ , and because the number of possible values of  $y_N(\cdot)$  in  $B(0, N^{-1/2}c_3)$  is uniformly bounded as N varies. Hence

$$P[\tau_{\{s_N\}} < \hat{\tau}_{0,2N^{-1/2}c_3} \mid y_N(0) \in B(0, N^{-1/2}c_3)] > \delta$$
(4.14)

for some  $\delta > 0$ . If the complementary event occurs, then  $B(0, N^{-1/2}c_3)$  is hit again by  $y_N$  before it leaves  $B(0, N^{1/2}c'_3)$  with probability at least

$$1 - KN^m e^{-(c'_3)^2 \beta N}$$

for some K, in view of (4.12). It thus follows that

$$1 - \tilde{r}_{C'(N)} \le \delta^{-1} K N^m \, e^{-(c'_3)^2 \beta N} = O(e^{-\beta' N}), \tag{4.15}$$

for any  $0 < \beta' < (c'_3)^2 \beta$ .

In order to control the mean time to hitting s for the process  $\widetilde{X}_N$ , we take  $f(r) := r^{-m} + \theta r$ , for m large enough and  $\theta$  small enough positive. Then  $(\mathcal{A}g)(y)$  once again has two principal negative contributions, the first, bounded above by  $-\frac{1}{2}\gamma\theta r_y^2$ , coming from the drift term, and the second, bounded above by  $-\frac{1}{2}mr_y^{-(m+1)}$ , from the variance term. The former dominates all positive terms for  $r_y \ge r_0$ , for some fixed  $r_0$ , and the second then dominates for the smaller values of  $r_y$ , if m is chosen large enough; the quantities  $\eta_l(y; g), 1 \le l \le 3$ , are treated as before, and the upper and lower bounds for  $r_y$  can be left unchanged. Hence, in the same range of y, we always have

$$(\mathcal{A}g)(\mathbf{y}) \le -\delta' < 0,$$

for some  $\delta' > 0$ . Applying the optional stopping theorem then yields

$$\delta' \mathbb{E}\{\hat{\tau}_{\rho,R} \mid r_{y_N(0)} = r\} \le F_{\rho}(r) \le \frac{\rho^{-m+1}}{m-1} + \frac{1}{2}\theta r^2,$$

if m > 1, uniformly in  $\rho$ , R such that  $N^{-1/2}c_3 \le \rho < R \le N^{1/2}c'_3$ . Take the extreme values for  $\rho$  and R. Then since, for this R, the process  $\widetilde{X}_N$  is returned directly to  $s_N$  if  $y_N(\hat{\tau}_{\rho,R}) \notin B(0, R)$ , and since the mean time to either hitting  $N^{-1/2}(s_N - Nc)$  or leaving  $B(0, 2N^{-1/2}c_3)$ , starting within  $B(0, N^{-1/2}c_3)$ , is uniformly bounded by some  $c_1 < \infty$ , a regenerative argument much as above shows that

$$\widetilde{T}^+_{C'(N)} \le c_0 \{ N^{(m-1)/2} + N \} + c_1 + (1-\delta) \widetilde{T}^+_{C'(N)},$$

for  $\delta$  as in (4.14), and hence that, uniformly in *N*,

$$\widetilde{T}^+_{C'(N)} \le C\{N^{(m-1)/2} + N\},\tag{4.16}$$

for some  $C < \infty$ .

Collecting the above bounds, we have enough to prove the following theorem.

**Theorem 4.1.** Suppose that X is a Markov population process with transition rates  $N\alpha_J$  as given in (4.1), and that the  $\alpha_J$  are such as to ensure that  $X_N$  is locally irreducible. Suppose also

that F(c) = 0 for some  $c \in \mathbb{R}^d$  with  $c_j > 0, 1 \le j \le d$ , and that all the eigenvalues of the matrix of derivatives DF(c) have negative real parts. Then there exist  $\alpha$ ,  $\beta_1$ ,  $\beta_2$  and  $c'_3 > 0$ , and  $C_1$ ,  $C_2$  and  $C_3 < \infty$ , depending only on the parameters of the process and not on N, such that, for all t,

$$d_{\text{TV}}(\tilde{\pi}_{C'(N)}^{\delta_s}, \mathcal{L}_s(X(t))) \le C_1 t N e^{-\beta_1 N} + C_2 t^{-1/2} N^{1+3\alpha/2} + C_3 e^{-\beta_2 t N^{-\alpha}},$$

where  $s = s_N$  is the nearest lattice point to Nc, and C'(N) is as defined in (4.13).

**Proof.** All that is needed is to apply the estimate given in Theorem 2.5. An upper bound on  $(1 - \tilde{r}_{C'(N)})$  is given in (4.15); a bound on  $\tilde{T}^+_{C'(N)}$  is given in (4.16); and  $1/\tilde{T}_{C'(N)}$  is bounded in (4.6). For the exponent  $\beta_1$ , any  $\beta'$  as for (4.15) can be taken;  $\alpha = \max\{(m-1)/2, 1\}$  as in (4.16); and  $\beta_2$  can be taken to be  $(1 - \log 2)/\{32C\}$ , for *C* as in (4.16).  $\Box$ 

The lower bound given here for the time at which the quasi-equilibrium approximation becomes accurate is very pessimistic. The main reason is that the general coupling strategy used to prove Theorems 2.4 and 2.5 can be very inefficient in specific instances, and is so here. Better results could be expected by using the methods to be found in Roberts and Rosenthal [18].

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