

FLUID APPROXIMATION AND A TIME CHANGE FOR AN EVOLUTION MODEL

KAIS HAMZA, HAYA KASPI, AND FIMA KLEBANER

ABSTRACT. In the Bare Bones Evolution Model of Sagitov, (see “Stochasticity in the adaptive dynamics of evolution: the bare bones”, [5]) the appearance of a new mutation in a resident established population is described as follows. The resident population, which is assumed to be around its carrying capacity K , evolves as a binary splitting process with probability of successful reproduction (division) dependent on the size of that population and also on the size of the new mutant population. The mutant population starts with a single individual and also evolves as a binary splitting with initially very high probabilities of successful division. Approximating this system for high values of carrying capacity K leads to a dynamical system with a small noise, which initially starts near an unstable fixed point. By a classical approximation Theorem the population densities converge to that unstable fixed point on any fixed finite time interval. In other words, the evolution does not produce a sizable effect in finite time. The shortcoming of approximations of processes on finite time intervals has been discussed already in Barbour (1980). The effect of evolution is therefore observed on intervals increasing to infinity with the size of carrying capacity. The same effect of “wrong” approximation on finite intervals is equally observed in deterministic systems. In this work we show that one needs intervals that increase as $\log K$ and describe the fluid approximation in deterministic as well as stochastic settings. The limiting dynamics after the proposed time change is given by the same dynamics but different initial conditions. In this approximation population densities converge to a stable fixed point as time goes to infinity.

Key Words: Branching process, fluid approximation, bare bones evolution, carrying capacity, dynamical systems.

1. INTRODUCTION. STOCHASTIC EQUATIONS

In the Bare Bones Evolution Model of Sagitov and co-workers, appearance of a new mutation in a resident established population is described as follows. The resident population, which assumed to be around its carrying capacity, evolves as a binary splitting process with probability of successful reproduction (division) dependent on the size of that population Z^1 and also the size of the new mutant population Z^2 . The mutant populations also evolves as a binary splitting with initially very high probabilities of successful division. These probabilities

are given below. Here ξ^1 and ξ^2 denote the generic random variables representing offspring distribution of the resident and the mutant populations. The population size is denoted by $\mathbf{Z} = (Z^1, Z^2)$.

$$\begin{aligned} \mathbf{P}(\xi^1 = 0 | \mathbf{Z}) &= \frac{Z^{(1)} + \gamma Z^{(2)}}{a_1 K + Z^{(1)} + \gamma Z^{(2)}}, \\ \mathbf{P}(\xi^1 = 2 | \mathbf{Z}) &= \frac{a_1 K}{a_1 K + Z^{(1)} + \gamma Z^{(2)}}, \end{aligned}$$

and

$$\begin{aligned} \mathbf{P}(\xi^2 = 0 | \mathbf{Z}) &= \frac{\gamma Z^{(1)} + Z^{(2)}}{a_2 K + \gamma Z^{(1)} + Z^{(2)}}, \\ \mathbf{P}(\xi^2 = 2 | \mathbf{Z}) &= \frac{a_2 K}{a_2 K + \gamma Z^{(1)} + Z^{(2)}}. \end{aligned}$$

In a corresponding birth-death process the probability splitting into two gives the birth rate, and the complimentary probability the death rate. Hence individual death and birth rates are

$$\begin{aligned} \mu^1(z^1, z^2) &= C_1(z^1 + \gamma z^2) \quad , \quad \lambda^1(z^1, z^2) = C_1 a_1 K, \\ \mu^2(z^1, z^2) &= C_2(\gamma z^1 + z^2) \quad , \quad \lambda^2(z^1, z^2) = C_2 a_2 K, \end{aligned}$$

where C_1, C_2 are constants. There is no unique translation to continuous time, but if we replace the unit of discrete time by the exponential waiting time with rate 1, then the birth and death rates add up to one. In this way the birth rate is exactly the splitting probability and the death rate is its complimentary probability.

Hence in the first population individual birth and death rates are

$$\lambda^1(z^1, z^2) = \frac{a_1 K}{a_1 K + z^{(1)} + \gamma z^{(2)}}, \quad \mu^1(z^1, z^2) = \frac{z^{(1)} + \gamma z^{(2)}}{a_1 K + z^{(1)} + \gamma z^{(2)}}.$$

For the second population it is similar,

$$\lambda^2(z^1, z^2) = \frac{a_2 K}{a_2 K + \gamma z^{(1)} + z^{(2)}}, \quad \mu^2(z^1, z^2) = \frac{\gamma z^{(1)} + z^{(2)}}{a_2 K + \gamma z^{(1)} + z^{(2)}}.$$

The rates in the whole populations are

$$z^1 \lambda^1(z^1, z^2) \text{ and } z^1 \mu^1(z^1, z^2); \quad z^2 \lambda^2(z^1, z^2) \text{ and } z^2 \mu^2(z^1, z^2).$$

If $Z(t)$ is a Markov jump process with a positive holding time parameter $a(x)$, the jump from x with mean $m(x)$ and second moment $v(x)$ then (eg. [4])

$$Z(t) = Z(0) + \int_0^t a(Z(s))m(Z(s))ds + M(s),$$

where $M(s)$ is a martingale with predictable quadratic variation

$$\langle M, M \rangle_s = \int_0^t a(Z(s))v(Z(s))ds.$$

In a Birth-Death process the holding parameter is $a(x) = \lambda(x) + \mu(x)$, where $\lambda(x)$ and $\mu(x)$ are birth and death rates of the population at x , i.e. at x the process stays for an exponentially distributed time with parameter $a(x)$ then jumps to the state $x + \xi(x)$, where

$$\xi(x) = \begin{cases} 1, & \text{with prob } \lambda(x)/a(x) \\ -1, & \text{with prob } \mu(x)/a(x). \end{cases}$$

$$a(x) = \lambda(x) + \mu(x)$$

and the first two moments of the jump $\xi(x)$ are

$$m(x) := E\xi(x) = \frac{\lambda(x) - \mu(x)}{\lambda(x) + \mu(x)}, \quad v(x) := E\xi^2(x) = 1.$$

Therefore we have the following representation for Z^1 and Z^2

$$\begin{aligned} Z_t^1 &= Z_0^1 + \int_0^t \frac{a_1K - Z_s^1 - \gamma Z_s^2}{a_1K + Z_s^{(1)} + \gamma Z_s^{(2)}} Z_s^1 ds + M_t^1 \\ Z_t^2 &= Z_0^2 + \int_0^t \frac{a_2K - \gamma Z_s^1 - Z_s^2}{a_2K + \gamma Z_s^{(1)} + Z_s^{(2)}} Z_s^2 ds + M_t^2, \end{aligned} \tag{1.1}$$

where

$$\langle M^1, M^1 \rangle_t = \int_0^t Z_s^1 ds, \quad \langle M^2, M^2 \rangle_t = \int_0^t Z_s^2 ds.$$

Note that these processes are indexed by K , which is implicit, we make it explicit when necessary. We want to give approximations for large values of K .

2. FLUID APPROXIMATION

Here we give fluid approximation for the population density process $\mathbf{X}(t) = \frac{1}{K}\mathbf{Z}(t)$.

Classical fluid approximation is given by a result of Kurtz (1970) [2].

Theorem 2.1. *If $X_0^i \rightarrow x_0^i$ then (X_t^1, X_t^2) converges in sup norm on any finite time interval $[0, T]$ to (x^1, x^2) defined a solution to the following system of equations*

$$\begin{aligned} x_t^1 &= x_0^1 + \int_0^t \frac{a_1 - x_s^1 - \gamma x_s^2}{a_1 + x_s^{(1)} + \gamma x_s^{(2)}} x_s^1 ds, \\ x_t^2 &= x_0^2 + \int_0^t \frac{a_2 - \gamma x_s^1 - x_s^2}{a_2 + \gamma x_s^{(1)} + x_s^{(2)}} x_s^2 ds. \end{aligned} \tag{2.1}$$

2.1. Fluid Approximation for small initial values and convergence to unstable fixed point.

2.1.1. *Fixed points of the deterministic system.* The system (2.1) has four fixed points, obtained by solving the system

$$(x_t^1)' = 0, \quad (x_t^2)' = 0.$$

They are: $(0, 0)$, $(0, a_2)$, $(a_1, 0)$ and

$$(x_1^*, x_2^*) = \left(\frac{a_1 - \gamma a_2}{1 - \gamma^2}, \frac{a_2 - \gamma a_1}{1 - \gamma^2} \right). \tag{2.2}$$

The parameters are chosen in such a way that $a_i > 0$, $0 < \gamma < 1$, $a_1 - \gamma a_2 > 0$ and $a_2 - \gamma a_1 > 0$, so that the last point is the only one in the positive quadrant.

The first three fixed points are unstable, and (x_1^*, x_2^*) is stable, and we shall see that solutions converge to it from any positive initial condition.

2.1.2. *Convergence to unstable fixed point.* In the Evolution model the initial number of new mutants is one, $Z_0^2 = 1$, while the initial number of the resident population is around its carrying capacity K . Thus $X_0^2 = 1/K$ and its limit as $K \rightarrow \infty$ is $x_0^2 = 0$.

In this case the fluid approximation is given by

$$\begin{aligned} dx_t^1 &= \frac{a_1 - x_t^1}{a_1 + x_t^1} x_t^1 dt \\ x_t^2 &= 0. \end{aligned} \tag{2.3}$$

The first equation integrates by writing $\frac{a_1 + x_t^1}{x_t^1(a_1 - x_t^1)} dx_t^1 = dt$. Further, for any initial point x_0^1 , $\lim_{t \rightarrow \infty} x_t^1 = a_1$, while if $x_0^1 = a_1$, then $x_t^1 = a_1$ for all t .

Thus it follows from Theorem 2.1 that the fluid approximation for the Evolution Model on any fixed time interval is the unstable fixed point $(a_1, 0)$. This is because for any fixed time T the evolution has not produce a sizable effect. The effect of evolution is therefore observed on intervals increasing to infinity $[0, T_K]$, with $T_K \rightarrow \infty$.

This effect of “wrong” approximation, when done on finite time intervals, equally holds for the deterministic system. in fact the “correct” approximation for the deterministic system also works in the stochastic case. That’s why we start with the system below. We want to describe the behaviour of the system (solutions are indexed implicitly by K)

(2.4)

$$\begin{aligned} (x_t^1)' &= \frac{a_1 - x_t^1 - \gamma x_t^2}{a_1 + x_t^{(1)} + \gamma x_t^{(2)}} x_t^1, \quad x_0^1 \geq a_1 \\ (x_t^2)' &= \frac{a_2 - \gamma x_t^1 - x_t^2}{a_2 + \gamma x_t^{(1)} + x_t^{(2)}} x_t^2, \quad x_0^2 = 1/K. \end{aligned} \tag{2.4}$$

for large but fixed K , when $t \rightarrow \infty$. As $K \rightarrow \infty$, for a fixed t , $(x_t^1, x_t^2) \rightarrow (a_1, 0)$. But with an appropriate change of time convergence to a stable fixed point (x_1^*, x_2^*) in (2.2) takes place. In the next section we look to change time in the deterministic system (2.4).

3. CHANGE OF TIME

In this section use notation $x^K(t) = x^1(t)$ and $y^K(t) = x^2(t)$ to make explicit dependence of K . Take an $\alpha > 0$, and denote by

$$\sigma_K = \inf\{t : y^K(t) = \alpha\}.$$

The required time change is

$$\tau^K(t) = t + \sigma_K, \quad t \geq 0.$$

Let $\mathbf{G}(\mathbf{x})$ be a vector function of two variables

$$\mathbf{G}(\mathbf{x}) = \begin{pmatrix} g_1(\mathbf{x}) \\ g_2(\mathbf{x}) \end{pmatrix} = \begin{pmatrix} x(a_1 - x - \gamma y)/(a_1 + x + \gamma y) \\ y(a_2 - \gamma x - y)/(a_2 + \gamma x + y) \end{pmatrix}. \quad (3.1)$$

Since \mathbf{G} is Lipschitz in the domain of interest $x, y > 0$, continuous dependence on the initial conditions applies and we have obtained the following result.

Theorem 3.1. *There exists $\lim_{K \rightarrow \infty} \mathbf{x}^K(\tau^K(t)) = \mathbf{x}_\alpha(t)$, that uniquely solves*

$$\mathbf{x}_\alpha(t) = \begin{pmatrix} \beta \\ \alpha \end{pmatrix} + \int_0^t \mathbf{G}(\mathbf{x}_\alpha(u)) du,$$

where

$$\beta = \lim_{K \rightarrow \infty} x^K(\sigma_K) = y(\alpha), \quad (3.2)$$

where $y(t)$ is the solution of the differential equation

$$y'(t) = F(t, y(t)), \quad y(0) = a_1,$$

with

$$F(t, y) = \frac{(a_1 - y - \gamma t)}{t} \frac{y(a_2 + t + \gamma y)}{(a_1 + \gamma t + y)(a_2 - \gamma y - t)}, \quad \text{for } t > 0.$$

It is easy to see that the time changed first co-ordinate function $y^K(t) = x^1(\tau_t)$, (bringing again explicit dependence on K) is given by

$$(y^K)'(t) = F(t, y^K(t)), \quad 1/K \leq t < x_2^*, \quad y^K\left(\frac{1}{K}\right) = x^1(0) = a_1. \quad (3.3)$$

Theorem 3.2. *The sequence $y^K(t)$ on $[0, d]$ is sequentially compact. Furthermore, the limit on a subsequence satisfies the differential equation*

$$y'(t) = F(t, y(t)), \quad t > 0, \quad y(0) = a_1. \quad (3.4)$$

This equation is extended to $t = 0$ by defining $F(0, a_1)$ by continuity

$$F(0, a_1) = \frac{-\gamma(a_2 + \gamma a_1)}{2(a_2 - \gamma a_1)}.$$

Theorem 3.3. *Differential equation (3.4) has at most one solution.*

Since outside zero $F(t, y)$ is Lipschitz, the classical result gives global existence. Existence in the neighbourhood of zero is established in Theorem 3.2, while global uniqueness by Theorem 3.3. Hence we obtain the global existence and uniqueness result of solution of (3.4).

Corollary 1. *The differential equation $y'(t) = F(t, y(t))$, $y(0) = a_1$ has a unique solution on $[0, x_2^*)$ (ie. on $[0, c]$ with $c < x_2^*$). The solution $y(t)$ is decreasing and is strictly positive with $\lim_{t \rightarrow x_2^*} y(t) = x_1^* > 0$.*

REFERENCES

- [1] Barbour, A. Density dependent Markov population processes In: Biological growth and spread, Eds W. Jäger, H. Rost and P. Tautu Lecture Notes in Biomathematics 38, 36-49, Springer, Berlin (1980)
- [2] Kurtz, T. G. (1970) Solutions of ordinary differential equations as limits of pure jump Markov processes. *J. Appl. Probab.*, 7, 49-58.
- [3] Klebaner F. C. (1994) Asymptotic Behaviour of Markov Population Processes with Asymptotically Linear Rate of Change. *JAP*, 31, 614-625.
- [4] Klebaner, F.C. Introduction to Stochastic Calculus with Applications. 3rd Ed. Imperial College Press, 2012.
- [5] Klebaner, F., Sagitov S., Vatutin V., Haccou P., Jagers P. (2011) Stochasticity in the adaptive dynamics of evolution: the bare bones. *J. of Biological Dynamics*, Vol 5, No 2, 147-162.

SCHOOL OF MATHEMATICAL SCIENCES, BUILDING 28M, MONASH UNIVERSITY, CLAYTON CAMPUS, VICTORIA 3800, AUSTRALIA.

E-mail address: kais.hamza@monash.edu

INDUSTRIAL ENGINEERING AND MANAGEMENT, TECHNION, HAIFA 32000, ISRAEL

E-mail address: iehaya@tx.technion.ac.il

SCHOOL OF MATHEMATICAL SCIENCES, BUILDING 28M, MONASH UNIVERSITY, CLAYTON CAMPUS, VICTORIA 3800, AUSTRALIA.

E-mail address: fima.klebaner@monash.edu