

# Exact solution of master equations for a simple model of self-organized biological evolution

Yu M Pismak†

II. Institut für Theoretische Physik†, Universität Hamburg, 22761 Hamburg, Germany

Received 8 December 1994

**Abstract.** The master equations for the random neighbour Bak–Sneppen model are solved explicitly.

## 1. Introduction

Recently, Bak and Sneppen proposed a model of biological evolution [1, 2]. It is a dynamical system describing the mutation and natural selection of interacting species. The most interesting point in this model is the phenomenon of self-organized criticality which is studied intensively by means of several different numerical and analytical methods [3–6]. Self-organized criticality is the asymptotical critical behaviour in dynamical systems which is achieved without any external fine tuning of their parameters [7]. One can hope that the Bak–Sneppen model (BSM) represents an important universal type of critical behaviour which is realized in many dynamical systems independent of their detailed properties. It would be natural to expect this from the point of view of present experience in studies of critical phenomena.

The formulation of BSM is simple. It describes an ecosystem of  $N$  species which has a state defined by the set  $\{x_1, \dots, x_N\}$  of  $N$  numbers,  $0 \leq x_i \leq 1$ . The state of the  $i$ th species  $x_i$  is called the barrier; it characterizes the effective barrier towards further evolution of the species. The BSM dynamics is the following. Initially, each  $x_i$  is set to a randomly chosen value. At each time step the barrier  $x_i$  with minimal value and  $K - 1$  other barriers are replaced by  $K$  new random numbers. In the random neighbour model (RNBSM) the  $(K - 1)$ -replaced non-minimal barriers are chosen at random. In the local or nearest-neighbour model (LBSM) these are the barriers of the nearest neighbours to the species with minimal barrier. In this version of the BSM the nearest neighbours of the species are assumed to be defined.

The study of LBSM is more complex compared to the RNBSM because of the non-trivial topology of the interspecies interaction in the LBSM. The analytical study of the BSM is based mainly on the mean field approximation [2, 3, 6]; some exact results are obtained for the RNBSM [3]. In this paper we obtain the explicit solution of the master equation used in [3] for the study of the RNBSM. We consider these equations for the case of an infinite ecosystem with an infinite number of species (in the thermodynamic limit) only. The exact

† Supported in part by EC–Russia Collaboration Contract ESPRIT P9282 ACTCS.

‡ Permanent address: Department of Theoretical Physics, State University of Sankt-Petersburg, Ul'yanovskaya 1, Stary Petergof, 198904 Sankt-Petersburg, Russia (e-mail pismak@ontl.phys.lgu.spb.su).

stationary solution of the RNBSM master equations obtained in [3] is the asymptotic of the time-dependent solution which is constructed by us.

## 2. Statement of the problem

The basic quantity used in [3] to study the RNBSM is the probability that at time  $t$  the number of barriers that have values less than a fixed value  $\lambda$  is  $n$ . It is denoted in [3] as  $P_n(t)$  and fulfils the following master equation representing the dynamics of the RNBSM:

$$\begin{aligned} P_n(t+1) &= \lambda^2 P_{n-1}(t) + 2\lambda(1-\lambda)P_n(t) + (1-\lambda)^2 P_{n+1}(t) \quad n \geq 3 \\ P_2(t+1) &= \lambda^2 P_1(t) + 2\lambda(1-\lambda)P_2(t) + (1-\lambda)^2 P_3(t) + \lambda^2 P_0(t) \\ P_1(t+1) &= 2\lambda(1-\lambda)P_1(t) + (1-\lambda)^2 P_2(t) + 2\lambda(1-\lambda)P_0(t) \\ P_0(t+1) &= (1-\lambda)^2 P_1(t) + (1-\lambda)^2 P_0(t). \end{aligned} \quad (1)$$

The initial values  $P_n(0)$  at  $t=0$  are assumed to be given. Equations (1) define the values of probabilities  $P_n(t)$  for  $t>0$ . These can be considered as the complete specification of the RNBSM dynamical rules.

It is convenient for us to rewrite the system of equations (1) in the form

$$P_n(t+1) = aP_n(t) + bP_{n+1}(t) + cP_{n-1}(t)(1-\delta_{n,0}) + (\alpha\delta_{n,0} + \beta\delta_{n,1} + \gamma\delta_{n,2})P_0(t) \quad (2)$$

where

$$\begin{aligned} a &= 2\lambda(1-\lambda) & b &= (1-\lambda)^2 & c &= \lambda^2 \\ \alpha &= (1-\lambda)(1-3\lambda) & \beta &= \lambda(2-3\lambda) & \gamma &= \lambda^2. \end{aligned} \quad (3)$$

By virtue of (3)

$$a + b + c = 1 \quad \alpha + \beta + \gamma - b = 0. \quad (4)$$

Hence, it follows from (2) that the common necessary condition for probabilities  $P_n(t)$  is

$$\sum_n P_n(t+1) = (a+b+c) \sum_n P_n(t) + (\alpha + \beta + \gamma - b)P_0(t) = \sum_n P_n(t) = 1.$$

In the more general case, when there are no representations of the form (3) for the parameters of dynamical system (2) but relations (4) are fulfilled,  $P_n(t)$  could be treated as a probability.

By introducing the operator

$$D_{m,n}(t, t') = \delta_{t+1, t'} \delta_{m,n} - \delta_{t, t'} L_{m,n} \quad (5)$$

where

$$L_{m,n} \equiv a\delta_{m,n} + b\delta_{m+1,n} + c\delta_{m-1,n}(1-\delta_{m,0}) + (\alpha\delta_{m,0} + \beta\delta_{m,1} + \gamma\delta_{m,2})\delta_{0,n}.$$

Equation (2) can be rewritten in the compact form

$$(DP)_m(t) \equiv \sum_{t', n=0}^{\infty} D_{m,n}(t, t') P_n(t') = \delta_{t,0} P_m(0). \quad (6)$$

Thus, if the solution  $\Delta_{m,n}(t, t')$  of the operator equation

$$D\Delta = 1 \quad (7)$$

is found, the solution of equation (6) can be constructed as

$$(P)_m(t) = \sum_{n=0}^{\infty} \Delta_{m,n}(t, 0) P_n(0). \quad (8)$$

Hence, the problem of solving the master equations is reduced to an inversion of the linear operators  $D$  (5). There is no obvious transformation which diagonalizes  $D$  directly. In this case the inversion of  $D$  would be trivial. However, the important property of operator  $\Delta$ , which makes the problem of its construction solvable, is that  $\Delta_{m,n}$  for  $n \neq 0$  can be expressed in a simple way through  $\Delta_{0,n}$  and the equation for  $\Delta_{0,n}$  can be solved explicitly.

### 3. Modified equations for $\Delta$

Let us define the auxiliary operator

$$\Delta_{n,m}^0(t, t') \equiv \frac{1}{2\pi i} \oint \frac{dz(a + bz^{-1} + cz)^{t-t'-1}}{z^{m-n+1}} \theta(t - t'). \tag{9}$$

Here, by definition,

$$\theta(t) \equiv 0 \text{ for } t \leq 0 \quad \theta(t) \equiv 1 \text{ for } t > 0.$$

Multiplying both sides of equation (7) by  $\Delta^0$ , one obtains an equation of the form

$$\Delta^0 D \Delta = \Delta^0. \tag{10}$$

If the operator  $V$  is defined as

$$\Delta^0 D = 1 - V \tag{11}$$

one can verify directly that

$$V_{m,n}(t, t') = V_m(t, t') \delta_{0,n} \tag{12}$$

where

$$V_m \equiv \frac{1}{2\pi i} \oint \frac{dz(a + bz^{-1} + cz)^{t-t'-1}}{z^{m+1}} (\alpha + \beta z + \gamma z^2 - bz^{-1}) \theta(t - t'). \tag{13}$$

Thus, by virtue of (11) and (12), equation (10) can be rewritten as

$$\Delta_{m,n} - V_m \Delta_{0,n} = \Delta_{m,n}^0. \tag{14}$$

Setting  $m = 0$  in (14), one obtains the equation for  $\Delta_{0,n}$ :

$$\Delta_{0,n} - V_0 \Delta_{0,n} = \Delta_{0,n}^0. \tag{15}$$

The main result is that to solve equation (14) for the matrix operator  $\Delta_{m,n}$  it is enough to find the solution of equation (15) for  $\Delta_{0,m}$ . If  $\Delta_{0,m}$  is known, the matrix elements  $\Delta_{m,n}$  for  $m \neq 0$  can be constructed as

$$\Delta_{m,n} = V_m \Delta_{0,n} + \Delta_{m,n}^0. \tag{16}$$

### 4. Useful integral transformation

We introduce a special integral transformation (SIT) for functions of a complex variable, which will be necessary to solve equation (15). Its definition for the function  $f(z)$  is written in the form

$$\mathbb{I}_r\{f\}(t) \equiv \oint_r \frac{dz}{2\pi iz} (v + z + z^{-1})^{t-1} f(z) \theta(t). \tag{17}$$

Here, the integration contour is the circle  $|z| = r$  of the radius  $r$  with the centre at  $z = 0$ ,  $v$  is a parameter. It is assumed that the integral on the right-hand side of (17) exists. We shall

consider the SITs as functions of integer variables. For the SITs we define a convolution operation as

$$\mathbf{I}_r^\nu\{f\} * \mathbf{I}_r^\nu\{g\}(t, t') \equiv \sum_{s=0}^{\infty} \mathbf{I}_r^\nu\{f\}(t-s) \mathbf{I}_r^\nu\{g\}(s-t').$$

For such defined SITs the following simple lemmas can be proven.

*Lemma 1.* If the function  $f(z)$  is analytical for  $z \neq 0$ ,  $z \neq \infty$  and

$$f_R(z) \equiv f(z^{-1}) \quad \bar{f} \equiv \frac{1}{2}(f + f_R)$$

then

$$\mathbf{I}_r^\nu\{f\} = \mathbf{I}_r^\nu\{f_R\} = \mathbf{I}_r^\nu\{\bar{f}\}.$$

*Lemma 2.* If the functions  $f(z)$  and  $g(z)$  are analytical for  $|z| \leq r$ , then

$$\mathbf{I}_r^\nu\{f\} * \mathbf{I}_r^\nu\{g\} = \mathbf{I}_r^\nu\{f * g\}$$

where

$$f * g(z) \equiv \frac{zf(z)g(z)}{1-z^2}.$$

With the help of the SITs, equation (15) can be solved explicitly for  $\Delta_{0,n}$ . They are also convenient for constructing the matrix elements of operator  $\Delta$  from (16).

## 5. Exact solution of equations for $\Delta$

It follows from definition (9) that the operator  $\Delta^0$  is proportional to the SIT of a power function:

$$\Delta_{m,n}^0(t, t') = U_{m,n}(t, t') \mathbf{I}_r^\nu\{z^{n-m}\} \quad (18)$$

where

$$U_{m,n}(t, t') \equiv c^{(m-n+t-t'-1)/2} b^{(n-m+t-t'-1)/2} \quad v \equiv \frac{a}{\sqrt{bc}}. \quad (19)$$

From (13) one obtains a similar representation for the operator  $V_m$ :

$$V_m = U_{m,0} \mathbf{I}_r^\nu\{z^{-m} Q(z)\} \quad Q(z) \equiv \alpha' + \beta'z + \gamma'z^2 - b'z^{-1}. \quad (20)$$

Here

$$\alpha' = \alpha \quad \beta' = \sqrt{\frac{b}{c}} \beta \quad \gamma' = \frac{b}{c} \gamma \quad b' = \sqrt{\frac{c}{b}} b = \sqrt{bc}.$$

By virtue of lemma 1 the operator  $V_0$  is represented by the SIT of a polynomial function:

$$V_0 = U_{0,0} \mathbf{I}_r^\nu\{Q(z)\} = U_{0,0} \mathbf{I}_r^\nu\{q(z)\} \quad q(z) \equiv \alpha' + (\beta' - b')z + \gamma'z^2. \quad (21)$$

Thus, it is natural to suppose that the operator  $\Delta_{0,n}$  has a representation of the form

$$\Delta_{0,n} = U_{0,n} \mathbf{I}_r^\nu\{f_n(z)\}. \quad (22)$$

It is assumed here that the function  $f_n(z)$  is analytical for  $|z| \leq r$ . By using (18), (19), (21) and (22), equation (15) can be written as

$$\mathbf{I}_r^\nu\{f_n(z)\} - \frac{1}{\rho} \mathbf{I}_r^\nu\{q(z)\} * \mathbf{I}_r^\nu\{f_n(z)\} = \mathbf{I}_r^\nu\{z^n\} \quad \rho \equiv \sqrt{bc}$$

It is fulfilled if

$$f_n(z) - \frac{f_n(z)q(z)z}{\rho(1-z^2)} = z^n.$$

The solution of this equation

$$f_n(z) = \frac{\rho z^n(1-z^2)}{\rho(1-z^2) - q(z)z}$$

is obviously an analytical function for  $|z| \leq r$  if the parameter  $r$  of the SIT is chosen to be sufficiently small. Thus, we obtain the solution of equation (15) in the form

$$\Delta_{0,n} = U_{0,n} \mathbb{I}_r^\nu \left\{ \frac{\rho z^n(1-z^2)}{\rho(1-z^2) - q(z)z} \right\} = U_{0,n} \mathbb{I}_r^\nu \left\{ z^n + \frac{z^{n+1}q(z)}{\rho(1-z^2) - q(z)z} \right\}. \tag{23}$$

Substituting (20) and (23) in (16) and by use of lemmas 1 and 2 we obtain the following representations for the other matrix elements of  $\Delta$ :

$$\begin{aligned} \Delta_{1,n} &= U_{1,n} \mathbb{I}_r^\nu \left\{ z^{n-1} + \frac{z^{n+1}q_1(z)}{\rho(1-z^2) - q(z)z} \right\} \\ \Delta_{m,n} &= U_{m,n} \mathbb{I}_r^\nu \left\{ z^{n-m} + \frac{z^{m+n-1}q_2(z)}{\rho(1-z^2) - q(z)z} \right\}. \end{aligned}$$

Here  $q_1(z), q_2(z)$  are the polynomials

$$\begin{aligned} q_1(z) &\equiv \beta' + (\alpha' + \gamma')z - b'z^2 \\ q_2(z) &\equiv \gamma' + \beta'z + \alpha'z^2 - b'z^3 \end{aligned}$$

and the parameter  $r$  of the SIT is defined as

$$\rho(1-z^2) - q(z)z \neq 0 \quad \text{for } |z| < r.$$

By using (3), the operator  $\Delta$  for the original master equations (1) can be represented as

$$\begin{aligned} \Delta_{m,n}(t, t') &= \lambda^{m-n+t-t'-1} (1-\lambda)^{n-m+t-t'-1} \oint_r \frac{dz(1+z)^{2(t-t')-2}}{2\pi iz^{t-t'+m-n}} \\ &\quad \times \left( 1 + z^{2m-1} \frac{1-\lambda-\lambda z}{\lambda-(1-\lambda)z} \right) \theta(t-t') \\ \Delta_{1,n}(t, t') &= \lambda^{t-t'-n} (1-\lambda)^{n+t-t'-2} \oint_r \frac{dz(1+z)^{2(t-t')-2}}{2\pi iz^{t-t'-n+1}} \\ &\quad \times \left( 1 + \frac{z^2(2-3\lambda-\lambda z)}{(z+1)(\lambda-(1-\lambda)z)} \right) \theta(t-t') \\ &= \lambda^{t-t'-n} (1-\lambda)^{n+t-t'-2} \oint_r \frac{dz(1+z)^{2(t-t')-3} (1-z)(\lambda+(3\lambda-1)z+\lambda z^2)}{2\pi iz^{t-t'+n+1}(\lambda-(1-\lambda)z)} \\ &\quad \times \theta(t-t') \\ \Delta_{0,n}(t, t') &= \lambda^{t-t'-n-1} (1-\lambda)^{t-t'+n-1} \oint_r \frac{dz(1+z)^{2(t-t')-2}}{2\pi iz^{t-t'-n}} \\ &\quad \times \left( 1 + \frac{z((1-\lambda)z+1-3\lambda)}{(z+1)(\lambda-(1-\lambda)z)} \right) \theta(t-t') \\ &= \lambda^{t-t'-n} (1-\lambda)^{t-t'+n-1} \oint_r \frac{dz(1+z)^{2(t-t')-3} (1-z)}{2\pi iz^{t-t'-n}(\lambda-(1-\lambda)z)} \theta(t-t'). \end{aligned}$$

Here, the integration contour is the circle  $|z| = r, r < \lambda/(1-\lambda)$ .

The integrals can easily be calculated in the case of  $\lambda = 1/2$ :

$$\Delta_{m,n}(t, t') = 4^{1-t+t'} \left( \frac{2(t-t'-1)!}{(t-t'+m-n-1)!(t-t'-m+n-1)!} + \frac{2(t-t'-1)!}{(t-t'-m-n)!(t-t'+m+n-2)!} \right)$$

$$\Delta_{1,n}(t, t') = 4^{1-t+t'} \left( \frac{2(t-t'-1)!}{(t-t'-n)!(t-t'+n-2)!} + \frac{(2(t-t')-3)!}{(t-t'-n-2)!(t-t'+n-1)!} \right)$$

$$= 4^{1-t+t'} \frac{(2(t-t')-3)!(3(t-t')^2-10(t-t')+n^2-3n+8)}{(t-t'-n)!(t-t'+n-1)!}$$

$$\Delta_{0,n}(t, t') = 4^{1-t+t'} \left( \frac{2(t-t'-1)!}{(t-t'-n-1)!(t-t'+n-1)!} - \frac{(2(t-t')-3)!}{(t-t'-n-2)!(t-t'+n-1)!} \right)$$

$$= 4^{1-t+t'} \frac{(2(t-t')-3)!(t-t'+n-1)}{(t-t'-n-1)!(t-t'+n-1)!}$$

For  $\lambda \neq 1/2$  the following asymptotic forms of  $\Delta(t, t')$  can be obtained for  $t-t' \rightarrow \infty$ :

$$\Delta_{m,n}(t, t') = (1-2\lambda)\lambda^{2m-2}(1-\lambda)^{-2m} + \frac{4^{t-t'}\lambda^{t-t'+m-n-1}(1-\lambda)^{t-t'+n-m-1}}{\pi^{1/2}t^{5/2}}$$

$$\times \left( m + \frac{1-\lambda}{2\lambda-1} \right) \left( n + \frac{1-\lambda}{2\lambda-1} \right) + O(t^{-7/2}) \quad (24)$$

$$\Delta_{1,n}(t, t') = \frac{\lambda(1-2\lambda)(2-\lambda)}{(1-\lambda)^2} + \frac{4^{t-t'-1}\lambda^{t-t'-n}(1-\lambda)^{t-t'+n-2}(5\lambda-1)}{\pi^{1/2}t^{5/2}(2\lambda-1)}$$

$$\times \left( n + \frac{1-\lambda}{2\lambda-1} \right) + O(t^{-7/2}) \quad (25)$$

$$\Delta_{0,n}(t, t') = 1-2\lambda + \frac{4^{t-t'-1}\lambda^{t-t'-n-1}(1-\lambda)^{t-t'+n-1}}{\pi^{1/2}t^{5/2}(2\lambda-1)} \left( n + \frac{1-\lambda}{2\lambda-1} \right) + O(t^{-7/2}) \quad (26)$$

if  $\lambda < 1/2$ , and

$$\Delta_{m,n}(t, t') = \frac{4^{t-t'}\lambda^{t-t'+m-n-1}(1-\lambda)^{t-t'+n-m-1}}{\pi^{1/2}t^{5/2}} \left( m + \frac{1-\lambda}{2\lambda-1} \right) \left( n + \frac{1-\lambda}{2\lambda-1} \right)$$

$$+ O(t^{-7/2}) \quad (27)$$

$$\Delta_{1,n}(t, t') = \frac{4^{t-t'-1}\lambda^{t-t'-n}(1-\lambda)^{t-t'+n-2}(5\lambda-1)}{\pi^{1/2}t^{5/2}(2\lambda-1)} \left( n + \frac{1-\lambda}{2\lambda-1} \right) + O(t^{-7/2}) \quad (28)$$

$$\Delta_{0,n}(t, t') = \frac{4^{t-t'-1}\lambda^{t-t'-n-1}(1-\lambda)^{t-t'+n-1}}{\pi^{1/2}t^{5/2}(2\lambda-1)} \left( n + \frac{1-\lambda}{2\lambda-1} \right) + O(t^{-7/2}) \quad (29)$$

if  $\lambda > 1/2$ .

## 6. Conclusion

The solution obtained for  $\Delta$  can be verified by its direct substitution in equation (7). The asymptotic forms of  $P_n(t)$  (24)–(29) are in agreement with the results of [3]; for  $t \rightarrow \infty$  these can be calculated with help of (8).

In our paper we only considered the main mathematical problem arising for the description of self-organized criticality in the framework of RNBSM; however, our results

allow us to calculate all the quantities of interest for the understanding of critical phenomena in RNBSM. We hope that they will be useful for analytical and numerical studies of self-organized criticality in more complicated models. They could also be helpful for the elaboration of renormalization group methods for the BSM [8,9].

### Acknowledgments

I would like to thank Professor G Mack, B Mikeska and Y Xylander for fruitful discussions and to thank the II. Institute for Theoretical Physics of Hamburg University for its hospitality.

### References

- [1] Bak P and Sneppen K 1993 *Phys. Rev. Lett.* **71** 4083
- [2] Flyvbjerg H, Sneppen K and Bak P 1993 *Phys. Rev. Lett.* **71** 4087
- [3] de Boer J, Derrida B, Flyvbjerg H, Jacson A D and Wettig T 1994 *Phys. Rev. Lett.* **73** 906
- [4] Ray T S and Jan N 1994 *Phys. Rev. Lett.* **72** 4045
- [5] Paczuski M, Maslov S and Bak P 1994 *Europhys. Lett.* **27** 97
- [6] de Boer J, Jackson S D and Wettig T 1994 Criticality in simple models of evolution *Preprint cond-mat* 9409074
- [7] Bak P, Tang C and Wiesenfeld K 1987 *Phys. Rev. Lett.* **59** 381; 1987 *Phys. Rev. A* **38** 364
- [8] Marsili M and Caldarelli G 1994 Memory and self-organization *Preprint cond-mat* 9410111
- [9] Marsili M 1995 Renormalization group approach to the self-organization of a simple model of biological evolution *Europhys. Lett.* submitted for publication