

Population Dynamics: Probabilistic Extinction, Stability, and Explosion Theorems

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Abstract

The relation between individual reproduction and the probability that populations die out is given. Populations that decrease on average will, of course, always die out, but populations whose expected sizes grow can also have a high probability of extinction. Malthus's law of exponential growth of populations, i.e., not dying out, holds in general, not only for populations of independently reproducing individuals, but also under some types of interaction. The stable age distribution and general stable composition, appearing as a consequence of exponential growth, are described. Finally, populations whose size and composition may influence individual reproduction are described.

Extinction, Stable Size, or Explosion?

Historically, probabilistic population theories originate from the *extinction problem*: suppose you know the probabilities of begetting 0, 1, 2, 3, ... children. Now determine the probability that a population of a known number of individuals will eventually die out. Already Malthus had noted that a rapid increase of the whole population could occur together with frequent extinction of the separate families constituting the population. Rephrased in the terminology of evolutionary biology, frequent extinction of species does not contradict a rapid growth of the biomass of the world.

The mathematical explanation of this apparent paradox is due to Bienaymé (1845) and independently, 30 years later and only in parts correctly, to Galton and Watson, who were later to lend their names to the simplest, generation-counting version of the so-called branching processes that provide the mathematical structure underlying most stochastic population dynamics. Indeed, if p_k denotes the probability of giving birth to k children, $k = 0, 1, 2, 3, \dots$, then the extinction probability of a population stemming from one ancestor will be the smallest nonnegative solution q of the equation,

$$\sum_k p_k q^k = q.$$

If we disregard the trivial case $p_1 = 1$, q will equal 1 if and only if the mean number of children,

$$m = \sum_k p_k k \leq 1.$$

If $m > 1$, then the population growth rate per generation will be m , and even though q must be less than 1 it can still be pretty large: it is easy to formulate demographically or biologically plausible cases, where, say, m exceeds 2 and q is still around 0.8.

The preceding argument presumes that individuals reproduce independently of one another. In deterministic population theories dependence structure is not made precise, and stable population sizes can arise, cf Keyfitz 1968. The situation

in stochastic models with interaction or dependence upon the population as a whole is therefore of great interest.

Population Growth

To describe population growth in real time rather than generation-wise, a more sophisticated description of individual life and reproduction is needed. Probabilistic population dynamics is *individual-based* in the sense that it starts from such a description. Deterministic theories, on the other hand, often start directly from an assumed behavior of the population as a whole. Demographic theory is often *pseudo-probabilistic*, in that, it uses probabilistic notions but makes conclusions only about the expected behavior of the population as a whole. (This is the reason why there exist deterministic populations with stationary sizes: if the underlying stochastic population is critical in the sense that on average each individual is replaced by one child, then the expected total population size will be stationary, whereas the population itself will die out sooner or later.)

The most general probabilistic formulation of individual life goes as follows: at birth an individual inherits a *type* from her mother. The type determines her survival distribution as well as the distribution of age at childbearing. It also determines the types of the children she will give birth to in her turn. (Think of the type as a genotype, or a genotype combined with the social and biological conditions of life.)

In the *supercritical* case, where there is a positive chance of nonextinction, the probability laws of survival and childbearing determine a positive *Malthusian* parameter that gives the rate of exponential growth. In the theory of branching processes this rate is usually denoted by α , so that the population will grow like $e^{\alpha t}$, as time t passes. In deterministic theory the conventional notation is often r instead.

Reproduction Influenced by the Population as a Whole, Extinction or Quasi-Stationarity

Now assume that individual reproduction can be influenced by the present state of the population as a whole, its size or its

composition or both, or only by special individuals like neighbors or close relatives.

If this is the case, the situation can be drastically different and it is easy to exhibit examples of populations with high growth rate ($m > 1$), which still are bound to extinction (Haccou et al., 2005). It can, however, be proved very generally that a stochastic population, which is not dying out, must grow beyond all limits (Jagers, 1991; see also Haccou et al., 2005). This is a consequence of stochasticity and the asymmetry between extinction and big sizes: however big the population, there remains an albeit small but still positive risk of extinction, whereas an extinct population cannot be resurrected.

Even though exponential growth appears to be a consequence of the independence assumed (tacitly or explicitly) between the reproduction of different individuals, it is interesting to note that such growth has been proved also to occur in many cases where individual reproduction depends upon the population as a whole, e.g., its size. For such results in the case of simple Galton–Watson branching processes, see Klebaner (1984). In cases where the reproduction approaches criticality as the population grows, nonMalthusian growth can occur nevertheless, e.g., in the form of linear growth (Klebaner, 1994).

But a finite world cannot sustain infinite growth. One can therefore argue that probabilistic population dynamics show that all real populations will die out sooner or later. But before that happens there may be a long period of growth, or even – as recent research has shown – long periods of quasi-stationarity.

Indeed, consider a population where individual reproduction at any time is influenced by total population size, and assume that there is a *carrying capacity* K , a numerical value above which the population is subcritical and cannot sustain itself, whereas it is supercritical below K . Then, if starting small, it may die out directly, or else in time span of order $\log K$, for large K , it will reach a band around the carrying capacity, where it will then stay during a period whose length is exponential in K , until it finally dies out (Jagers and Klebaner, 2011).

Stable Population Theory

In contrast to population size, the composition of growing populations, where individuals reproduce independently, tends to stabilize. The description of this composition, or rather the various stable compositions pertaining to different reproduction and survival laws, is the object of stable population theory.

The most well-known aspect of stable population composition is the stable age distribution, first described by Euler in 1760 and since then rediscovered repeatedly: if the Malthusian parameter is $\alpha > 0$ and all individuals have the same survival

function ℓ , then the age of an individual sampled at random in an old population will have the density

$$\frac{e^{-\alpha a} \ell(a)}{\int_0^\infty e^{-\alpha u} \ell(u) du}$$

at age a , exactly as in deterministic theory. This is, of course, a law-of-large-numbers effect; we are considering ever-increasing populations.

If, as in the general setup mentioned above, there are several types of individuals, each with its own life span distribution, then the situation will be more complex. First of all, the type distribution will converge to a stable type law, determined by an eigen-measure property. Then the survival function ℓ , above will have to be replaced by an average of all the different survival functions weighted by the stable type distribution.

But the stable composition describes many other aspects of a balanced growing population besides ages. For example, the probability of being firstborn can be calculated as well as other aspects of family structure. In modern evolutionary biology the genealogy of individuals and, say, the mutational history play an important role. In an old population this is described by a stable, typical ancestry, which can be used to determine time back to some event like divergence between species. In a strict sense, such results have yet been proven only for populations of independently reproducing individuals. Little is known about stabilization during the quasi-stationary stage in population size dependence.

See also: Population Dynamics: Mathematic Models of Population, Development, and Natural Resources; Population Dynamics: Momentum of Population Growth; Population Dynamics: Theory of Nonstable Populations.

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