Random steps in evolution and point processes

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Academic dissertation

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List of Publications

This thesis is based on the following four papers, which are referred to by the Roman numerals given here.

(I) M. Gyllenberg and R. Service. *Necessary and sufficient conditions for the existence of an optimisation principle in evolution*, J. Math. Biol. 62 (2011) 359-369.

(II) M. Gyllenberg, H. Metz and R. Service. *When Do Optimisation Arguments Make Evolutionary Sense?* in *The Mathematics of Darwin's Legacy*, 233-268, Springer Verlag, Basel, 2011.

(III) R. Service. *An easier extra head scheme for the Poisson process on* $\mathbf{R}^n$, Proc. Amer. Math. Soc. 138 (2010), 3703-3705.

(IV) R. Service. *Independent particle processes and local observations.* (submitted manuscript)

Author's contribution

Following the tradition in the mathematics literature, the authors are listed alphabetically in papers (I) and (II). The mathematical ideas and proofs in paper (I) are mine, as well as most of the actual writing. In the second paper, I wrote mainly the parts that overlap with, and expand upon, the material of paper (I) and also contributed to editing the manuscript as a whole.

Introduction

The papers included in this thesis address somewhat varied problems, both in terms of the motivation and background and the mathematical methods employed. This horizontal rather than vertical structure presents something of a challenge for writing an introduction. To meet this challenge, I decided to concentrate more on questions that are a little more general in nature than those addressed in the individual papers and try to give the reader an overview of large parts of mathematical biology. Of course, in addition, I give summaries of the results and some specific background for each paper.

The main scientific work in this thesis consists of the four papers listed. The papers (I) and (II) clearly address the same topic. They have a somewhat different flavour, however, in that the first paper has a very clear and relatively narrow focus. It was written to answer a specific question implicit in the work of Hans Metz and some of his colleagues and addresses a specific question touching on the foundations of the mathematical theory of evolution, an area of mathematical biology I will attempt to describe below in this introduction. By contrast paper (II) expands on the results of (I), but has a much broader aim, in that it includes a rather lengthy discussion on optimisation in evolution in terms of more detailed ecological models and attempts to present the role of optimisation models in the broader context of the mathematical theory of evolution.

Paper (III) is again very narrowly focused, built essentially around the statement and proof of a proposition. It came about purely thanks to a talk given at the monthly departmental colloquium of the Department of Mathematics and Statistics in the spring of 2009 by Yuval Peres. It touches on one of the more abstract parts of the theory of point processes, that focuses on some aspects of symmetry. Again I give a quick account of this area of mathematics in this introduction in the section entitled "Projections and extra head schemes". The paper deals with the theory of so-called extra head schemes, otherwise known as shift-couplings of the Palm and ordinary versions of a process. A quick explanation of the background to the theory is found below in this introduction.

Finally, acting as a kind of bridge between evolution and the theory of point process, paper (IV) presents some results that fall between pure and applied mathematics. The setup is a rather general one of stochastic processes of a locally compact metric space. The idea is very simple: given the law of a Markov process on such

a space, define a new process where individual agents move independently in the space according to the law of the original process. A requirement that arises quite naturally is that any compact set in the space be populated by but a finite number of individuals at each time, when the set of all individuals is infinite. The first half of the paper develops some basic theory for such processes, while the second half addresses a question of conditioning the process on certain types of observations of local events. The original motivation for writing the paper was simply to get some insight into the behaviour of a cloud of independent particles conditioned on the event that no particle enters a given region in the state space in some given time interval $[0, t]$.

What is mathematical biology?

To help explain how I came to work on the topics of the papers included in this thesis, it seems appropriate to give a quick overview of mathematical biology in general. Let me begin by giving a a very imprecise answer to the question headlining this section: Mathematical biology is a field in which a student sitting through, seminars, schools and conferences during his time in graduate school is able to come across a great number of practical, biologically motivated problems that lend themselves to solution by mathematical methods from diverse fields, such as the theory of dynamical systems, stochastic processes, functional analysis and elementary probability. This answer may be wholly unsatisfactory as an attempt to describe a field in general, but it explains the somewhat eclectic nature of the thesis at hand. It is therefore given with a view to explaining how three distinct topics are covered in the four papers that make up the body of the thesis.

A more standard attempt to describe mathematical biology would probably be to say that it an interdisciplinary field in which mathematics is used to address questions arising in biology. However, according to standard usage, not all research meeting this definition is classified as mathematical biology. Thus a lot of applied work with an emphasis on statistical or computational methods is not called mathematical biology, but falls under such descriptions as bioinformatics or computational biology. Of course in many cases it is difficult to draw a line as to which title to apply to a particular piece of research work. What is clear is that a clearly differentiated research community defining it self as mathematical biology or biomathematics has grown up with its own journals and conferences and that there is a new generation of students specialising in mathematical biology already in their undergraduate studies. Whether the application is to cell biology, evolution, epidemiology or any other one of the large number of areas in biology to which one can apply mathematics, the approach associated with biomathematics tends to rely more on building and analysing exact, if simplified, models of biological phenomena, rather than direct statistical conclusions.

This thesis contains papers, notably (III) and (IV), which, taken individually do not fit nicely under the categorisation of mathematics applied to biology. Hence this work should be considered a thesis in the area of mathematical biology in

the extended and informal sense I put forth right at the beginning of this section. A peculiar feature is that to read and understand the mathematical content of each of the papers does not require very deep specialised knowledge. However, the motivation for all of the results is based on some awareness of work done on the various topics, so I will do my best to convey enough background in this introduction to motivate the specific results found in the papers.

My perhaps more colourful than strictly informative summary of the specific emphasis of mathematical content in journals such as the Journal of Mathematical Biology, is: mathematical biology is an attempt to do biology as if it were physics. I use the word "attempt", since it is widely accepted that physics provides us with the clearest and most impressive examples of advanced mathematical methods at work in empirical science. It is the obvious model for success of mathematics in science, whereas biology has, until recent times, been less reliant on mathematics.

Physics plays a special role among the natural sciences in that it studies the most basic level of the physical reality on which all of the phenomena studied by science is based. But even more importantly, since the era of Newton, there has been a great overlap between the groups of scientists working to advance physics and mathematics.

So why is mathematics so succesful in physics? Taken as a philosophical question, this is definitely beyond the scope of the current discussion and the interested reader is directed to the famous essay [16] as a starting point for that discussion. On a superficial level, however, it seems that physics is fundamentally simple. To take the example of mechanics, it is not a priori obvious that the analysis of the movements of point masses acting via Newton's inverse square law of gravitation can be simplified via the Lagrangian and Hamiltonian formalisms. Furthermore, the way this mathematical development lends itself to an extension when classical mechanics is replaced by quantum mechanics has been seen as rather miraculous, as discussed in the book [17]. The extra ingredients needed, principally the theory of Hilbert spaces and spectral theory, were developed by mathematicians primarily motivated by problems in ordinary and partial differential equations that were of greater scope than their applications to physics at the time would have required.

Let us now consider the success of mathematics in biology. Let us take as an analogue of the mechanical equations of motion in physics the Lotka-Volterra predator-prey equations of mathematical ecology:

$$\dot{x} = x(\alpha - \beta y) \tag{1}$$

$$\dot{y} = -y(\gamma - \delta x) \tag{2}$$

Here x denotes the prey population size and y denotes the predator population size. In the absence of the predator, the prey population grows at an exponential rate. I turns out that the solutions of the equations (1) are periodic when one starts at any positive initial conditions for x, y. However, when one wants to make the model more realistic, by for example including a simple self-limiting mechanism for prey

$$\dot{x} = x(\alpha - \beta y - \eta x)$$

one easily destroys this nice structural property of the solutions (see e.g. the textbook [2] for details). Thus studying the simple case gives rather limited insight into the general case.

In physics, certain very general and abstract principles are seen to be fundamental. The most familiar example is probably the principle of conservation of energy. Thus, a physicist who sets up a model in which the conservation of energy does not hold, is unlikely to conclude that a triumphant advance through counterexample has been found, but rather will most likely draw the frustrated conclusion that the definition of energy used for the model is wrong.

By contrast, among the models of population dynamics that have been studied in the literature, one does not expect to find fundamental principles analogous to the conservation of energy that hold universally. Instead many papers cite as their main result the discovery of a model that satisfies some combination of features that was previously thought counterintuitive, if not outright impossible (see for example [14]). It seems therefore that while biology may serve to supply and motivate an abundant supply of examples of dynamical systems and mathematical problems related to them, there are few general constraints on such systems that could be characterised as inherent to ecological models.

One attempt to simplify the zoo of different population dynamical models put forth in the paper [3] is captured in the motto "all population dynamical equations can be written as delay equations". This is briefly touched upon in the paper (II) appearing in this thesis. The idea is roughly that the birth rate $b(t)$ of a species at time t is a deterministic function of the history of the birth rate itself up to time t and that of the state I of the environment, allowing one to write population dynamics as a coupled system of Volterra and differential delay equations. Another, quite different approach to imposing some regularity on population dynamics via physical constraints is the Dynamic Energy Budget theory developed principally by Bas Kooijman (see [11]).

It is undeniable that biology has benefitted from the work of mathematicians and statisticians and will do so even more in the future. On the other hand, it must also be admitted that the application, especially of advanced mathematics, bears a closer resemblance to the situation in economics than to that in physics. That is, one expects somewhat less order, less miraculous simplifying conspiracies thrown in by nature itself.

Background to papers (I)-(II)

In comparing the applications of mathematics to biology and physics, I claimed that there seem to be few general constraints on models of population dynamics that arise purely from biological considerations, differentiating them from dynamical systems in general. One example of a very general and simple, biologically motivated, constraint is that for dynamical systems on $\mathbf{R}^n$ with coordinates representing populations or abundances of resources, the relevant phase space should consist of some

subset of $\mathbf{R}^n_+$, the space of vectors with nonnegative coordinates. Thus when the dynamical system is given as a system of ODEs, such as the Lotka-Volterra equations given above, where the right hand side is given by an expression that is defined on all of $\mathbf{R}^n$, a basic criterion for plausibility of a model is that the cone of nonnegative vectors remain invariant, as is indeed the case for (1). A nice consequence of the invariance is that it simplifies analysis of the so-called invasion problem that is central to the mathematical theory of evolution and adaptive dynamics in particular.

For sake of concreteness, suppose that a population dynamical model is given by a system of ODEs. We consider an unstructured population for simplicity of exposition, so let the population of a given species i be $x \in \mathbf{R}_+$ and let $y \in E \subset \mathbf{R}^n$ be a vector representing all of the other variables in the model, such as the abundance of various resources or other environmental factors that play a role in the population dynamical model. Then the general form of a ODE population model for an unstructured population without migration is

$$\dot{x} = xf(x, y) \tag{3}$$

$$\dot{y} = g(x, y) \tag{4}$$

where $f : \mathbf{R}_+ \times E \to \mathbf{R}^n$ and $g : \mathbf{R}_+ \times E \to \mathbf{R}^n$ are (usually) continuous functions. The reason for writing the growth rate of x in the above form is that $f(x, y)$ then has the natural interpretation of a per capita population growth rate, which combines the underlying effects of mortality and reproduction. We consider this model here simply to illustrate the central ideas of adaptive dynamics, without getting bogged down in technicalities one encounters when dealing with structured populations.

The set $\{0\} \times E$ is invariant under the flow. The invasion problem consists of determining whether a small population of species s will grow or decline to 0. Frequently it is the case that the invariant set determined by the condition $x = 0$ has a stable equilibrium $(0, y_0)$. Then, if $f(0, y_0) > 0$, it follows from the continuity of f that $\dot{x} > 0$ for small values of x and one then says that the species i can invade the equilibrium $(0, y_0)$. Analogously, if $f(0, y_0) < 0$, a small population of s will decline and one says that the the equilibrium cannot be invaded by species s.

Now let us consider evolution in this simple context. Let I be a space of possible phenotypes (or strategies). In order to be able to consider evolution, the model must facilitate the possible coexistence of different strategies. Even in the simple case at hand, where individual phenotypes are represented by an unstructured population, one needs to be rather heavy-handed with abstract definitions to be entirely rigorous. To represent all feasible states of the system, allowing any number of phenotypes to coexist, we take as the state space $\ell^1(I)^+ \times E$, where

$$\ell^1(I)^+ = \{u : I \to \mathbf{R}_+ : \sum_{s \in S} u(s) < \infty\}.$$

A function $u \in \ell^1(I)^+$ thus represents the population sizes $u(i) \geq 0$ of each phenotype i, giving a finite total population size. The complete population dynamics is

governed by a master equation of the form

$$\dot{u}(i) = u(i)F(u, s, i) \tag{5}$$

$$\dot{y} = G(u, y). \tag{6}$$

The term $F(u, y, i)$ has the interpretation of being the per capita population growth rate for the phenotype i in an environment set by the population structure u and other environmental variables captured y.

Note that for any set $I' \subset I$, the set $\{(u, y) : u(i) = 0 \text{ whenever } i \notin I'\}$ is invariant. In particular, when the initial condition u_0 for u has finite support, (5) - (6) is really just a roundabout way of writing a finite system of ODEs. For a monomorphic population, $u(i) = 0$ for all but at most one value of i. Substituting $u(j) = x\delta_{ij}$, where $\delta_{ij} = 1$, if $j = i$ and $\delta_{ij} = 0$ otherwise, one gets again a system of the form (3)-(4).

Now, if (u, y) is an equilibrium of (5) - (6) and $i \in I$ is such that $u(i) = 0$, one can consider the invasion problem for phenotype i into the environment (u, y) in the obvious way. If $F(u, y, i) < 0$, the equilibrium cannot be invaded by i. If $F(u, y, i) < 0$, a small population of phenotype i will grow. It is frequently the case that the population dynamics then converges to a new equilibrium (u', y'). Let us assume this is always the case for the model we are considering. In fact we assume even more:

Assumption. *There exists a nonempty set $E' \subset E$ with the following properties.*

1. *$E' \times \ell^1(I)^+$ is invariant under (5) - (6).*
2. *For any finite set $C \subset I$ there exists a unique equilibrium attr(C) such that the trajectory for any initial condition (u_0, y_0) with supp$(u_0) = C$ and $y_0 \in E'$ converges to attr(C).*

Note though, that checking whether this holds is for a concrete model is often a non-trivial task. Typically the set E' needs to be distinct from E when one wants to rule out e.g. extinction of other species included in the model, since otherwise one may fail to get uniqueness of the attractor.

Now we are at the starting point of adaptive dynamics, where one thinks of the population dynamics as happening on a faster timescale than the introduction of new mutants. One looks at a sequence of phenotype coalitions $C_0, C_1, \ldots$ as follows. At each stage k one adds a new mutant phenotype i_{k+1}, not present in C_k. One then assumes that the population dynamics converges quickly to attr$(C_k \cup \{i_{k+1}\})$ and takes the set C_{k+1} of phenotypes present as the next coalition. One can then look at various mechanisms for the mutation process, typically making the assumption that i_{k+1} must be close in some sense to one of the phenotypes present in C_k.

Let us consider monomorphic evolution, where attr(C) always has just one phenotype present. Then an additional assumption, which seems to hold in most models one encounters (but not all, see [14]) is that if i_1 can invade attr$(\{i_2\})$

then it will drive i_2 extinct. In this case, to determine possible courses for evolution one need only look at the invasion fitness function, defined for $i, j \in I$ by $s_i(j) = F(\mathrm{attr}(\{i\}), j)$.

Papers (I) and (II) deal with a question of when evolution optimises some numerical quantity. This means that there exists a function $\varphi : I \to \mathbf{R}$ such that for all $i, j \in I$ $\varphi(i) < \varphi(j)$ holds if and only if $s_i(j) > 0$. When this happens one can usually predict the outcome of evolution, simply by finding the maximum for the function φ, if it is unique. Of course, φ may still have distinct local maxima, so an assumption that mutational steps are small may mean that evolution gets stuck at a local maximum away from the maximum of φ over the whole set I.

Finding conditions for optimisation is the subject of papers (I) and (II). Since the latter paper contains a very complete introduction to the topic, it seems unnecessary to go into more detail here. Instead, let me remark that the ODE model considered here was merely for convenience. The whole framework of considering evolution based on an underlying ecological dynamical model carries over in great generality to the case of structured populations. One can also consider the invasion problem when the resident population is not at equilibrium, but at some other attractor of the dynamics, e.g. a limit cycle. Other generalisations, such as stochastic fluctuations are also accommodated without much difficulty on the theoretical level, although calculating numerical values for the invasion fitness function can present problems.

The framework of adaptive dynamics, originally developed by Geritz and Metz, has turned out to be very popular, due in part to the wide applicability of the approach. Since the aim here was merely to give an adequate introduction to the papers in this thesis, little of the essential ideas was really touched upon, beyond the essential idea of building a model of evolution on top of a model of ecology. See [4] for a brief overview of the idea of a adaptive dynamics and [5] for a somewhat more complete exposition. Paper (II) contains a large number of references to more recent work in adaptive dynamics.

Background to paper (III)

Paper (III) is based on one simple idea. Let me therefore take the opportunity to give some background on the body of research work that this contribution fits into.

A point process is, loosely speaking, a random set of points in some space. It turns out to be convenient, from a technical standpoint, to give the following precise definition. Let S be a locally compact separable metric space and let $\mathcal{N}(S)$ be the set of Borel measures N on S such that $N(A)$ is an integer for each compact set $A \subset S$. The space $\mathcal{N}(S)$ is equipped with a natural Borel structure induced by the family of maps $N \mapsto N(A)$ where A ranges over the compact subsets of S.

A random element $N \in N(A)$ is called a point process on S. With this definition it becomes transparent that point processes are special cases of random measures. A point process N is called simple, if $N\{x\} \leq 1$ holds on some event of probability 1 uniformly for all $x \in S$. A simple point process N is uniquely defined by the discrete set of points $x \in S$ for which $N\{x\} = 1$, justifying the heuristic description

as a random set of points. General point processes instead allow more than one point to be placed at the same site $x \in S$.

Suppose a point process N is defined on a locally compact group G. Given $g \in G$ one can then define a shifted process $T_g N$ via $T_g N(A) = N(g^{-1}A)$. Note that if one writes formally $N = \sum_k \delta_{x_k}$, where (x_k) is a sequence of points in G, $T_g N = \sum_k \delta_{g x_k}$. Now a point process is called stationary (or left-stationary in the general noncommutative case), if $N \stackrel{d}{=} T_g N$ for all $g \in G$. Note that the same definition applies to more general random measures.

A stationary random measure ξ is called ergodic, if the only translation invariant events have probability 0 or 1. Note that in the case of compact groups G, the probabilistic structure of ergodic random measures is rather trivial, as they are obtained from a random shift, distributed by normalised Haar measure, of a single measure.

For a point process or random measure ξ the expression $E\xi(A)$ defines a (deterministic) measure in A called the intensity $E\xi$ of ξ. If the process is stationary then $E\xi(A)$ is a left invariant measure. An important special case of point processes is a Poisson process N, which is defined with respect to a reference measure μ by the property that $EN = \mu$ and $N(A_1), \ldots, N(A_n)$ are independent Poisson variables whenever the sets $A_1, \ldots, A_n$ are pairwise disjoint. The distribution of Poisson point process is uniquely defined by its expectation.

Let ξ be a stationary random measure on a locally compact group G. In this case $E\xi = c\lambda$, where λ is left Haar measure on G and $c \in [0, \infty]$. When $c \in (0, \infty)$ one defines the Palm distribution as follows:

Definition 0.1. Given a stationary random measure ξ on G with $E\xi = c\lambda$, where λ is left Haar measure and $0 < c < \infty$, define the Palm measure Q_ξ on $\mathcal{N}(G)$ by the condition

$$\int f dQ_\xi = \frac{1}{E\xi(A)} \int_A f(T_{g^{-1}}\xi)\xi(dg)$$

for all measurable $f : \mathcal{N}(G) \to [0, \infty]$, where $A \subset G$ is some fixed Borel set with Haar measure $0 < \lambda(A) < \infty$.

It can be easily shown using stationarity that the definition of Q_ξ does not depend on the choice of the set A. It is not hard to show that Q_ξ is a probability measure. In the case of a point process N, Q_N assigns probability 1 to the event $\{N(e) \geq 1\}$, where e is the neutral element of G. Any process with distribution Q_ξ is simply referred to as the Palm version of ξ, the use of the definite article being justified by uniqueness of the distribution.

The definition of the Palm distribution may look a little cryptic at first. The informal intuition in the case of a simple point process N is that Q_N is obtained as a conditional distribution by conditioning on the event $\{N\{e\} = 1\}$. In case G is discrete, this is in fact rigorous, but in the general case it must be thought of as shorthand for a statement about an appropriate limit, since $P\{N\{e\} = 1\} = 0$ when G is not discrete. For general stationary random measures ξ, one thinks of the

Palm distribution as arising through shifting a random point to the origin, where the distribution of the random point is weighted by the random measure ξ itself.

In the paper [15] the Icelandic probabilist Hermann Thorisson proved the following result.

Theorem 0.2. *Let a second countable locally compact group G act measurably on an arbitrary measurable space $(S, \mathcal{S})$. Let X, X' be random elements in S defined on some probability space. Then the distributions of X, X' agree on all G-invariant measurable subsets of S if and only there exists a random $g \in G$, defined on some extension of the original probability space, such that $gX \stackrel{d}{=} X'$.*

If G is a second countable locally compact group then G acts on $\mathcal{N}(G)$ measurably by translation. If N is a stationary ergodic point process on G, then the distribution of N and that of its Palm version $N^\star$ agree on translation invariant sets. Thus Theorem 0.2 implies that there exists a random element $g \in G$, such that $T_g N$ is the Palm version of N.

A noteworthy special case of a random measure N is when $G = \mathbf{Z}$ and $N\{k\}$ are i.i.d. Bernoulli variables with a common expectation $p \in [0, 1]$. This has the familiar and intuitive interpretation of a doubly infinite sequence of independent tosses of a biased (if $p \neq \frac{1}{2}$) coin. Interpreting the event $N\{k\} = 1$ as a head for the k:th coin toss gives rise to the name "extra head scheme" for a random element g in a group satisfying the condition in Theorem 0.2. This usage has been adopted for the general case, even though there is no useful interpretation in terms of coin tosses for point processes on non-discrete groups.

An extra head scheme picks out a generic head and shifts it to the origin, so that the shifted process is the Palm version of the original process. The question then arose as to when one could find an extra head scheme as a deterministic function of N, without additional randomness. It is perhaps surprising that deterministic extra heads do in fact exist in a number on non-trivial cases. In particular, the paper [12] presents an explicit construction for an extra head scheme for simple ergodic processes on $\mathbf{Z}$ and $\mathbf{R}$. A general solutions for $\mathbf{Z}^n$ and $\mathbf{R}^n$ were presented in [9]. A highly recommended source containing a complete and very elegant solution to the n-dimensional case is [8].

Paper (III) in this thesis sidesteps the intricacies of the known solution to finding an extra head scheme in $\mathbf{R}^n$ in the Poisson case by reducing the problem to the one-dimensional one. To illustrate the idea, take the case $n = 2$. Consider the strip $\mathbf{R} \times (-\frac{1}{2}, \frac{1}{2})$ and project all points in the strip onto the line $\{0\} \times \mathbf{R}$ according to the mapping $(x, y) \mapsto (x, 0)$ as illustrated in Figure 1. If the original process was a Poisson process in $\mathbf{R}^2$ then this projection construction gives a Poisson process on the one-dimensional line. Now, crucially, if one uses a one-dimensional extra head scheme to find a projected point $(x, 0)$, then taking the a.s. unique point of the original process $(x, y) \in (-\frac{1}{2}, \frac{1}{2}) \times \mathbf{R}$ gives an extra head scheme for the original process.

An obvious generalisation of this construction works in $\mathbf{R}^n$ and this fact is shown rigorously in the paper (III). This gives a shortcut to finding an extra head scheme in n dimensions, by reducing to the one-dimensional case.

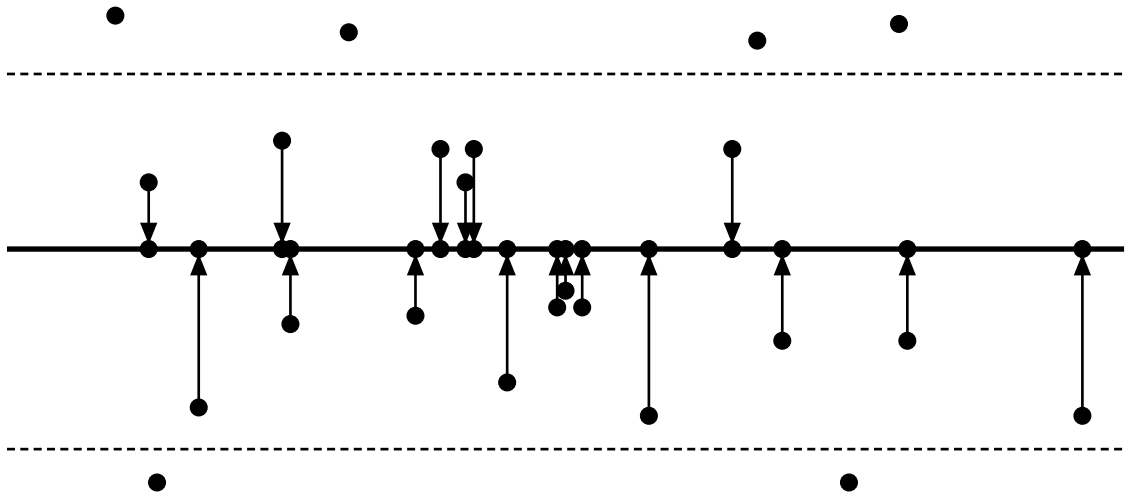

FIGURE 1. Replacing points in a strip with points on a line.

BACKGROUND TO PAPER (IV)

Paper (IV) started from a desire to understand the following simple problem. Suppose that a number of individuals are executing indpendent random walks on the lattice $\mathbf{Z}^n$. One is a able to observe the state of a single site, say 0, but no other information of the state of the whole system is given. What can one then say about the conditional distribution of the system, given the observed data?

It turns out that one can give a satisfactory answer in a much more general setting. Namely, one can consider the individuals as living in a general space without all of the symmetries and discrete structure of the lattice. The first part of the paper is therefore dedicated to developing the appropriate framework, where one allows infinitely many individuals moving in a locally compact metric space, imposing the key requirement that at any time each compact set be occupied be a finite number of individuals.

This leads to the point of view of considering a stochastic process with a state space consisting of counting measures on a locally compact space. For applications to biology, it would be desirable to have a theory allowing for interactions between the individuals, but the paper included here concentrates only on the simple case without interactions. It is given the name independent particle process.

The fact that individuals are assumed to have independent trajectories has two consequences. First, it allows one to solve the question about conditioning on local

observations explicitly in many cases, thanks to the role played by Poisson processes as stationary distributions. Second, it provides a new perspective for the abstract theory of general stochastic processes, since the process of independent individuals can be constructed without much in the way of restrictions on the original process.

The role of Poisson processes as stationary distributions for independent particle processes stems from the fact that randomisations of Poisson processes are again Poisson (see e.g. [10] for definitions). I use this opportunity to present a proof of a classical theorem related to this fact, due to Moran.

Theorem 0.3 (Moran, 1950)**.** *Let $(X_k) \in \{0,1\}^{\mathbf{Z}_+}$ be a sequence of independent Bernoulli variables with $EX_k = p$ for all k, $0 < p < 1$ and let $N \in \mathbf{N}$ be a random variable independent of (X_k). Then the following conditions are equivalent*

(1) *N has a Poisson distribution.*
(2) *$\sum_{k=1}^N X_k$ and $\sum_{k=1}^N (1 - X_k)$ are independent*

Proof. Let $Y = \sum_{k=1}^N X_k$ and $Z = \sum_{k=1}^N (1 - X_k)$. Denote by f, g, h the respective probability generating functions of N, Y, Z. Let

$$F(x,y) = \sum_{i,j} P[Y = i, Z = j] x^i y^j.$$

Now

$$P[Y = k|N] = P[Z = N - k|N] = \binom{N}{k} p^k (1-p)^{N-k}. \tag{7}$$

Conditioning on N shows that $F(x,y) = f(px + qy)$, $g(x) = f(px + q)$ and $h(x) = f(qx + p)$, where we write $q = 1 - p$.

Suppose now that N has a Poisson distribution with $EN = \lambda$. Then $f(x) = e^{\lambda(x-1)}$ which implies

$$F(x,y) = e^{\lambda(px+qy-1)} = e^{\lambda p(x-1)} e^{\lambda q(y-1)} = g(x)h(y),$$

showing that Y and Z are independent.

Let us start conversely from the assumption that Y and Z are independent. This is equivalent to $F(x,y) = g(x)h(y)$. Combining this with the equations noted above, one sees that

$$f(px + qy + 1) = f(p(x+1) + q(y+1)) = g(x+1)h(x+1) = f(px+1)g(qy+1).$$

It follows that the analytic function $\phi(x) = f(x+1)$ satisfies Cauchy's functional equation $\phi(x+y) = \phi(x)\phi(y)$ in some neighbourhood of 0 and hence has the form $\phi(x) = e^{\lambda x}$, so the generating function of N is that of a Poisson variable. □

Actually, the fact that randomisations of Poisson processes are Poisson really boils down to just the implication (1) ⇒ (2) and a few easy measure theoretic technicalities. My excuse for including the above formulation here is simply that the result is perhaps less well known than it deserves, given the simple and beautiful proof "from the book", to use the famous phrase attributed to Paul Erdös (see [18]).

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