

Branching processes as population dynamics

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Branching processes were once born out of a question from (human) population dynamics. Lately the driving forces have been, and continue to be, more of pure mathematical nature. Nevertheless, the resulting theory turns out to solve many classical problems from general, usually deterministic, population dynamics. These will be reviewed, with an emphasis on basic structure and on problems of the rate of population growth and the ensuing population composition. Special attention will be paid to possible interaction between individuals, or between the environment or population as a whole and individual reproduction behaviour. But the framework will remain the general model without explicit special assumptions about the form of interactions, lifespan distribution or reproduction.

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Population dynamics, and even a concern for the destiny of human populations, is certainly what once gave birth to branching processes, and did so on repeated occasions. Bienaymé (1845) formulated what later became known as the Galton–Watson process with the purpose of studying the ‘fate [of extinction] that allegedly hangs over the aristocracy and middle classes’. Galton’s own formulation, in terms of the possible survival of the family names of N adult males who colonize a district, has become more than famous (Galton 1873).

Still half a century later, when Andrei Nikolaevich Kolmogorov (1903–87) worked on branching processes, population dynamical questions seemed very much in focus. His works have titles like ‘The solution of a biological problem’ and ‘The transition of branching processes into diffusion processes and related genetic problems’ (Kolmogorov 1938; 1959).

Among them you may also notice a short work with the astounding title ‘On a new confirmation of Mendel’s laws’ (Kolmogorov 1940). The point is the year, during the Hitler–Stalin pact, when Lysenko’s grip over Soviet genetics was firm. I have included it to honour Kolmogorov as a scientist in the widest sense of the word. It certainly deals with population dynamics but lies far from branching processes: it presents a statistical analysis of what fluctuations to expect in Mendelian schemes. The conclusion reached is that a paper by one of Lysenko’s followers (Ermolova), claiming to refute Mendel, on a closer examination turns into a confirmation of his theories. There are also openly disdainful comments upon another anti-Mendelian paper by a then quite illustrious Marxist philosopher, Kolman. For such matters people – at that time, in that country – were indeed, at the very least, risking their jobs.

Since Kolmogorov, branching processes have certainly changed their focus. They have grown into fully-fledged mathematical theories, well integrated into probability theory, and with some connections to statistical inference. In their turn, they have given rise to still more theoretical mathematics, such as measure-valued or so called superprocesses. But relations to the outside world

are often only weak. This is the usual development, from relevance to sophistication, from answering questions posed from a general point of view to dealing with the intricate details of elaborate theories (or, from another perspective, from models with broad ambitions to conceptually simpler frameworks, which, however, yield a rich mathematical theory). In happy cases, the sadness of this evolution is alleviated by the advent of new, more or less unexpected applications. And indeed, after maybe too long in mathematical celibacy, branching processes today find fascinating use in as disparate areas as the analysis of computer algorithms and the fractal descriptions of complicated geophysical phenomena.

And the roots still offer much of interest. To the mathematically inclined I hope to show that there are challenging tasks in general population dynamics. Those primarily interested in the dynamics of populations *per se*, biology or demography and the statistics that goes with it, will find contributions, and perhaps even insight, hard to obtain except by using the impressive power of modern probability theory. In that sense, this paper provides a defence of some mathematical *art pour l'art*: it would be hard, if not impossible, to understand more general population schemes without access to detailed and mathematically sophisticated knowledge of conceptually simplistic artefacts, like the Galton–Watson process, studied merely for mathematical curiosity.

It is to the basic and general problems of population dynamics that we shall address ourselves. If a population does not die out, can its size stabilize? If not, how quickly must it grow? Will its composition then stabilize? To what? And if it has a stable composition, what was its path towards it; what is the history of a stable population? In this manner, can we even hope to say something about how populations on earth may have evolved to what they are today?

In parts, these are matters that have a long scientific tradition, in parts they are prompted by recent advances in evolutionary theory, molecular biology, or cell kinetics. Trying to answer them we shall have the general pattern in mind all the time, rather than specific populations. In this respect we differ both from really applied population biology, and from the rich deterministic mathematical population dynamics, based on partial differential equations and analogies with classical physical reasoning of the fluid dynamics type. These both tend to concentrate upon specific natural, or quasi-natural, populations. And we also deviate from what is possibly the mainstream of present-day applied probability, the analysis of quite special distributional structures. Here there will be no particular distributions, no Poissonian births, exponential lifespans, or normally distributed weights.

The one important restriction will be the one historically defining the theory: that individuals, once born into the population, live and reproduce independently of one another. Though conceptually clean, and methodologically fundamental for the hundred years during which branching processes have been studied, this presumption certainly limits the theory. If there is one thing we know about life, it is that it is full of interaction. Still independence remains a natural idealization: indeed, populations change by their members changing. Individual dynamics comes first, population dynamics later. But once the theory is established, it is important to proceed beyond it and investigate what kinds of dependence it can accommodate, between individuals, between the population as a whole and its members, or between a varying environment and the populations it can support. We shall end by saying some words about the complications of such interaction.

But first the established theory. In this, as we have seen, your mother is the only person to depend upon. She is the one to make the choice whether you will be born into life or not, and then also at

what time this will happen. And in giving birth, she passes on to you the genetic imprint that constitutes your *type* and determines the probability measure over all your possible life careers. Thus, the process marches on, Markovian in the pedigree, though certainly not generally so in real time. Allow me to stress this last point: Markovianness of population growth in real time either requires biologically unreasonable assumptions on the individual level, essentially the absence of ageing effects, or else it leads to strange, untreatable state spaces. Much pain in theoretical demography has resulted from the stubborn reluctance to realize that if there is a Markov structure at all in population growth, then it resides in the tree structure of the pedigree rather than in real time.

On the population level, the Markov tree property manifests itself in regeneration at so called *lines* or *cuts*. These are sets of individuals, which are thin in the sense that no member of a set may be a descendant of any other member. A generation thus constitutes a typical line. Another is the Nerman line at a time t , the set of individuals not yet born at t , whose mothers have, however, been born then (Nerman 1981). For any line, once the types (and birth times) of the individuals in it are given, their progeny will be independent of the rest of the population. This is one of the two properties heavily used in the analysis of population evolution, the other – actually a consequence of the Markovianness – is that the population must also be *branching* in the sense we have referred to as almost defining the subject, that disjoint daughter populations are conditionally independent of one another, given the initiator's types and birth times.

Now, start the population, at the dawn of time, from an Eve of some given type, and henceforth measure it by some measure that is additive over individuals, i.e. at each time point we measure all individuals one by one – perhaps just count them – and add the measures together. Let the measure of an individual possibly depend on the individual's type, and at each time point also on her age then. Assume that the measure – at this stage – is otherwise independent of the individual's past and indeed identically distributed. Such a measure is called a *characteristic*, and at any point in time the process, as measured by that characteristic, is obtained by summing over the values of all characteristics then. We assume that the measure vanishes at negative ages, i.e. you make no contribution until you are born.

It is now well known that such processes, and indeed much more general populations, either die out or grow to infinity. In order to get interesting models for persisting populations, it seems necessary to think of infinite populations in some grand macrocanonical space, and then possibly focus on the finite population that dwells in some bounded subset of the space. This is an active area of research (cf. Wakolbinger 1995) which I shall not go into. Actually, I am not at all convinced that the extinction–explosion dichotomy renders branching-style processes as unsuitable as long-range biological models, as many, among them Kolmogorov, have argued. Indeed, in a recent book, with the quite suitable title *Extinction*, the palaeontologist David Raup (1991) argues that 99.9% of all species that ever existed are now extinct.

If populations do not die out, then it has been the established truth – since Thomas Malthus's famous essay of 1798 – that, under broad conditions, growth must occur at an exponential rate. The fact that in this growth the population composition must stabilize, is a more recent insight. But one aspect of it, the so called *stable age distribution*, has a rich history. It was basically known already to Euler – who also knew about exponential growth well before Malthus (see Euler 1767). Since then it has been rediscovered over and over again, by demographers, actuaries, population biologists, and most recently cell researchers.

Generally, the stable population composition is best described in terms of a typical individual, i.e. one chosen at random. What is her age distribution? What is the probability that she was first-born, that she is pregnant or, say, in mitosis? However, the sampling frame should not be the population of those alive right now, but rather the (admittedly somewhat theoretical but none the less well-defined) total population of all those born, dead or alive, since the inception of the population. This may seem strange. But logically it is being born into the population that is the primary concept. Then you may display various other properties, like belonging to a certain age group, being of a certain type, or for that matter remaining alive. The probability of these will follow through simple conditioning.

By exponential growth, the typical individual will have an exponentially distributed age, with the Malthusian growth rate α as its parameter. If she was sampled only from those alive, the classical stable age distribution of the population will appear, by the conditioning argument: it is the age distribution, when sampling from the total population, but conditioning upon the individual sampled being alive.

And her history, her mother's type and age when she was born, her grandmother's and so forth, constitute a Markov renewal process, as time rolls back. Its parameters are determined in a beautiful way by the entity that turns out to govern most of population growth, the individual *reproduction kernel*, which is the expected number of children of various types, to be obtained at various ages by a mother of a given type,

$$\mu(s, A \times B) = E[\#A\text{-type children from an } s\text{-type mother of age } \in B].$$

Thus, first the Malthusian parameter is chosen as the discount factor to render the reproduction kernel integrated over all ages,

$$\hat{\mu}(s, A) := \int_0^\infty e^{-\alpha t} \mu(s, A \times dt),$$

a transition operator with Perron root 1. What this actually is (cf. Shurenkov 1989; or 1984), may be of less importance to readers of this paper. What matters is that it is well determined. Usually we shall have the so called *supercritical* case in mind, where $\alpha > 0$, by definition. Under suitable recurrence and communication conditions – basically it should be possible for individuals of any type to have descendants of any other type, sooner or later, and this is important to bear in mind, as we shall see when we turn to cases with dependence – if the type space is not too unwieldy in this sense, then the transition operator can further be shown to have an eigenfunction h and an eigen probability measure π ,

$$\int_S h(s) \hat{\mu}(r, ds) = h(r),$$

$$\int_S \hat{\mu}(s, A) \pi(ds) = \pi(A).$$

These are the *reproductive value* function and *stable population* measure, respectively: h indicating the relative reproductive efficiency – or fitness – of the genotype s , whereas π , as the name implies, gives the asymptotic stable distribution over types in the population.

In summary:

1. We have a strict mathematical definition of the otherwise somewhat vague biological concept of fitness.
2. The Malthusian growth is e^{at} . It is independent of the starting type and of the particular way of measuring the population.
3. While growing, the population's composition settles down to the stable population composition determined by the reproduction kernel. In particular, the type and age distributions stabilize.
4. Looking backwards, the typical ancestry of an individual in the asymptotic stable population is a Markov renewal process, again determined by the reproduction kernel. The probability of an r -individual having a mother with type $\in ds$, who gave birth to that individual at age $\in du$, is

$$\pi(ds) e^{-au} \mu(r, ds \times du) / \pi(dr).$$

5. The long run average age at childbearing is the proper time-scale of growth, the generation time.

The renewal structure of a typical ancestry is not only a picturesque piece of information for the amateur genealogist, wanting to know where in the archives to search for her forebears. It may shed light upon virtually any aspect of population history, e.g. the much debated questions of the role of neutral mutations in evolution, and their establishing a possible molecular clock of the evolution of species (Taib 1992).

To this end, interpret a mutation, in a gene or protein, say haemoglobin or mitochondrial DNA, as initiating a new super or macro individual, as it were. In this manner we obtain a pruned population tree, which is the realization of a new branching process. In the latter births occur only with mutations, and tracing ancestry backwards in it is precisely investigating the stream of mutations in evolution.

We conclude at once that this is a renewal process. Not really a Poisson process, in the strict sense of the word, and as the proponents of the molecular clock hypothesis might express themselves, but close enough. It is also easy to see that the stream should be independent of variations in population size, and actually it is determined by the mutation rate, two important but debated tenets of modern evolutionary theory. Thus we obtain a sort of checklist for the molecular clock hypothesis in terms of an alternative, branching model, and we may conclude that it basically fares well.

Turning back to the general results about growth, asymptotic composition, and history of old branching populations, they are typically derived in two steps. First, expected populations are considered, then results are extended to the processes themselves. The mean analysis boils down to the application of either functional analysis, or better, of Markov renewal theory in the strong formulations now available, again thanks to the development of quite abstract probability theory.

The approach towards it starts from the – more than trivial – observation that each individual x divides the population in two parts, those stemming from it, the daughter process as it might suitably be termed, and the rest. In the classical branching framework the daughter process constitutes a new population, which is indeed independent of the rest, given x 's type. Furthermore, the expected population size is the expectation of the sum of individual sizes. But the expectation of a sum is the sum of expectations, and for each individual we can replace her size by a

conditional size, given all information not in her daughter process. And in the classical set-up, by independence the expected size will have the simple form that it is a function of the individual's type and age. But certainly, conditional independence is an exorbitant price for such a cheap property. Why not just assume the property itself, that there exists a function ϕ such that the conditional expectation can be thus written?

Thus, define the *ancestry* and *daughter process* of any individual x to be $\mathcal{A}_x := \sigma$ (the lives of all x 's ancestors) and $\mathcal{D}_x := \sigma$ (the lives of all x 's progeny, including herself), respectively. Write σ_x for x 's type and τ_x for the time of her birth, and χ_x for the characteristic measuring her size. The characteristic may depend upon x 's type and age, but otherwise it must be measurable with respect to x 's daughter process. Thus, by definition the population size, as measured by χ at time t , is

$$z_t^\chi := \sum_x \chi_x(\sigma_x, t - \tau_x).$$

The sum here is over all possible individuals, and the χ_x may be taken as non-negative and bounded, so as to avoid complications. Recall that they vanish if $\tau_x > t$.

Refraining from classical independence requirements, we make the following assumptions:

Assumption 1

There exist a historical σ -algebra \mathcal{H}_x such that

$$\mathcal{A}_x \subseteq \mathcal{H}_x \subseteq \sigma(\text{the lives of all those } \textit{not} \text{ stemming from } x),$$

and a function ϕ such that

$$E\{\chi_x(\sigma_x, t - \tau_x) | \mathcal{H}_x\} = \phi(\sigma_x, t - \tau_x).$$

Assumption 2

There is a reproduction kernel μ satisfying

$$E\{\# \textit{A-children from } x \text{ of age } \in B | \mathcal{H}_x\} = \mu(\sigma_x, A \times B).$$

Then we will be able to step backwards along x 's ancestry, to regain the renewal expression that may yield the expected asymptotics. Indeed, repeating the verbal argument above in terms of formulae,

$$\begin{aligned} E_s(z_t^\chi) &= E_s \left(\sum_{x \in I} \chi_x(\sigma_x, t - \tau_x) \right) \\ &= \sum_{x \in I} E_s [E\{\chi_x(\sigma_x, t - \tau_x) | \mathcal{H}_x\}] \\ &= \sum_{x \in I} E_s \{\phi(\sigma_x, t - \tau_x)\}. \end{aligned}$$

In this $E_s[\phi(\sigma_x, t - \tau_x)] = \phi(s, t)$ for x being the ancestor, born at time 0 and of type s . Then the conditioning can be repeated for the first generation, and these arguments finally lead to the Markov renewal type expression looked for (Jagers 1995).

Now, the requirements made are strange in the sense that they turn vacuous if you can choose the type space freely, so that it can carry all the relevant information contained in the conditioning. The

proper question becomes whether the type space can be chosen neat enough, so that some Markov renewal theory can be brought to bear on it. And this is precisely what may not be the case, if the individual's behaviour is influenced by too many factors, if there is interaction, and we have chosen the historical σ -algebras to be maximal, i.e. equal to the complement of the daughter process. Therefore, it is important to be able to choose the historical σ -algebras to be smaller. Then, we would average many dependencies out, and have a greater chance that a nice little compact type space could channel all appropriate information. The reason for giving some leeway in the choice of historical σ -algebras, and not simply always choosing it to equal the ancestry, is that it might be smoother to include some information into the conditioning that is not contained in the latter, e.g. a total population size dependence.

The abstract form of the assumptions may well seem abominable, and the precise meaning elusive. But the substance is straightforward: we can forget about dependencies between the individual considered and individuals not in the historical σ -algebra. Hopefully we can choose the latter so that the way it affects the future is easily expressed through a type.

Three obvious examples, or test cases, spring readily to mind, the first a local form of dependence, the second and third more global forms:

1. Dependencies that are local in the family tree, and simply disappear in averaging when $\mathcal{H}_x = \mathcal{A}_x$, as in interaction between siblings, cousins, etc.
2. A random environment, so that each individual obtains a type that is influenced by the environment prevailing (at her time of birth). For the ordinary theory such an environment should then vary in a nice recurrent fashion.
3. The type may be influenced by the total population size at that time, or earlier.

In all of them, and certainly much more generally, the approach sketched yields the expected evolution of populations even with some dependence between individuals. This is important – results about means tend to be underestimated by probabilists, even though they are the core of much classical applied mathematics. Nevertheless, the real pride and glory of branching process theory remains the fact that supercritical processes themselves behave like their expectations. Unfortunately, this is harder to prove and indeed, for some cases with dependence, as in a random environment, it will not even be true. The reasons for this become clear if we recall the type of law-of-large-numbers reasoning that establishes the asymptotics of population processes.

At any given time, the population can be viewed as essentially consisting of disjoint subpopulations, stemming from some line long ago. In the classical branching case these will be conditionally independent and suitable forms of the law of large numbers apply, to yield the desired stabilization of the process around its mean.

In the present situation, matters are more complicated. It is not clear how to transfer properties of conditioning per individual, as it were, to a situation where you want to condition upon a whole, say, generation of individuals. And, anyhow, the covariances between daughter processes need no longer vanish. But, in cases of only local dependencies most of them nevertheless will. (For a strict analysis of this case, in somewhat different terms, see Olofsson 1994.) And in cases of competition – for example, if there are limited resources – the correlations between daughter population sizes will be negative, and thus just enhance the stabilization of actual population composition. For these reasons, classical results, about exponential growth as well as about the ensuing stable composition, will remain true in many cases with complicated dependence.

For an illustration, let us look at a straightforward, but much studied tumour model, which aims at describing the fact that as a tumour grows bigger, its rate of increase tends to slow down. Tumour cells either become quiescent, with a probability that depends upon the tumour size, or else they enter a cell cycle, which ends by division. And so the history repeats itself. Assume that the cell cycle has a distribution function, G . For the time perspective that we have in mind, we may safely think of quiescent cells as relishing eternal life.

Write $m(s)$ for the expected number of daughter cells of a cell that is born into a tumour of size s , so that $m(s)$ is twice the probability of entering the cell cycle. While the cell then cycles, the population will grow. It is tempting to presume that if the cell cycle is of length u , then the population size, when the cycle ends, will equal, say, r , with some probability $p_u(s, r)$. However, this would lead us into the pitfall of assuming that the population size is Markov in real time, and even homogeneously so. And this may have unwanted consequences on the individual level, as we have already pointed out. However, that can rather easily be avoided by a slightly more general approach, where one considers the more complicated state space S of non-increasing positive but ultimately vanishing functions on the positive half-line, with the interpretation that $s(t)$ is the size t time units ago. Then, the existence of a transition probability kernel $p_u(s, dr)$ should not seem so threatening.

Forgetting about such complications we would arrive at a reproduction kernel and expected weight function

$$\begin{aligned}\mu(r, ds \times du) &:= 2p(r) p_u(r, ds)G(du), \\ \phi(s, a) &:= 1 - p(s)G(u),\end{aligned}$$

seemingly well suited for our analysis.

But there is more to be beware of. Biologically we should consider means $m(s)$ that decrease, the bigger the tumour the greater the necrosis, and other complications to wild growth. Thus $m(s) \downarrow$ some number $m > 1$, as $s \rightarrow \infty$. But there is no extinction in this model, and then the population size must tend to infinity. The situation lacks all recurrence properties necessary for Markov renewal theory!

We need some transient renewal theory, catching cases where the type in some sense tends to infinity, while reproduction stabilizes.

Indeed, endow the type space with some topological structure and some element of infinity. Furthermore, assume that the reproduction kernel converges, as the mother's type approaches infinity, and that individuals of type infinity can bear children only of that same type. Define the Malthusian parameter to be the proper discount factor for the infinity type reproduction kernel, and assume that the types must tend to the infinity element, unless the population dies out. Then, a Markov renewal theory can be established, yielding the desired Malthusian growth and composition stabilization under certain, unfortunately rather strong, conditions (Thorisson, personal communication, 1994).

It might not be worthwhile formulating those in the general case. But in special cases, such as a Galton–Watson version of our tumour model, quite an elegant characterization follows directly. Provided the expected number of children settles down quickly enough, as the population grows,

$$\sum_k \{m(k) - m\} < \infty,$$

the tumour grows at the same Malthusian rate as one without tumour size dependence, m being the expected number of children per cell. This should be compared to Klebaner's (1984) corresponding, essentially necessary and sufficient, condition for L^1 -growth, $\sum_k \{m(k) - m\}/k < \infty$.

This little example was chosen in order to illustrate what is new in this paper, the possibility of including certain interdependencies in general branching structures. But it has another, more far-reaching message, that could have been conveyed by any of the many applications of branching processes. And that is that the general is not all that far from precise special models, in spite of all seemingly verbose and formula-ridden abstraction. Indeed, the basic message of this paper is that the essence of population growth, the individual branching off into new individuals, is a strong pattern, tending to pervade structures where it is present, and dominate whatever other properties there may be, be it the special qualities of cells, fish, moose, elementary particles or search algorithms. And of course the message is that this essence can be studied in an astonishing generality. Thus, I dare hope that I have made a plausible case that the general stochastic theory of population dynamics, based on branching processes, is important for our understanding the dynamics of real populations.

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