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Space-time dependence dynamics for birth-death point processes*

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Abstract

This paper analyses the space-time interdependency of a spatially explicit birth-death process based on the intensity function. Based on intensity functions, these formulations can be, to some extent, analytically solved to obtain explicit formulae of, for instance, the total point population size contained in the unit torus at equilibrium. The definition of continuous space-time processes based on point intensities opens up new promising lines of research to analyse ecological dynamics: our spatially explicit birth-death process can be easily expanded to mimic other realistic ecological scenarios. Note that although space-time stochastic processes are (generally) intractable, theoretical development of their corresponding intensity function provides useful insights into these complex dynamics. Hence, the analytical analysis of the point intensity provides a complementary method to simulation-based analyses of complex space-time processes.

2000 Mathematics Subject Classification: 60G55; 60K35; 62H11; 62M30.

Keywords and Phrases: Birth-death processes, Ecological dynamics, Intensity function, Point processes, Space-time interdependency, Space-time stochastic processes, Strauss process

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1. Introduction

The incorporation of spatial elements into ecological models has become increasingly popular during the last few decades. The development of computer software such as Geographic Information Systems (GIS) and the dramatic increase in processing speed and memory on personal computers have clearly contributed to such tendency. Moreover, the incorporation of spatial information has revealed, and continues revealing, unexpected results on stability and dynamics from local (i.e. non-spatial) models. For instance, several authors suggest that the spatial structure of ecological dynamics affects population as much as average birth and death rates, competition and predation do (see, amongst others, Tilman and Kareiva, 1997; Bascompte and Solé, 1998).

Although considerable attention has been paid to model spatio-temporal ecological dynamics of populations, including diffusion-reaction models (Skellam, 1951; Levin, 1979; Kareiva, 1990; Okuvo and Levin, 2001), lattice-base models (Durret and Levin, 1994) and metapopulation models (Hanski, 1999), rather less research has been done to analyse continuous spatio-temporal dynamics of "single" individuals. The assumption of individual organism information is crucial to understand ecological phenomena where different type-class of organisms, such as organism size and species, are exploiting the same region but at distinct distinguished locations. For instance, Pacala and Deutschman (1995) show how crucial the spatial distribution of individual trees can be to maintain forest ecosystem function.

A natural way to analyse and model continuous space-time dynamics of single individuals can be done through the development of spatial point processes. Loosely speaking, a spatial point process is a stochastic mechanism which generates a countable set of events x_i in a bounded region A(see, for instance, Stoyan *et al.*, 1995 or Diggle, 2003). Point process theory plays a fundamental role to analyse and model ecological patterns. Since the Neyman's (1939) pioneering paper suggesting the use of spatial point processes to model the spatial distribution of insect larvae, a large amount of spatially explicit approaches has been formulated to generate purely spatial patterns (see, for instance, Diggle, 2003). Relevant examples include the family of cluster processes, based on the contagious distribution of Neyman (1939), conceived to generate aggregated spatial patterns of individuals, inhomogeneous Poisson processes to create spatial heterogeneity, and Gibbs processes to generate inhibitory point patterns. However, most of these point process models generate spatial patterns in terms of purely spatial relationship, though in real life biological population of plants and animals evolve through time.

A novel way to analyse space-time processes can be done through the development of *multi-generation* point processes (Diggle, 2003; Comas and Mateu, 2007). These type of point processes have the potential to generate spatial point patterns evolving through discrete time. Moreover, given that they are (usually) defined by fairly tractable mathematical formulations, it is possible to make substantial analytical progress of such approaches (Comas and Mateu, 2007). However, although multi-generation point processes can be a reasonable approximation for population reproducing at discrete interval of times (such as annual plants), these type of processes may not satisfactorily analyse dynamics of individuals reproducing continuously through time.

Renshaw and Särkkä (2001) formulate a continuous space-time stochastic process to generate spatial patterns of (marked) points on the unit torus. Although this approach defines a simple and flexible framework to generate spatial patterns where the underlying point structure is constantly changing, this model is based on the simulation of growing and interacting (marked) points rather than on the simulation of the underlying marked point intensity measure (i.e. first order properties; see, for instance, Stoyan *et al.*, 2005). This paper expands the work of Comas and Mateu (2007) by analysing several continuous space-time processes formulated through the point intensity, assuming a spatially explicit birth-death process.

The main purpose of this paper is to study the space-time interdependency of continuous spacetime stochastic processes through the analysis of the underlying intensity function. Specific aims and features are to (i) formulate a spatially explicit birth-death process dependent on the spatial configuration of points and based on the intensity function, and (ii) provide conditions for stability of such a model. In particular, we start in Section 2 with a simple spatially explicit birth-death process. Then, in Section 3, we consider a more realistic approach by introducing parent-to-parent interaction effects to limit offspring production, providing the condition for stability. Finally, in Section 4, we discuss the applicability of such formulation and suggest a tentative way to simulate such processes.

2. A simple continuous space-time birth-death process

Let $Z(\mathbf{x}; t)$ be the random intensity function depending on a spatial location $\mathbf{x} \in \mathbb{R}^2$ and a temporal instant t of a point process $\Phi_t \subset \mathbb{R}^2$, where the subindex denotes the temporal instant t. Then, in the subsequent small time interval of length dt, the increase in point intensity due to the reproduction of a single organism is αdt , and consequently, the increase in size due to all organisms located over a given region $A \subset \mathbb{R}^2$ is

$$\alpha \int_A Z(\mathbf{y}; t) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} dt$$

where $g(\mathbf{x} - \mathbf{y})$ is a time invariant radially symmetric bivariate probability density function (p.d.f.), i.e. the offspring spatial distribution around "parent" events. Moreover, in this subsequent small time interval the decrease in population size due to the death of a single organism is μdt , and the point mortality due to all $Z(\mathbf{x}; t)$ points is $\mu Z(\mathbf{x}; t) dt$. Hence

$$Z(\mathbf{x};t+dt) = Z(\mathbf{x};t) + \alpha \int_{A} Z(\mathbf{y};t)g(\mathbf{x}-\mathbf{y})d\mathbf{y}dt - Z(\mathbf{x};t)\mu dt$$
(2.1)

which, on dividing both sides by dt, gives

$$dZ(\mathbf{x};t)/dt = \alpha \int_{A} Z(\mathbf{y};t)g(\mathbf{x}-\mathbf{y})d\mathbf{y} - Z(\mathbf{x};t)\mu.$$
(2.2)

Note that $Z(\mathbf{y}; t)$ could be the intensity function of a Poisson cluster process (i.e. a Cox process). Also notice that a symmetric p.d.f. $g(\cdot)$ and a stationary "parent" event distribution (i.e. the points at time t) implies stationarity in the resulting point distribution at time t + dt. Furthermore, we can consider that

$$\int_{A} Z(\mathbf{y}; t) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} \equiv \sum_{i=1}^{N(t)} g(\mathbf{x} - \xi_i)$$
(2.3)

where $\xi_i \in \Phi_t$ are points located in A at time t, and N(t) is the total number of points in A at time t, i.e. $N(t) = \int_A Z(\mathbf{x}; t) d\mathbf{x}$. The relation in (2.3) is due to the fact that only those spatial positions $\mathbf{y} \in \mathbb{R}^2$ where there is a point $\xi_i \in \Phi_t$ at time t contribute to the birth process. Moreover, on applying standard mathematical results, we obtain that

$$\frac{dN(t)}{dt} = \int_{A} \frac{dZ(\mathbf{x};t)}{dt} d\mathbf{x},$$
(2.4)

which is valid as long as $dZ(\mathbf{x};t)/dt$ is continuous in both t and **x**. On substituting (2.3) into (2.2), and integrating both sides of (2.2) over the region A, we obtain

$$dN(t)/dt = \int_{A} \left(\alpha \sum_{i=1}^{N(t)} g(\mathbf{x} - \xi_i) - Z(\mathbf{x}; t) \mu \right) d\mathbf{x}$$
(2.5)

which can be further simplified to give EPTED MANUSCRIPT

$$dN(t)/dt = \int_{A} \alpha \sum_{i=1}^{N(t)} g(\mathbf{x} - \xi_i) d\mathbf{x} - N(t)\mu, \qquad (2.6)$$

yielding

$$dN(t)/dt = N(t)\alpha - N(t)\mu, \qquad (2.7)$$

since $\int_A g(\mathbf{x} - \xi_i) d\mathbf{x} = 1$, assuming that the area of region A is "big enough". Solving the equation (2.7) leads to the relation

$$N(t) = N(0) \exp\{(\alpha - \mu)t\}.$$
(2.8)

Expression (2.8) is the non-spatial expression of the population size growth for a simple linear birth-death process (see, for instance, Renshaw, 1991), which results in an exponential growth. Note that this population growth is independent of the spatial distribution of offspring around parent-events, which is expected since offspring distribution neither affect the birth rate nor the death rate. This model can be a reasonable approximation for a population when there is no limit in the available food resource to ensure that there is no competition between individuals. However, if the availability of food resources and space is limited, population cannot grow without limit; individuals start to interact with each other reducing the total number of individuals.

3. Introducing a birth rate dependent on the spatial point structure

A first choice to ensure that the process (2.2) remains bounded is to consider that the birth rate α depends on the spatial configuration of points. Usually, in real life, one may expect that the interaction between parent-individuals affects negatively/positively the resulting reproduction dynamics. For instance, certain types of trees reduce their canopy size as the result of interaction pressure. Having smaller canopies, these interacting trees produce far less number of seeds than those trees which are isolated.

Consider that the birth rate is positively/negatively affected by the distance between parentevents. Thus, the offspring production due to the point intensity located at \mathbf{y} at time t can be defined as

$$\alpha Z(\mathbf{y};t) \exp\left(-\int_{A} d(\|\mathbf{y}-\mathbf{z}\|) d\mathbf{z}\right).$$
(3.9)

Here $d(\cdot)$ is a time invariant function relating parent spatial configuration and offspring production. A possible choice of $d(\cdot)$ includes the Strauss-like *pair potential* function (Strauss, 1975), for which

$$d(\|\mathbf{y} - \mathbf{z}\|) = \begin{cases} c & \text{if } \|\mathbf{y} - \mathbf{z}\| < R, \mathbf{y} \text{ and } \mathbf{z} \text{ contain a point and } \mathbf{y} \neq \mathbf{z} \text{ at time } t \\ 0 & \text{otherwise} \end{cases}$$
(3.10)

where R is the interaction distance, i.e. the interaction range, and c is a constant interaction effect. Whilst under c > 0 interacting parents reduce offspring production, for c < 0 parent-toparent interaction favours offspring production. Then, substituting the density-dependent offspring production due to the point intensity $Z(\mathbf{y}; t)$ (expression (3.9)) into (2.2) we obtain

$$dZ(\mathbf{x};t)/dt = \alpha \int_{A} Z(\mathbf{y};t) \exp\left(-\int_{A} d(\|\mathbf{y}-\mathbf{z}\|) d\mathbf{z}\right) g(\mathbf{x}-\mathbf{y}) d\mathbf{y} - Z(\mathbf{x};t)\mu,$$
(3.11)

which is the increase in point intensity assuming a birth rate dependent on the spatial point structure. Moreover, on noting that

$$\int_{A} d(\|\mathbf{y} - \mathbf{z}\|; t) d\mathbf{z} = c \, u(\mathbf{y}; t), \tag{3.12}$$

where $u(\mathbf{y}; t)$ is the number of points that interact with the spatial position \mathbf{y} at time t, expression (3.11) can be written as

$$dZ(\mathbf{x};t)/dt = \alpha \int_{A} Z(\mathbf{y};t) \exp(-c \, u(\mathbf{y};t)) g(\mathbf{x}-\mathbf{y}) d\mathbf{y} - Z(\mathbf{x};t) \mu.$$
(3.13)

Since $u(\mathbf{y};t) = 0, 1, 2, \dots$ it follows that

$$\int_{A} Z(\mathbf{y};t) \exp(-c \, u(\mathbf{x};t)) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} = \int_{A_0(t)} Z(\mathbf{y};t) \exp(0) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} + \int_{A_1(t)} Z(\mathbf{y};t) \exp(-c) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} + \int_{A_2(t)} Z(\mathbf{y};t) \exp(-2c) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} + \dots$$
(3.14)

where $A_i(t)$, for i = 0, 1..., denotes a subregion of A where i balls b(0, R) (see (3.10) for the Strauss process) with radius R centrered at an arbitrary point 0 overlap with each other at time t. Following expression (2.3) we can write

$$\int_{A_i(t)} Z(\mathbf{y}; t) \exp(-ic) g(\mathbf{x} - \mathbf{y}) d\mathbf{y} \equiv \exp(-ic) \sum_{j=1}^{N_i(t)} g(\mathbf{x} - \xi_j)$$

where $\xi_j \in \Phi_t$ is any point located in A at time t interacting with i neighbours, and $N_i(t)$ is the total number of points in A at time t interacting with i neighbours. Whence we can rewrite (3.14) via

$$\int_{A} Z(\mathbf{y};t) \exp(-c \, u(\mathbf{x};t)) g(\mathbf{x}-\mathbf{y}) d\mathbf{y} = \sum_{i=0}^{\infty} \exp(-ic) \sum_{j=1}^{N_i(t)} g(\mathbf{x}-\xi_j).$$
(3.15)

On substituting (3.15) into (3.13), we obtain

$$dZ(\mathbf{y};t)/dt = \alpha \sum_{i=0}^{\infty} \exp(-ic) \sum_{j=1}^{N_i(t)} g(\mathbf{x} - \xi_j) - Z(\mathbf{y};t)\mu$$
(3.16)

which on integrating over A yields

$$dN(t)/dt = \int_{A} \left(\alpha \sum_{i=0}^{\infty} \exp(-ic) \sum_{j=1}^{N_{i}(t)} g(\mathbf{x} - \xi_{j}) \right) d\mathbf{x} - N(t)\mu.$$
(3.17)

This can be further simplified to give

$$dN(t)/dt = \alpha \sum_{i=0}^{\infty} \exp(-ic)N_i(t) - N(t)\mu$$
 (3.18)

given that for a given i (in (3.17))

$$\int_{A} \exp(-ic) \sum_{j=1}^{N_{i}(t)} g(\mathbf{x} - \xi_{j}) d\mathbf{x} = \exp(-ic) \int_{A} g(\mathbf{x} - \xi_{1}) d\mathbf{x} + \dots + \int_{A} g(\mathbf{x} - \xi_{N_{i}(t)}) d\mathbf{x}$$
$$= \exp(-ic) N_{i}(t)$$

since $\int_A g(\mathbf{x} - \xi_j) d\mathbf{x} = 1$ assuming a "large enough" area A. Notice that $N_i(t)$, i.e. the number of points that interact with i neighbours, is fully dependent on the spatial distribution of offspring

around "parent" events. Thus if c = 0, i.e. the interaction between parents does not affect the production of offspring (see expression (3.10)), from (3.18) we obtain

$$dN(t)/dt = \alpha \sum_{i=0}^{\infty} N_i(t) - N(t)\mu$$

i.e. $dN(t)/dt = \alpha N(t) - \mu N(t)$, since $\sum_{i=0}^{\infty} N_i(t) = N(t)$, the population size grows/decays exponentially (see expression (2.7)). Then we can write $N_i(t)$ as

$$N_i(t) = N(t)P(b(0,r) = i;t)$$

where P(b(0, r) = i; t) is the conditional probability of having *i* points within a ball b(0, R) (see the interaction expression (3.10)) with radius *R* centrered at an arbitrary point 0. Hence expression (3.18) can be written via

$$dN(t)/dt = \alpha \sum_{i=0}^{\infty} \exp(-ic)N(t)P(b(0,r) = i;t) - N(t)\mu.$$

From this equation we see that in equilibrium

$$\alpha \sum_{i=0}^{\infty} \exp(-ic) P(b(0,r) = i; t) N^* - N^* \mu = 0, \qquad (3.19)$$

where N^* is N(t) in equilibrium (assuming this equilibrium exists). Expression (3.19) suggests two equilibrium states, an unstable situation when $N^* = 0$, and a stable one when

$$\sum_{i=0}^{\infty} \exp(-ic)P(b(0,r)=i;t) = \mu/\alpha.$$

Then given that $\sum_{i=0}^{\infty} P(b(0, r) = i; t) = 1$ and $0 \leq P(b(0, r) = i; t) \leq 1$ (i.e. a probability), if c = 0, i.e. the interaction between parents does not affect the production of offspring, an equilibrium state is only reached when $\mu = \alpha$ (see also expression (2.7)). Moreover, if c < 1, i.e. parent-to-parent interaction favours offspring production, it is required that $\mu < \alpha$ to have a stable equilibrium. In words, if the interaction between parents promotes offspring production, the rate of mortality has to be larger than the birth rate in order to bound the population growth. Finally, if c > 1, i.e. parent-to-parent interaction effects reduce offspring production, it is required that $\mu < \alpha$, i.e. the rate of mortality has to be smaller than the birth rate to have a stable state.

4. Final remarks

Few approaches have been formulated to analyse continuous space-time interdependencies (see, amongst others, Renshaw and Särkkä, 2001; Särkkä and Renshaw, 2006; Comas and Mateu, 2007). For instance, Renshaw and Särkkä (2001) formulate an immigration-growth-spatial interaction process to generate spatial patterns of marked points. This approach is based on the simulation of growing and interacting marked points rather than on the simulation of the underlying marked point intensities (i.e. first order properties). As such, they analyse such complex space-time interdependency of distinct growth and interaction functions, and Renshaw and Comas (2005) study the limiting case when random point mortality tends to zero $\mu \rightarrow 0$. Moreover, Comas and Mateu (2007) show that the formulation of multi-generation (i.e. discrete time) point processes

based on the point intensities permits analytical analysis of such complex point process models. Their results suggest that analytical analyses of the underlying intensity function of such complex space-time models provide a complementary method to simulation-based analyses in order to study these complex dynamics.

This paper, therefore, has expanded the work of Comas and Mateu (2007) by analysing a continuous space-time birth-death process, confirming that the analitical study of the underlying intensity function can provide a novel way to formulate and analyse continuous space-time stochastic processes. Note that although in this paper we have focused our attention on a spatially explicit birth-death process assuming density-dependent effects on parent offspring production, this model can be easily expanded to mimic other realistic ecological scenarios. For instance, far more complex models can be formulated by changing the robust and easy-to-interpret Strauss-type interaction function by other interaction mechanisms.

Regarding the simulation of these continuous space-time stochastic processes, it can be done through the evaluation of the $Z(\mathbf{x}; t)$ for those spatial positions that contain an already established point and spatial positions of tentative newly arrived points to test for point establishment, mortality and interaction effects. As such, the simulation of these point processes is based on point positions rather than on intensity functions (see, for instance, Renshaw and Särkkä, 2001). This clearly does not limit the potential number of point positions (as for a process in the lattice space), because newly arrived points can explore any spatial location, while keeping the procedure reasonably fast in terms of required computing time.

Finally, we conclude this paper by saying that the definition of continuous space-time processes based on the point intensity opens up new promising lines of research to analyse realistic ecological dynamics.

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References

- Bascompte, J. and Solé, R.V. (1998), Modeling spatiotemporal dynamics in ecology, Springer, New York.
- Comas, C. and Mateu, J. (2007), Multi-generation space-time point processes, Statistics, to appear.
- Diggle, P.J. (2003), Statistical Analysis of Spatial Point Patterns, Hodder Arnold, 159pp.
- Durret, R. and Levin, S. (1994), The importance of being discrete (and spatial), *Theor. Pop. Biol.* **46**, 363-394.
- Ford, E.D. and Renshaw, E. (1984), The interpretation of process from pattern using two-dimensional spectral analysis: modelling single especies patterns in vegetation, Vegetatio 56, 113-123.

Hanski, I. (1999), Metapopulation Ecology, Oxford University Press.

- Kareiva, P. (1990), Population dynamics in spatially complex environments: theory and data. In Population regulation and dynamics, M.P. Hassell and R.M. May, eds., Royal Society, London.
- Levin, S.A. (1979), Nonuniform stable solutions to reaction-diffusion equations: aplications to ecological pattern formation. In *Pattern formation by dynamic systems and pattern recognition*, H. Haken, ed., Springer, Berlin.

- Neyman, J. (1939), On a new class of contagious distributions, applicable in entomology and bacteriology. Annals of Mathematical Statistics 10, 35-57.
- Okubo, A. and Levin, S.A. (2001), Diffusion and Ecological Problems, Springer, 2nd edition.
- Pacala, S.W. and Deutschman, D.H. (1995), Details that matter: the spatial distribution of individual trees maintains forest ecosystem function, Oikos 74, 357-365.
- Ripley, B.D. (1976), The second-order analysis of stationary point processes, *Journal of Applied Probability* **13**, 255-266.
- Renshaw, E. (1991), Modelling biological populations in space and time, Cambridge Univ. Press.
- Renshaw, E. and Särkkä, A. (2001), Gibbs point processes for studying the development of spatialtemporal stochastic processes, *Computational Statistics and Data Analysis* 36, 85-105
- Renshaw, E. and Comas, C. (2005), Space-time generation of high-intensity patterns using growthinteraction processes, Conference on *Stochastic Geometry and its Applications*, 3-7 October, Bern, Switzerland.
- Salonen, V., Penttinen, A. and Särkkä, A. (1992), Plant colonization of a bare peat surface: population changes and spatial patterns, J. Vegetation Sci. 3, 113-118.
- Särkkä, A. and Renshaw, E. (2006), The analysis of marked point patterns evolving through space and time, *Computational Statistics and Data Analysis* **51**, 1698-1718.
- Skellam, J.G. (1951), Random dispersal in theoretical populations, *Biometrika* 38, 196-218.
- Stein, A., Goergiadis, N. and Khaemba, W. (2004), Spatial statistics to quantify patterns of herd dispersion in a savanna herbivore community. In *Spatial point process modelling and its applications*, A. Baddeley, P. Gregori, J. Mateu, R. Stoica and D. Stoyan, eds., Universitat Jaume I. Castellón, Spain.
- Stoyan, D., Kendall, W.S. and Mecke, J. (1995), *Stochastic Geometry and its Applications*, New York: John Wiley and Sons.
- Strauss, D.J. (1975), A model for clustering, Biometrika 62, 567-475.
- Tilman, D. and Kareiva, P. (1997), Spatial Ecology, Princeton University Press, Princeton.