

# Stochastic Modelling of Spatial and Dynamic Patterns. Applications in Ecology

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- revised version -

**Abstract.** Time dependent Poisson point processes are considered to describe spatial point patterns in time. Asymptotic equilibrium, extinction and explosion as long-time behaviour of the system may (eventually) occur. To lay the appropriate foundation for programming adaption of such processes to discrete and finite structures will be investigated. A further type of data from ecological case studies are spatially aggregated counts. An open stochastic network model will be proposed to describe the time dependent abundance of different species in a finite number of observation windows considering simple kinds of interaction.

**Keywords.** Stochastic point processes, stochastic networks, spatial and dynamic pointpatterns, spatially aggregated counts

## 1 Time Dependent Poisson Point Processes on $\mathbb{R}^d$

Time dependent Poisson point processes  $\{\xi_t\}_{t \geq 0}$  on  $\mathbb{R}^d$ ,  $d \in \mathbb{N}$ , of the following form

$$\xi_t = \sum_{k=1}^{C(t)} \mathbb{1}_{\{T_k > t\}} \varepsilon_{X_k(t)}, \quad t \geq 0$$

are investigated in the paper by Pfeifer, Bäumer, and Albrecht (1993).

$\{C(t)\}_{t \geq 0}$  denotes a Poisson counting process on  $\mathbb{R}^+ = \{x \in \mathbb{R} | x \geq 0\}$  with finite cumulative intensity measure  $E[C(t)] = \Lambda(t)$ .  $\Lambda(t)$  is some weakly increasing absolutely continuous function with  $\Lambda(0) \geq 0$ ,  $t \geq 0$ . This Poisson process governs the birth of particles.  $I_k(t) = \mathbb{1}_{\{T_k > t\}}$  is the indicator variable of the event  $\{T_k > t\}$  where  $\{T_k\}_{k \in \mathbb{N}}$  is a family of iid random variables with absolutely continuous cdf  $F$ ,  $F(0) = 0$ , and density  $f = F'$ .  $T_k$  controls the life length of each particle.  $\{X_k(t)\}_{t \geq 0, k \in \mathbb{N}}$  denotes a family of iid random variables with  $X_k(t) \in \mathbb{R}^d$  which controls the location of each particle in  $\mathbb{R}^d$ . For each Borel set  $B$   $\varepsilon_x(B)$  denotes the Dirac measure with mass 1 at  $x \in B$ .

In short, given a Borel set  $B$ ,  $\xi_t(B)$  describes the number of particles with  $X_k(t) \in B$  which have an expiring date later than  $t$ .

Weak convergence of the Poisson point processes  $\xi_t$  to some Poisson point process  $\xi$  with an appropriate intensity measure  $\mu$  is proven in Pfeifer, Bäumer, and Albrecht (1993), p. 251 ff.

The long-time behaviour of such Poisson point processes  $\{\xi_t\}_{t \geq 0}$  is studied with the following specifications. The cumulative intensity  $\Lambda(t)$  of the Poisson birth process  $\{C(t)\}_{t \geq 0}$  is given by  $\Lambda(t) = t^{d/2} \exp(c\tau t) + \Lambda(0)$ ,  $t \geq 0$ ,  $c \geq 0$ ,  $\tau > 0$ . The lifetime density is  $f(t) = \tau \exp(-\tau t)$ . The initial location is distributed as  $\mathcal{N}(\mathbf{0}, \sigma_0^2 \mathbf{I})$ ,  $\sigma_0^2 > 0$ . Here  $\mathbf{I}$  denotes the identity matrix. The movement of particles is governed by a componentwise independent Brownian motion  $B_t$  distributed as  $\mathcal{N}(\mathbf{0}, \sigma^2 t \mathbf{I})$ ,  $\sigma^2 > 0$ . The intensity measure  $\mu$  of  $\xi$  is proportional to  $m_d$ , the  $d$ -dimensional Lebesgue measure. In the case of  $c=1$ , an asymptotic equilibrium of the system will be achieved. For  $c < 1$  extinction (eventually) occurs, and for  $c > 1$  the system (eventually) explodes (cf. Pfeifer, Bäumer, and Albrecht (1993), p. 252 ff.).

As an introduction to random point processes on  $\mathbb{R}^d$  the monograph of König and Schmidt (1992) is recommended.

For computational purposes the model has to be adapted to discrete and finite structures.

## 2 Adaption to Discrete and Finite Structures

The Poisson point processes  $\{\xi_t\}_{t \geq 0}$  will be considered in discrete time steps of length  $h$ ,  $h > 0$ . Setting  $d=2$ , a circle of finite radius  $R$  around the origin is proposed as spatially finite structure in  $\mathbb{R}^2$ . To determine an appropriate  $R$ , the movement and lifetime of particles as well as hardware restrictions have to be taken into account. To visualize realizations of the Poisson point processes  $\xi_{kh}$ ,  $k=0,1,\dots,n$  on a screen a suitable square submatrix of the pixel matrix available is assumed a square of side length  $SL$  with the origin as midpoint. Particles trying to cross the boundary of the circle of radius  $R$ ,  $R > \sqrt{2}SL$ , become caught at the boundary. Then, the Poisson point processes  $\{\xi_t\}_{t \geq 0}$  are split up into three independent Poisson point processes. For the Poisson point processes in the open circle weak convergence to some Poisson point process  $\xi_C$  with an intensity measure proportional to  $m_2$  is preserved.

The probability  $\beta$ ,  $0 < \beta < 1$ , to survive  $m$  successive time steps  $h$  is  $\beta = \exp(-\tau mh)$ . Truncating  $\ln(\beta)/(-\tau h)$  to an integer is a conservative choice of  $m$ .

The location of particles at time  $t+h$  is controlled by iid random variables  $X_k(t+h) = X_k(t) + Z_k(h)$  which are distributed as  $\mathcal{N}(\mathbf{0}, (\sigma_0^2 + \sigma^2(t+h))\mathbf{I})$  where  $Z_k(h)$  is distributed as  $\mathcal{N}(\mathbf{0}, \sigma^2 h \mathbf{I})$ . Let  $L_{\max}$  denote the Euclidean distance between  $X_k(t)$  and  $X_k(t+mh)$  which will maximally be covered by a particle during  $m$  successive time steps  $h$  with probability  $1-\alpha$ . The random variable  $Y_m = \|Z_k(mh)\|^2 / (m\sigma^2 h)$  is distributed as  $\chi_{\text{df}=2}^2$

implying  $L_{\max} = \sqrt{m\sigma^2 k \chi_{df=2; q=1-\alpha}^2}$ . Then, each particle with an Euclidean distance to the origin equal to or greater than  $R = L_{\max} + \sqrt{2}SL$  will be captured at the boundary of the circle.

The net increase of particles in the open circle of radius  $R$  after a discrete time step  $h$  will be determined next. The Poisson birth processes  $C(t), C(t+h)$  are independent implying  $C(t+h) - C(t)$  to be a Poisson process  $\psi$  with intensity measure  $E\psi = E[C(t+h)] - E[C(t)] = \Lambda(t+h) - \Lambda(t)$ . In the case of  $d=2$  the intensity measure  $E\psi$  is  $\exp(c\tau t) [t(\exp(c\tau h) - 1) + h\exp(c\tau h)]$ . With the lifetime density  $f(t) = \tau \exp(-\tau t)$  the cdf is  $F(t) = 1 - \exp(-\tau t) = P(T_k \leq t)$ . Regarding a  $p$ -thinning of the Poisson process  $\psi$  with  $p = P(T_k > t+h) = 1 - F(t+h) = \exp(-\tau(t+h))$  a Poisson process  $\zeta$  results with intensity measure  $E\zeta = pE\psi = \exp(-\tau(t+h))E\psi$ . Considering the spatial restriction to the open circle around the origin with radius  $R$  leads to the probability  $p^* = P(\|X_k(t+h)\| < R) = 1 - \exp(-R^2 / (2(\sigma_0^2 + \sigma^2(t+h))))$ . Then, by a  $p^*$ -thinning of the Poisson process  $\zeta$ , a Poisson process  $\zeta^*$  results with the intensity measure  $E\zeta^* = p^*E\zeta = (1 - \exp(-R^2 / (2(\sigma_0^2 + \sigma^2(t+h)))) \exp(-\tau(t+h))E\psi$ . The Poisson process  $\zeta^*$  describes the net increase of particles in the open circle of radius  $R$  in the time interval  $[t, t+h]$ .

The location of particles belonging to the net increase is governed by iid random variables  $R_k(t+h) \in \mathbb{R}$  (distance from the origin) and iid angles  $\varphi_k$  which are uniformly distributed over the interval  $[0, 2\pi]$ . The conditional cdf of  $R_k(t+h)$  given  $\|X_k(t+h)\| < R$  is obtained

as  $F_{t+h}(r) = \frac{1 - \exp(-r^2 / (2(\sigma_0^2 + \sigma^2(t+h))))}{1 - \exp(-R^2 / (2(\sigma_0^2 + \sigma^2(t+h))))}$  with  $r \in [0, R]$  and  $F_{t+h} = 0$  elsewhere.

Let  $M_t$  be the number of particles with  $T_k > t$ , then the number of particles with  $T_k \leq t+h$  is binomially distributed as  $B(M_t, p_b)$  with  $p_b = 1 - \exp(-\tau h)$ . By inversion of the binomial distribution  $B(M_t, p_b)$  the number of particles with  $t < T_k \leq t+h$  is obtained.

### 3 Applications to Ecological Case Studies

On the basis of the theoretical results mentioned above a programme was implemented in Borland Pascal, version 7.0, using the object oriented library Vision. Input parameters are  $c, \tau, \sigma_0, \sigma, \Lambda(0)$ , and  $h$  with default value 1. User specified scale of time and scale of length are optional input. As a facultative feature of the programme time dependent planar Poisson Voronoi diagrams are generated.

For spatial tessellations and especially for applications of Poisson Voronoi diagrams the monograph of Okabe, Boots, and Sugihara (1992) may be consulted.

In the monograph of Richter and Söndgerath (1990) as well as in some recent papers (e.g. Pfeifer, Schleier-Langer, and Bäumer (1994)) applications of point process theory to ecological case studies are discussed. Simulation of features of the ecological process of repopulation of artificially depopulated experimental fields in the Lower Saxony Wadden Sea is a further example (cf. Bäumer, H.-P. (1994)). Substantive interpretation of the time dependent variation of the abundance of the gastropod *Hydrobia ulvae* repopulating the experimental fields implies the hypothesis of equilibrium as long-time behaviour. Adults of this species are smaller than 1 mm. Setting  $c$  to 1, time dependent planar Poisson point processes are applied starting with no individuals in the experimental field. Their number is gradually increased approaching an equilibrium with  $E\xi_c(B) \approx m_2(B)$ ,  $B \in \mathcal{B}^2$ , the Borel  $\sigma$ -field over  $\mathbb{R}^2$ .

Often in ecological case studies spatially aggregated data are gathered. As an example the abundance of two among several benthic species in each square of 4 cm<sup>2</sup> of a multicorer sample is presented in the following scheme.

245	142	326	52	293
222	368	84	18	67
239	25	477	213	204
18	570	183	494	47
238	119	126	591	20

0	1	2	0	2
4	4	1	3	2
1	0	5	1	1
0	1	1	2	0
0	0	1	2	0

Here, for a number of disjoint observation windows  $W_i, i=1, \dots, J$ , the abundance of different species  $s_1, \dots, s_N$  in the window at time  $t$  is known, but the location of each individual is not. The observation windows are neither necessarily adjacent nor of equal area as in the scheme above.

Such a configuration is basic to multiclass queueing networks consisting of a set  $\mathcal{J} = \{1, \dots, J\}$  of queues and a set  $\mathcal{C} = \{c_1, \dots, c_N\}$  of customer classes. A network is said to be open if customers are allowed to leave or enter it.

A relatively simple open stochastic network model will be proposed to describe the dynamics of an assemblage of several species in the following section.

## 4 Rethinking an Open Stochastic Network Model

Let  $\mathcal{W} = \{W_1, \dots, W_J\}$  denote a set of observation windows and  $\mathcal{S} = \{s_1, \dots, s_N\}$  a set of faunal species. At a given time  $t, t \geq 0$ , each organism in the open system belongs to one of the  $N$  species and is in one of the  $J$  observation windows. Then  $n_{s,i}(t), s=1, \dots, N$ , denotes the abundance of species  $s$  in the window  $W_i$  at time  $t$ . The sum of the  $n_{s,i}(t), s=1, \dots, N$ , is  $n_i$ , the total count of organisms in window  $W_i$ . Immigration, movement of individuals between observation windows, emigration, distribution and consumption of resources with regard to simple kinds of interaction as aggregation and repulsion are considered in the model.

For each species  $s$  the number of individuals immigrating into window  $W_i$  at time  $t$  is described by an independent Poisson count process  $C_{s,i}(t), t \geq 0$ , with intensity  $\mu_{s,i} = a_{s,i}t = E[C_{s,i}(t)] \geq 0$ . The vector  $A_s = (a_{s,i})_{i=1,\dots,J}$  is called vector of immigration rates. The conditional probability for an immigrating individual to arrive in window  $W_i$  is  $p_{s,0i} = a_{s,i} / a_s$  where  $a_s$  denotes the sum of the  $a_{s,i}, i = 1, \dots, J$ . An individual emigrating from the system will never return.

The movement of organisms of species  $s$  in the system is described by the routing matrix  $P_s = (p_{s,ik})_{i,k=1,\dots,J}$ . The probabilities  $p_{s,ik}$  govern the internal transition of an individual of species  $s$  from  $W_i$  to  $W_k$ . Let  $p_{s,i}$  denote the sum of the  $p_{s,ik}, k = 1, \dots, J$ . Then,  $p_{s,i0} = 1 - p_{s,i}$  is the probability for an individual of species  $s$  to emigrate directly from window  $W_i$ .

Assuming the probability for an organism of species  $s$  to leave the system directly or indirectly to be larger than 0 ensures that the absolute largest eigenvalue of  $P_s$  is positive and less than 1 (cf. Brauer, A. (1961), p. 443). Then,  $\mathbf{I} - P_s$  has an inverse which equals a convergent (von Neumann) series. Therefore, there exists a unique vector  $Q_s$  with  $Q_s^T = A_s^T (\mathbf{I} - P_s)^{-1} = A_s^T \sum_{k=0}^{\infty} P_s^k$ , with  $P_s^0 = \mathbf{I}$ .

The nonnegative components  $q_{s,i}$  of the vector  $Q_s$  may be considered as the equilibrium immigration rate for individuals of species  $s$  in observation window  $W_i$ .

For each species  $s$  let  $\{R_{s,i}\}_{i=1,\dots,J}$  denote a family of independent random variables with values in  $\mathbb{R}^+$ , cdf  $F_{s,i}$ , and finite expectation  $E[R_{s,i}] = r_{s,i}$ .  $R_{s,i}$  controls the resources available for species  $s$  in window  $W_i$ . In particular, the random variable  $R_{s,i}$  governs the portion of these resources available to the  $j$ -th organism of species  $s$  in window  $W_i$ . At the arrival of the  $j$ -th individual of species  $s$  in window  $W_i$  at time  $t_a$  its resources  $r_{s,i,j}(t_a)$  are a realization of random variable  $R_{s,i}$ . The individual resources  $r_{s,i,j}(t_a)$  are spent with a rate which is proportional to some given function  $v_i(n_i(t))$ . In the case of  $r_{s,i,j}(t) = 0$  the  $j$ -th individual immediately moves to another window  $W_k$  according to  $p_{s,ik}$  of the routing matrix  $P_s$ .

To investigate the long-time behaviour of the system the processes  $\eta(t) = (\eta_1(t), \dots, \eta_J(t))$  with  $\eta_i(t) = (n_i, \varphi_{i,1}, \dots, \varphi_{i,n_i})$  are introduced. The organisms are indexed with regard to their arrival time. With  $\varphi_{i,j} = \varphi_{i,j}(t) = (s_j, r_{i,j}, z_{i,j}(t))$ , where  $s_j$  denotes the species of the  $j$ -th organism,  $r_{i,j}$  denotes the individual resources, and the  $z_{i,j}(t)$  denote the resources already spent by the  $j$ -th organism at time  $t$ , the processes  $\eta(t)$  are Markovian. So, several important equilibrium properties of the model exist (cf. Pollett (1986), p. 395 ff.).

To assert the most relevant property set  $b_{s,i} = q_{s,i}r_{s,i}$  which may be considered as the average amount of resources carried by organisms of species  $s$  in the window  $W_i$ , and let  $b_i$  denote the sum of the  $b_{s,i}$ ,  $i = 1, \dots, J$ . Let further denote  $d_i(n)$  the product of the  $jv_i(j)$ ,  $j = 1, \dots, n$ , with  $d_i(0) = 1$ . Then, if  $e_i^{-1} = \sum_{n=0}^{\infty} b_i^n / d_i(n)$  is finite for each window  $W_i$  an equilibrium distribution for  $\eta(t)$  exists. In this case the  $n_i$  are independent under the equilibrium distribution and the probability that  $n$  organisms are in window  $W_i$  is given by  $P(n_i = n) = e_i b_i^n / d_i(n)$ .

Under the simplifying conditions that all parameters are independent of the choice of the index  $i$  of the windows the equilibrium distribution is Poissonian if no interaction between organisms is assumed. In the case of aggregation the equilibrium distribution is geometric. Taking the carrying capacity of each window into account and considering thinning out the equilibrium distribution is binomial. Assuming further that the windows are adjacent squares of equal area and combining no interaction and aggregation in the specification of the function  $v = v_i$  allows to model the well known empirical relation of sample mean and variance observed for spatially aggregated counts.

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