

Complexity and demographic stability in population models

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Abstract

This article is concerned with relating the stability of a population, as defined by the rate of decay of fluctuations induced by demographic stochasticity, with its heterogeneity in age-specific birth and death rates. We invoke the theory of large deviations to establish a fluctuation theorem: The demographic stability of a population is positively correlated with evolutionary entropy, a measure of the variability in the age of reproducing individuals in the population. This theorem is exploited to predict certain correlations between ecological constraints and evolutionary trends in demographic stability, namely, (i) bounded growth constraints—a uni-directional increase in stability, (ii) unbounded growth constraints (large population size)—a uni-directional decrease in stability, (iii) unbounded growth constraints (small population size)—random, non-directional change in stability. These principles relating ecological constraints with trends in demographic stability are shown to be far reaching generalizations of the tenets derived from classical studies of stability in an evolutionary context. These results thus provide a new conceptual framework for explaining patterns of variation in population numbers observed in natural populations.

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1. Introduction

A population defined by an age-specific fecundity and survivorship schedule which is a decreasing function of the population size will ultimately attain a steady state in which the relative number of individuals in the different age classes remains invariant in time and total population numbers remain constant. In natural populations, however, this constancy may not prevail indefinitely. Perturbations in the age-specific birth and death rates due to events intrinsic to the demographic process will induce variations in the age-distribution, and fluctuations in population numbers. Such fluctuations may have important ecological and demographic consequences. In animal populations of small size—typical of systems under conservation—the fluctuations, if sufficiently large and not rapidly attenuated, may lead to the rapid extinction of the population. In human populations, such chance variations in birth and death rates can generate large variations in the stable age-distribution; phenomena which may incur social cost

since they may induce changes in the labor force which are incongruent with the demand for labor. Accordingly, the rate of decay of fluctuations to the equilibrium state—a property which characterizes demographic stability, becomes of critical import in population studies.

The problem which this situation evokes can be stated as follows: Does there exist some measurable property of a population which will predict its degree of demographic stability, that is, its resilience or resistance to withstand perturbations from the steady state condition?

Perturbations will necessarily drive the population to a non-equilibrium condition. Consequently, the fluctuation decay rate towards the equilibrium state will be an intrinsically non-linear phenomenon regulated by the interaction, due to the birth and death process, of the individuals in the population. The problem we now confront is: Can this inherently non-linear process be described in terms of an operationally measurable function of the equilibrium state?

The problem has been addressed by demographers in the context of the Leslie matrix. A central theme that recurs in this analysis is the fact that the asymptotic rate

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of convergence to the stable age-distribution is determined by the relative sizes of the dominant eigenvalue and the second largest root of the characteristic equation of the matrix. Coale (1972) and Keyfitz (1972), however, recognized that the fluctuation decay rate after a perturbation from the steady state will typically involve transients of the process, and consequently, other complex roots of the characteristic equation will be implicated. These authors have therefore argued that demographic stability should be described by statistical parameters, such as the second and third moments of the net-maternity function—variables which would incorporate the effects of the other eigenvalues. However, efforts to describe these components in terms of a unique macroscopic variable have not been successful.

Demetrius (1977) brought a new perspective to the problem by invoking the notion evolutionary entropy, a mathematical concept which provides a measure of the heterogeneity in the age-specific birth and death rates in a population. In an effort to resolve the problems raised by the work of Coale and Keyfitz, the following hypothesis was proposed: *evolutionary entropy is positively correlated with demographic stability*. In other words, the larger the entropy, the more rapid the fluctuation decay rate to the steady state condition.

This hypothesis derives from the observation that demographic heterogeneity—the variability in age-specific birth and death rates, and fluctuation intensity—the deviation from the predicted population size which is induced by intrinsic stochastic effects, both issue from two related phenomena, developmental noise and demographic stochasticity.

Developmental noise refers to the chance variations in the sequence of ontogenetic events that transform the zygote into an adult, Waddington (1942). The random epigenetic variations entail, for example, that a clone of cells, descendants from the same mother cell and hence genetically identical, will vary in terms of the distribution of their metabolic components. Since these components affect cellular birth and death rates, the individuals in the clone will traverse the different stages of the cell cycle at different rates. Demographic heterogeneity is thus a necessary outcome of developmental noise and represents a fundamental property of any population of reproducing organisms.

Individuals who are apparently identical and are subject to similar environmental conditions may have different survivorship rates and produce different numbers of offspring. The term demographic stochasticity pertains to these variations in individual birth and death rates which typically have their origin in chance perturbations in developmental processes. In view of these chance variations, the trajectory of population numbers will not be defined by its predicted values but deviations from these values will occur. Accordingly,

fluctuations in population numbers is thus an inevitable outcome of demographic stochasticity, and also an intrinsic property of the population process.

Since developmental noise and demographic stochasticity are both expressions of the same phenomena, namely, the stochastic nature of biological processes at the epigenetic level, we predict that demographic heterogeneity and the fluctuation intensity of population numbers should be related—the greater the degree of heterogeneity, the smaller the deviation of population size from its mean value, or equivalently, the faster the fluctuation decay rate. The entropy-stability hypothesis derives from the above considerations, and the fact that entropy is a measure of demographic heterogeneity.

Partial support for the hypothesis has emerged from both theoretical and empirical studies. Demetrius (1977) showed, using the Lotka model, that the conjecture is valid for the special case of populations with life cycle distributions described by extremal values—maxima and minima—of entropy. Tuljapurkar (1982, 1993) provided insights into the problem from many different perspectives. One of the many achievements of Tuljapurkar's work is the derivation of a relation between entropy and the moments of the net-maternity function—the indices of demographic stability considered by Coale (1972) and Keyfitz (1972). Schoen and Kim (1991), Kim and Schoen (1993) expanded on these ideas and showed empirically, using human demographic data, that certain functions of the mean and variance of the net-maternity function are positively correlated with entropy.

This article will invoke the theory of large deviations to provide a complete analytical support for the entropy-stability hypothesis. We will establish the following result.

Fluctuation theorem: The rate of decay of fluctuations to the steady state is positively correlated with entropy.

Evolutionary entropy is a macroscopic variable which, in populations structured by age, is given by

$$H = - \frac{\sum p_j \log p_j}{\sum j p_j} \equiv \frac{S}{T}.$$

The quantity p_j is the probability that the mother of a randomly chosen newborn belongs to age class j . The numerator $S = -\sum p_j \log p_j$ describes the uncertainty in the age of the mother of a randomly chosen newborn. The denominator $T = \sum j p_j$ describes the generation time, the mean age of mothers at the birth of their offspring.

The fluctuation decay rate is also a macroscopic property which derives from a certain stochastic process which underlies demographic models. A mathematical representation of this stochastic process involves the notion of a genealogy, that is, a sequence which characterizes for each individual her age, the age of her mother at her birth, the age of her grandmother at

her mothers birth ... and so on, Demetrius (1974, 1983), Tuljapurkar (1982), Arnold et al. (1994). To a genealogy constituting n such events, we can associate a net offspring production which is derived by considering the reproduction and survivorship rates of the individuals that define the genealogy. As n increases, the net-offspring reproduction generated by the genealogy will converge to the net-offspring production of the population. Let $Q_n(\varepsilon)$ denote the probability that the net-offspring production at the “time” n differs from the predicted value by more than ε . As n increases $Q_n(\varepsilon)$ will tend to zero. The fluctuation decay rate, denoted by \mathcal{R} , is the asymptotic rate at which the number $Q_n(\varepsilon)$ tends to zero. Analytically, we have

$$\mathcal{R} = \lim_{n \rightarrow \infty} -\frac{1}{n} \log Q_n(\varepsilon).$$

We append some heuristic remarks to clarify this technical definition. The net-offspring production is a fundamental population observable. Its asymptotic value refers to the value which is predicted by the population process. The value at some instant n , defined by a genealogical trajectory, corresponds to a sample of the observable at the given instant. Hence, the quantity $Q_n(\varepsilon)$ can also be interpreted as the probability that the sample mean, defined at the instant n , differs from the asymptotic mean.

Formally, the fluctuation theorem asserts

$$\Delta \mathcal{R} \Delta H > 0. \quad (1)$$

Here ΔX is the change in the macroscopic variable X induced by a change in the age-specific fecundity and mortality variables at steady state.

The fluctuation decay rate is a non-linear property derived from the interaction between the individuals when the population is in the neighborhood of the steady state. The entropy describes a macroscopic variable defined at steady state. Hence, inequality (1) characterizes a non-linear phenomenon in terms of an equilibrium property, which can be described by an operationally measurable quantity, namely entropy.

Our proof of the fluctuation theorem appeals to the theory of large deviations, a mathematical theory concerned with the exponential decay of certain probabilities. The large deviation formalism has its origin in the work of Boltzmann who brought probability ideas into thermodynamic theory in his effort to characterize energy and density fluctuations in physical systems. Due primarily to the efforts of Cramér (1938), Donsker and Varadhan (1983) and Wentzell (1990), the original ideas of Boltzmann were systematized and integrated into a new mathematical discipline. The formalism has generated applications in a wide variety of domains, stochastic optimal control theory, Dupuis

and Ellis (1995); geometry, Varadhan (1984); partial differential equations, Dupuis et al. (1990); statistical mechanics, Ellis (1985, 1995).

In this article, we apply large deviation theory to population processes. This new application is a natural outcome of certain connections between population processes and thermodynamic theory, Demetrius (1983), Arnold et al. (1994). The relation between population dynamics and thermodynamic processes is embodied in the following variational principle: The asymptotic growth rate of a population satisfies an extremal principle which is formally analogous to the minimization of the Gibbs free energy in statistical mechanics. This result was shown to imply the following formal correspondence between population parameters and thermodynamic variables, namely: growth rate—free energy; generation time—reciprocal temperature; evolutionary entropy—the Boltzmann entropy. The formal relation furthermore suggests that the methods introduced by Boltzmann to analyze equilibrium fluctuations in physical systems should be pertinent to the study of non-equilibrium fluctuations in biological systems. The conceptual framework which this paper articulates is based on this observation.

The fluctuation theorem will be shown to have important implications for understanding patterns of variation in the demographic stability of natural populations: This results from a characterization of evolutionary trends in stability which this article delineates. Evolutionary changes in demographic stability can be inferred using Eq. (1) and appealing to directionality theory, the analysis of changes in entropy under mutation and natural selection, Demetrius (1992), Arnold et al. (1994).

Directionality theory classifies populations in terms of the ecological constraints (bounded, unbounded growth) they experience throughout their evolutionary history. Bounded growth pertains to populations which spend the greater part of their evolutionary history with stationary size or with a growth rate bounded by entropy. Unbounded growth refers to populations defined, throughout their evolutionary history, by a growth rate which exceeds entropy. Directionality theory predicts certain correlations between these ecological constraints and evolutionary changes in entropy. In this article, we will invoke the directionality principles for entropy and exploit the fluctuation theorem to predict the following correspondence between ecological constraints and evolutionary trends in stability.

- (I) *Bounded growth*: a uni-directional increase in stability.
- (II) *Unbounded growth* (large population size): a uni-directional decrease in stability.

(III) *Unbounded growth* (small population size): random, non-directional change in stability.

These dependences suggest that the dynamical changes in stability observed in natural populations (see, for example, Turchin and Taylor, 1992, Ellner and Turchin, 1995) may not necessarily reflect seasonal variation and environmental noise, but may be driven by intrinsic ecological constraints (bounded, unbounded growth). The principles relating ecological factors and trends in demographic stability which the integration of the fluctuation theorem and directionality theory predicts, thus provide a new framework for explaining empirical patterns in the demographic stability of natural populations. Our characterization of evolutionary changes in demographic stability will be shown to be a generalization of the classical studies of stability based on the McArthur–Wilson *r–K* model of evolution.

The paper is organized as follows. Section 2 gives an outline of the demographic model we analyze. In this section, which is mainly review, we will focus on the elucidating the concept of a genealogy which will be the critical parameter in our derivation of the fluctuation theorem. Section 3 develops the large deviation formalism which we will use to derive our main result. Numerical examples to illustrate the fluctuation theorem are given in Section 4.

The evolutionary changes in demographic stability are discussed in Section 5. In Section 5.1 we give a brief synopsis of directionality theory. Section 5.2 integrates directionality theory with the fluctuation theorem to derive correlations between ecological factors and evolutionary changes in demographic stability. The basic principles that underlie the McArthur–Wilson *r–K* selection model are described in Section 5.3. In Section 5.4, we evaluate the *r–K* model and directionality theory in terms of the ability of these two theories to explain evolutionary trends in demographic stability. We will show that the *r–K* model, which pertains to demographically homogeneous populations, can be considered a singular limit of directionality theory, which refers to demographically heterogeneous populations.

2. A structured population model

Age-structured models with non-linear dynamics can be described by the difference equation

$$u(t + 1) = A(t)u(t), \quad u(0) = u_0. \tag{2}$$

Here $A(t) = (a_{ij}(t))$ is a matrix with non-negative entries, and $u(t) = (u_j(t))$, where $u_j(t)$ denotes the number of individuals in age-class j at time t . The total population size at time t is given by $N(t) = \sum_{j=1}^d u_j(t)$.

This model was introduced by Leslie (1945). The particular nature of birth and death transitions in populations structured by age entails that the matrix assumes the form

$$A = \begin{pmatrix} m_1(t) & m_2(t) & \dots & \dots & m_d(t) \\ b_1(t) & 0 & \dots & \dots & 0 \\ 0 & b_2(t) & \ddots & & \vdots \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \dots & 0 & b_{d-1}(t) & 0 \end{pmatrix}.$$

Here $m_j(t) \geq 0$ denotes the mean number of offspring produced by an individual in the j th age class, and $b_j(t)$, $0 < b_j(t) \leq 1$, represents the proportion of individuals surviving from age-class j to age-class $j + 1$.

We assume that $m_j(t)$ and $b_j(t)$ are expressed in the form

$$\begin{aligned} m_j(t) &= m_j \exp\left(-\sum_{k=1}^d \mu_{jk} u_k(t)\right), \\ b_j(t) &= b_j \exp\left(-\sum_{k=1}^d \beta_{jk} u_k(t)\right). \end{aligned} \tag{3}$$

In (3), $\mu_{jk} \geq 0$, $\beta_{jk} \geq 0$. In view of the definition $N(t) = \sum_{j=1}^d u_j(t)$ we can interpret $\sum_{j=1}^d \mu_{jk} u_j(t)$ and $\sum_{j=1}^d \beta_{jk} u_j(t)$ as generalized population sizes, quantities which reduce to $N(t)$ when $\mu_{jk} = \beta_{jk} = 1$.

We observe from (3) that when $\mu_{jk} = \beta_{jk} = 0$, then $m_j(t) = m_j$ and $b_j(t) = b_j$. Hence (3) includes linear models defined by a constant matrix, and non-linear models where birth and death rates are density dependent.

We will assume that the system described by the non-linear dynamical system (2) converges to a steady state in which the proportion of individuals in each category remains invariant and the population size is constant. We should note that this situation can be guaranteed only under additional conditions (see for example Liu and Cohen (1987)). Hence at steady state the transition will be described in terms of a constant matrix $\tilde{A} = (\tilde{a}_{ij})$ where the \tilde{a}_{ij} are the steady state values of $a_{ij}(t)$. This matrix is non-negative. We will assume that it is irreducible and also primitive: The Perron–Frobenius theory ensures that \tilde{A} has a dominant eigenvalue λ and unique corresponding positive right and left eigenvectors u and v , respectively. We have

$$\tilde{A}u = \lambda u, \quad v\tilde{A} = \lambda v, \quad (u, v) = 1. \tag{4}$$

Due to the attractive state which we assume, we must have $\lambda = 1$, a condition which is equivalent to zero growth rate and a constant population size.

In the analysis we develop we will be concerned with both linear and non-linear models, whose dynamics converges to a unique steady state in which condition (4) holds. In linear models, the steady state will be characterized by the property $\lambda \geq 1$. In non-linear

models we have the relation $\lambda = 1$. Accordingly, to include both the linear and non-linear cases, we will assume that at the steady state defined by (4), the condition $\lambda \geq 1$ holds.

2.1. The steady state: age structure

The dominant eigenvalue λ is the unique real root of the characteristic equation

$$1 = \sum_{j=1}^d \frac{\ell_j m_j}{\lambda^j}, \tag{5}$$

where

$$\ell_j = \begin{cases} 1 & \text{for } j = 1, \\ b_1 \dots b_{j-1} & \text{for } j > 1. \end{cases}$$

We write

$$p_j = \frac{\ell_j m_j}{\lambda^j}. \tag{6}$$

The right and left eigenvectors are given by

$$u_j = \frac{\ell_j}{\lambda^j}, \tag{7}$$

$$v_j = \frac{1}{T u_j} \sum_{k=j}^d m_k u_k, \quad \text{where } T = \sum_j j p_j. \tag{8}$$

The quantity T is the mean age of mothers at the birth of their offspring, and gives a measure of the generation time.

The Malthusian parameter is defined by $r = \log \lambda$ with $\lambda = 1$ in the case of the non-linear model and $\lambda \geq 1$ for the linear model. It yields the asymptotic growth rate of actual population numbers. The population size $N(t)$ at time t is given by

$$N(t) = \sum_{j=1}^d u_j(t).$$

The Perron–Frobenius theorem (cf. Demetrius, 1971; Cohen, 1979) can be invoked to show that

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log N(t) = r. \tag{9}$$

Hence $N(t) \sim \exp(rt)$, and for large t we have

$$\frac{N(t+1)}{N(t)} \approx e^r. \tag{10}$$

Eq. (10) thus provides a method for evaluating r distinct from solving the characteristic equation (5).

2.2. The steady state: genealogies

The dynamics of the population at steady state can be described in terms of genealogies generated by individuals in the population at steady state. We first observe that the matrix at steady state admits a graphical

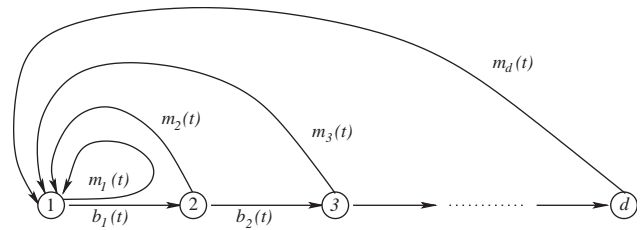


Fig. 1. Life cycle graph for a Leslie matrix.

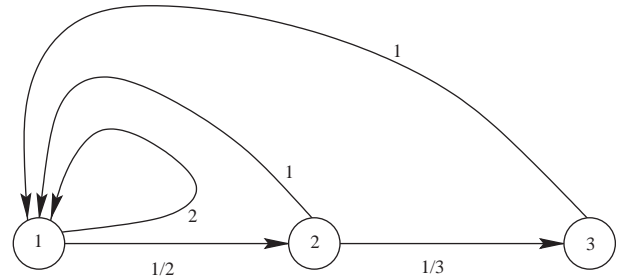


Fig. 2. Life cycle graph for the Leslie matrix in our example.

representation. In this graph, see Fig. 1, we join node (i) to node (j) if $a_{ij} > 0$.

Let Σ denote the set of all infinite backwards paths of the graph \mathcal{G} . A path in the graph can be described by a sequence

$$x = (x_0, x_1, x_2, \dots),$$

where $x_i \in \{1, \dots, d\}$ and $a_{x_{i+1}, x_i} > 0$.

Such a path is called a genealogy, as it represents a recording of successive ancestral states of a particular individual which at time 0 is in the class x_0 .

Example. Consider the population process given by

$$\begin{pmatrix} 2 & 1 & 1 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{pmatrix}.$$

The corresponding graph is shown in Fig. 2.

The genealogies generated by an individual in age class (1) are of the form

- (a) 1211... (b) 1231... (c) 1212...

The genealogy (a) describes the following sequence of events: individual in age class (1) at time 0, the same individual in age class (2) at time 1; an offspring of this individual in age class (1) at time 2; an offspring of this individual in age class (1) at time 3. The genealogies given by (a), (b) and (c) can be described by the graph in Fig. 3.

The genealogies generated by a single individual in age class (1) at time 0 will be characterized by a certain

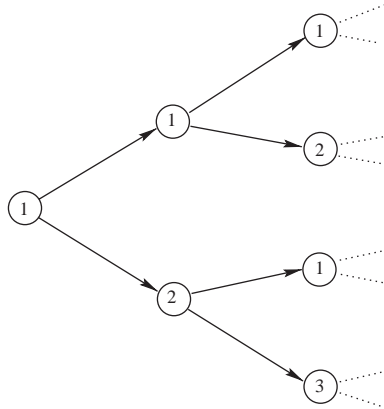


Fig. 3. Genealogies.

distribution which we calculate from the Markov chain induced from the transition matrix A .

Consider the stochastic matrix $P = (p_{ij})$ given by

$$p_{ij} = \frac{a_{ji}v_j}{\lambda v_i}, \tag{11}$$

where $v = (v_j)$ is the left eigenvector associated with the dominant eigenvalue λ . We can appeal to the expression for v_j given by (8) and compute p_{ij} explicitly (see Arnold et al., 1994). The matrix $P = (p_{ij})$ is given by

$$P = \begin{pmatrix} p_1 & 1-p_1 & 0 & \dots & \dots & 0 \\ \frac{p_2}{1-p_1} & 0 & \frac{1-p_1-p_2}{1-p_1} & 0 & \dots & \vdots \\ \vdots & 0 & \ddots & \ddots & \ddots & \vdots \\ \vdots & \vdots & \ddots & \ddots & \ddots & \frac{p_d}{p_d+p_{d-1}} \\ \frac{p_d}{1-\sum_{i=1}^{d-1} p_i} = 1 & 0 & \dots & \dots & \dots & 0 \end{pmatrix},$$

where p_j is given by (6).

The stationary distribution $\pi = (\pi_i)$ for the stochastic matrix P is given by

$$\pi_i = u_i v_i.$$

The Markov measure $\tilde{\mu}$ associated with this matrix P has the representation

$$\tilde{\mu}\{x_n = i_n, \dots, x_{n+k} = i_{n+k}\} = \pi_{i_n} p_{i_n i_{n+1}} \dots p_{i_{n+k-1} i_{n+k}}. \tag{12}$$

As shown in, say Arnold et al. (1994), this measure $\tilde{\mu}$ determines the distribution of the genealogies generated when the steady-state condition of the population is attained.

The concept of evolutionary entropy, denoted by H , is defined to be the entropy of the Markov chain (P, π) . As shown in, for example, Billingsley (1965), the entropy of the Markov chain is given by

$$H = - \sum_{i,j} \pi_i p_{ij} \log p_{ij}.$$

We write

$$H = - \sum_i \pi_i \sum_j p_{ij} \log p_{ij}. \tag{13}$$

Now, in view of (7) and (8), we observe that

$$\pi_1 = \frac{1}{T}, \quad \pi_i = \frac{1}{T} \left(1 - \sum_{j=1}^{i-1} p_j \right) \quad \text{for } 2 \leq i \leq d,$$

where $T = \sum_{j=1}^d j p_j$.

In view of the structure of the matrix P , the expression for H reduces to

$$H = \left(-\frac{1}{T} \right) \sum p_j \log p_j,$$

which we write as

$$H = - \frac{\sum_j p_j \log p_j}{\sum j p_j},$$

where p_j is given by (6).

The entropy H defined in the context of the genealogies, is the analogue of the Malthusian parameter r defined in the context of age-distribution dynamics. The entropy H determines the asymptotic rate of increase of the effective population size, $N^*(t)$, a quantity defined as follows (Demetrius, 1983).

Let $\Sigma^{(t)}$ denote the set of genealogies generated by a single individual during the time interval $(0, t)$ and let E denote a subset of $\Sigma^{(t)}$. We associate with the set E a probability measure as follows: Consider an element $z \in E$, where

$$z = (z_0, \dots, z_{t-1})$$

and write $[z] = \{x \in \Sigma : x_i = z_i, 0 \leq i \leq t-1\}$. We now write

$$\mu_t(E) = \sum_{z \in E} \mu[z].$$

The effective population size $N^*(t)$ is defined by

$$N^*(t) = \min \{ \text{card } E : E \subset \Sigma^{(t)}, \mu_t(E) > 1 - \varepsilon \}. \tag{14}$$

Thus the effective size describes the minimal number of genealogies whose total probability exceeds $1 - \varepsilon$.

The Shannon–McMillan theorem (cf. Demetrius, 1983), can be invoked to show that

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log N^*(t) = H. \tag{15}$$

Hence $N^*(t) \sim \exp(Ht)$ and for large t we have

$$\frac{N^*(t+1)}{N^*(t)} \approx e^H.$$

A heuristic interpretation of the effective size concept can be expressed as follows: We can assert that for arbitrarily small $\varepsilon > 0$ and $\delta > 0$, and for sufficiently large

t , all genealogies can be separated into two classes S_1 and S_2 such that

(a) for every genealogy x in class S_1

$$\left| \frac{\log \tilde{\mu}(x)}{t} + H \right| < \varepsilon,$$

(b) the sum of the probabilities of genealogies belonging to the class S_2 is less than δ .

For all genealogies $x \in S_1$, we have that $(-\frac{1}{t}) \log \tilde{\mu}(x)$ is close to H . Therefore, all genealogies of the class S_1 have approximately the same probability, namely e^{-tH} . This means that the number of genealogies in this class is approximately e^{tH} . This number characterizes the effective size $N^*(t)$. It describes the number of “typical” genealogies generated by an individual in the population.

2.3. The steady state: the thermodynamic formalism

One of the central themes exploited in the analysis of population processes is the following mathematical fact: The probability measure $\tilde{\mu}$ defined by (12) can be characterized in terms of a variational principle, Demetrius (1983), Arnold et al. (1994). This fact forces certain relations between population processes and thermodynamic theory and is the basis for the application of the large deviation formalism to the analysis of fluctuations in population processes. We refer to Ruelle (1978) for a general account of the thermodynamic formalism.

We now recall the main elements of the variational principle. Let M denote the set of probability measures on Σ which are invariant under the shift transformation $\tau : \Sigma \rightarrow \Sigma$ defined by

$$(\tau(x))_i = x_{i+1} \quad \text{for } i \geq 0 \text{ with } x = (x_i).$$

Let $h_\mu(\tau)$ denote the Kolmogorov–Sinai entropy of the system (Σ, μ, τ) . Consider a genealogy

$$(x_0, x_1, x_2, \dots). \tag{16}$$

The product

$$a_{x_0 x_1} a_{x_1 x_2} \dots a_{x_{n-1} x_n}$$

represents the net-offspring production of the individuals that describe the genealogy defined by (16).

Consider the function $\varphi : \Sigma \rightarrow \mathbb{R}$ defined by

$$\varphi(x) = \log a_{x_0 x_1}. \tag{17}$$

The function φ , called a potential, assigns to each genealogy $x \in \Sigma$, a real number which represents the net-reproduction function associated with the coordinates x_0, x_1 .

As observed (see for example Arnold et al., 1994), the population growth rate r defined by (9) satisfies an

extremal principle. We have

$$r = \log \lambda = \sup_{\mu \in M} \left[h_\mu(\tau) + \int \varphi d\mu \right]. \tag{18}$$

Moreover the supremum in (18) is attained by the Markov measure $\tilde{\mu}$ defined by (12) and we have

$$r = \log \lambda = h_{\tilde{\mu}}(\tau) + \int \varphi d\tilde{\mu}.$$

The dynamical entropy is precisely the entropy of the associated Markov chain as defined in Billingsley (1965). Hence we have $h_{\tilde{\mu}}(\tau) = -\sum_{i,j} \pi_i p_{ij} \log p_{ij}$. The computation in (13), using the Markov chain P , shows that

$$H = h_{\tilde{\mu}}(\tau) = -\frac{\sum p_j \log p_j}{\sum j p_j}, \tag{19}$$

where p_j is given by (6).

The quantity $\int \varphi d\tilde{\mu}$ is called the reproductive potential and denoted Φ .

In view of the Markov properties of the measure $\tilde{\mu}$, the potential Φ becomes

$$\Phi = \frac{\sum p_j \log V_j}{\sum j p_j} = \frac{E}{T}. \tag{20}$$

The expression E describes the net-reproductive rate $\log V_j$ averaged over all age-classes. In view of (18) we have the identity

$$r = H + \Phi. \tag{21}$$

From (21) we observe that

$$\begin{aligned} \Phi < 0 &\Rightarrow r < H, \\ \Phi = 0 &\Rightarrow r = H, \\ \Phi > 0 &\Rightarrow r > H. \end{aligned} \tag{22}$$

An example of a system with $\Phi = 0$ is given by the condition

$$V_j = l_j m_j = 1, \quad \text{i.e. } m_j = 1/l_j.$$

The transition matrix then has the form

$$\begin{pmatrix} 1 & \frac{1}{b_1} & \frac{1}{b_1 b_2} & \dots & \frac{1}{b_1 b_2 \dots b_{d-1}} \\ b_1 & 0 & 0 & \dots & 0 \\ 0 & b_2 & 0 & \dots & \vdots \\ \vdots & 0 & b_3 & \dots & \vdots \\ 0 & \dots & 0 & b_{d-1} & 0 \end{pmatrix}.$$

2.4. Census size and effective size

The census size $N(t)$ and the effective size $N^*(t)$, as shown in (9) and (15) satisfy the asymptotic relations $N(t) \sim e^{rT}$, $N^*(t) \sim e^{HT}$.

The function Φ can be used to illustrate the distinction between these two quantities.

We obtain from (22) and Eqs. (9) and (21) the following implications:

$$\begin{aligned} \Phi < 0 &\Rightarrow N(t) < N^*(t), \\ \Phi = 0 &\Rightarrow N(t) = N^*(t), \\ \Phi > 0 &\Rightarrow N(t) > N^*(t). \end{aligned} \tag{23}$$

Example. Consider the following Leslie matrices:

$$(A) \begin{pmatrix} 1 & 2 & 6 \\ 1/2 & 0 & 0 \\ 0 & 1/3 & 0 \end{pmatrix}.$$

Here, $\Phi = 0$ and $r = H \approx 0.61$, i.e. both $N(t)$ and $N^*(t)$ grow with the same exponential rate ≈ 0.61 .

$$(B) \begin{pmatrix} 2/3 & 2/3 & 4/3 \\ 2/3 & 0 & 0 \\ 0 & 1/3 & 0 \end{pmatrix}.$$

Here H takes the same value as in (A), but $\Phi \approx -0.23 < 0$ and $r \approx 0.37$ is considerably smaller than in (A). Hence in this case $N^*(t) \approx \exp(0.6t) > N(t) \approx \exp(0.37t)$.

$$(C) \begin{pmatrix} 3/2 & 1 & 1 \\ 1/2 & 0 & 0 \\ 0 & 2/5 & 0 \end{pmatrix}.$$

In this case $\Phi \approx 0.15 > 0$. The actual population grows with rate $r \approx 0.61$, but the effective population only with rate $H \approx 0.46$.

A deeper insight into the distinction between census size $N(t)$ and the effective size $N^*(t)$ may be obtained by considering the dynamics of the population in terms of the genealogies generated. In this context, the census size and the effective size can be considered as two distinct ways of enumerating the size of a population. The census size $N(t)$ is derived by assigning equal weight to each genealogy. In view of (14), the effective size $N^*(t)$ is derived by assigning equal weights to the typical genealogies and zero weight to the atypical genealogies.

Our analysis shows that $N(t) \approx N^*(t)$ when either $\Phi = 0$, or when the population size is effectively infinite.

Now a large body of theory in population dynamics revolves around the population growth rate. An example in this regard are models of population genetics which are based on the population growth rate as a measure of Darwinian fitness. Our observations indicate that this body of theory can be considered as the singular limit ($\Phi \rightarrow 0, N(t) \rightarrow \infty$) of theories which revolve around entropy, in particular models which invoke entropy as the measure of fitness.

3. Large deviations and demographic stability

The analysis of population models predicts that at steady state, the population will be described by a stable age distribution, and total population numbers will remain constant or increase exponentially at some constant rate. However, empirical observation of measurable quantities such as population numbers over time, will invariably show fluctuations. These fluctuations typically derive from two main sources (i) random individual variations in age-specific fecundity and mortality which is characteristic of all natural populations (demographic stochasticity), and (ii) the impact of wars, famines, inducing transient variations in the fecundity and mortality rates (extrinsic perturbation). We will be concerned with the effects of demographic stochasticity, and we will analyze the intensity of the fluctuations they generate. We will provide an analytical description of the fluctuation decay rate and show that changes in this quantity are positively correlated with changes in entropy.

In our analysis, we will appeal to the statistical mechanics representation of the population given in Section 2.2. According to this model the population at steady state can be described in terms of the dynamical system $(\Sigma, \tilde{\mu}, \tau)$ where Σ denotes the space of genealogies, $\tilde{\mu}$ the probability measure on Σ , and τ the shift operator on Σ .

Now, for a genealogy (x_0, x_1, x_2, \dots) consider the function $\varphi(x) = \log a_{x_0 x_1}$ defined in (17) and write

$$S_n \varphi(x) = \sum_{j=0}^{n-1} \varphi(\tau^j x). \tag{24}$$

We have

$$\begin{aligned} S_n \varphi(x) &= \log a_{x_0 x_1} + \log a_{x_1 x_2} + \dots + \log a_{x_{n-1} x_n} \\ &= \log a_{x_0 x_1} a_{x_1 x_2} \dots a_{x_{n-1} x_n}. \end{aligned}$$

Hence $S_n \varphi(x)$ represents the net-offspring production rate of the individuals that describe the genealogy.

By the ergodic theorem, we have

$$\lim_{n \rightarrow \infty} \frac{1}{n} S_n \varphi(x) = \int \varphi d\tilde{\mu} = \Phi = \frac{\sum p_j \log V_j}{\sum j p_j} \tag{25}$$

with probability one with respect to $\tilde{\mu}$.

Eq. (25) asserts that if we choose a genealogy $x = (x_0, x_1, x_2, \dots)$, then with probability one the long-term mean of its net-offspring production equals the normalized average Φ given in (25) taken over all genealogies with respect to $\tilde{\mu}$.

Now write

$$P_n(\varphi) = \left| \frac{1}{n} S_n \varphi(x) - \Phi \right|. \tag{26}$$

The quantity $P_n(\varphi)$ represents the deviation of the sample mean $\frac{1}{n} S_n \varphi(x)$ from the normalized average value Φ .

Since $r = H + \Phi$, the magnitude of this deviation from the average value Φ will be correlated with the magnitude of the deviation of the sample mean of the population size from its average value. Accordingly, the quantity $P_n(\varphi)$ characterizes the intensity of the fluctuations of any macroscopic variable from its average value. We are interested in the rate of decay of these fluctuations.

Given $\varepsilon > 0$, consider the probability $Q_n(\varepsilon)$ that the sample mean $\frac{1}{n}S_n\varphi(x)$ differs from the mean value Φ by more than ε , that is

$$Q_n(\varepsilon) = \tilde{\mu}\{x \in \Sigma : P_n\varphi(x) > \varepsilon\}.$$

We have, by the ergodic theorem of Birkhoff, that

$$\lim_{n \rightarrow \infty} Q_n(\varepsilon) = 0. \tag{27}$$

The convergence to zero, as indicated by (27), is at least exponential. We have, that for any $\varepsilon > 0$, there exist positive constants C, M , such that for every n ,

$$\tilde{\mu}\{x \in \Sigma : P_n\varphi(x) > \varepsilon\} \leq Ce^{-Mn}. \tag{28}$$

In order to characterize the fluctuation decay rate, we ask, in view of (28): How fast on a logarithmic scale does the value $Q_n(\varepsilon)$, the probability that the sample mean differs from the mean value by more than ε , go to zero.

The rate, denoted by \mathcal{R} , is given by

$$\mathcal{R} \equiv \mathcal{R}(\varepsilon) = \lim_{n \rightarrow \infty} -\frac{1}{n} \log Q_n(\varepsilon). \tag{29}$$

The quantity \mathcal{R} characterizes the asymptotic value of the probability measure of the set of trajectories that deviate up to ε from the behavior of the typical trajectory.

Now, as observed earlier, the population at steady state can be described in terms of the dynamical system (Σ, μ, τ) and hence to each population we can also define an entropy $h_\mu(\tau)$, the entropy of the dynamical system. This entropy, as (19) indicates is precisely the evolutionary entropy H . As noted in (14), we can also define an effective size $N_n^*(\varepsilon)$, which represents the minimal number of genealogies which total probability exceeds $1 - \varepsilon$. Moreover (cf. Demetrius, 1983), we have

$$H = \lim_{n \rightarrow \infty} \frac{1}{n} \log N_n^*(\varepsilon). \tag{30}$$

The quantity H , a measure of the variability in the age of reproducing individuals in the population, thus embodies information regarding the asymptotic value of the minimal number of genealogies whose total probability exceeds $1 - \varepsilon$.

Now, heuristic considerations suggest that the *greater* the minimal number of genealogies whose total probability exceeds $1 - \varepsilon$, the *smaller* will be the measure of the set of genealogies that deviate up to ε from the behavior of the typical genealogy. In view of (29) and (30), these considerations entail the following property: the larger the entropy, the more rapid the fluctuation

decay rate. This property is consistent with the original conjecture proposed on the basis of purely qualitative arguments.

We will now invoke the theory of large deviations and perturbation analysis developed in Arnold et al. (1994) to give an analytical proof of the fluctuation-stability property.

We will consider a population model defined by the matrix $A = (a_{ij})$ and its representation at steady state (Σ, μ, τ) . The fluctuation decay rate \mathcal{R} and the entropy H constitute macroscopic parameters of the model. We then consider a perturbation given by the matrix $A(\delta) = (a_{ij}^{1+\delta})$. The corresponding representation at steady state is $(\Sigma, \mu(\delta), \tau)$ where $\mu(\delta)$ denotes the unique equilibrium state, with fluctuation decay rate $\mathcal{R}(\delta)$ and entropy $H(\delta)$. Write $\Delta\mathcal{R} = \mathcal{R}(\delta) - \mathcal{R}(0)$ and $\Delta H = H(\delta) - H(0)$. We will establish the following result.

Theorem. *The evolutionary entropy H and the fluctuation decay rate \mathcal{R} are positively correlated, that is*

$$\Delta\mathcal{R}\Delta H > 0$$

for sufficiently small δ .

The proof of our result draws from certain characterizations of \mathcal{R} in terms of a variational principle.

Recall that (29) says

$$\mathcal{R} = \lim_{n \rightarrow \infty} \frac{1}{n} \log \tilde{\mu} \left\{ x \in \Sigma : \left| \frac{1}{n} S_n \varphi(x) - \Phi \right| > \varepsilon \right\}.$$

In order to find a characterization of \mathcal{R} we first define the more general decay rates

$$\begin{aligned} \bar{\mathcal{R}}(\varphi, E) &= \limsup_{n \rightarrow \infty} \frac{1}{n} \log \tilde{\mu} \left\{ x \in \Sigma : \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x) \in E \right\}, \\ \underline{\mathcal{R}}(\varphi, E) &= \liminf_{n \rightarrow \infty} \frac{1}{n} \log \tilde{\mu} \left\{ x \in \Sigma : \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x) \in E \right\} \end{aligned} \tag{31}$$

for arbitrary subsets E of the real line. The case we are mostly interested in corresponds to $E = \{s : |s - \Phi| > \varepsilon\}$.

Consider the function

$$h_\nu(\tau) + \int \varphi \, d\nu$$

where ν denotes a probability measure in Σ which is invariant under the shift operator τ .

As above shown in (18), we have

$$r = \sup_\nu \left[h_\nu(\tau) + \int \varphi \, d\nu \right],$$

where $r = \log \lambda$. Write

$$G(\nu) = \left[r - (h_\nu(\tau) + \int \varphi \, d\nu) \right]$$

and consider the function $k_\varphi(s)$ defined by

$$k_\varphi(s) = \inf \left\{ G(v) : v \text{ invariant under } \tau \right. \\ \left. \text{and } \int \varphi dv = s \right\}. \tag{32}$$

Applying the definition of $G(v)$ and taking into account that we have to restrict our attention to measures with $\int \varphi dv = s$, we obtain

$$k_\varphi(s) = r - s - \sup \left\{ h_v(\tau) : v \text{ invariant under } \tau \right. \\ \left. \text{and } \int \varphi dv = s \right\}. \tag{33}$$

As shown by Young (1990) (see also Orey and Pelikan, 1988), the functions $\underline{\mathcal{R}}(\varphi, E)$ and $\bar{\mathcal{R}}(\varphi, E)$ defined in (31) can be expressed by the relations

$$\underline{\mathcal{R}}(\varphi, E) \geq - \inf \{k_\varphi(s) : s \in E\} \text{ for every open set } E$$

and

$$\bar{\mathcal{R}}(\varphi, E) \leq - \inf \{k_\varphi(s) : s \in E\} \text{ for every closed set } E.$$

Moreover, the function k_φ defined by (33) satisfies the following relations: k_φ is continuous, and by the variational principle given in (18), $k_\varphi(\Phi) = 0$.

The continuity of k_φ implies that in the case $E = \{s : |s - \Phi| > \varepsilon\}$ with some fixed $\varepsilon > 0$ the lim sup and lim inf in (31) are actually limits and therefore,

$$\mathcal{R} = \underline{\mathcal{R}}(\varphi, E) = \bar{\mathcal{R}}(\varphi, E) = - \inf \{k_\varphi(s) : s \in E\} \\ = - \min \{k_\varphi(\Phi - \varepsilon), k_\varphi(\Phi + \varepsilon)\}. \tag{34}$$

Let us now consider the perturbed population model given by the matrix $A(\delta) = (a_{ij}^{1+\delta})$. Here $\varphi(x) = \log a_{x_0, x_1}$ has to be replaced with the function $\varphi(\delta) = (1 + \delta)\varphi$, which describes the net offspring production rate of the individuals that describe the genealogy. An application of the ergodic theorem, cf. (25), yields

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\delta)(\tau^j x) = \int \varphi(\delta) d\tilde{\mu}(\delta) \equiv \Phi(\delta) \tag{35}$$

for genealogies x with probability one with respect to $\tilde{\mu}(\delta)$, the unique equilibrium state corresponding to $\varphi(\delta)$.

Using $\varphi(\delta) = (1 + \delta)\varphi$ and dividing by $1 + \delta$, (35) yields,

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x) = \int \varphi d\tilde{\mu}(\delta). \tag{36}$$

Genealogies for which the sample mean $\frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x)$ after finite time n , deviates by more than ε from the expected mean value $\int \varphi d\tilde{\mu}(\delta)$, are thus characterized by

$$\left| \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x) - \int \varphi d\tilde{\mu}(\delta) \right| > \varepsilon. \tag{37}$$

Multiplying (37) by $(1 + \delta)$ we have

$$\left| \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\tau^j x)(1 + \delta) - \int \varphi(1 + \delta) d\tilde{\mu}(\delta) \right| \\ > \varepsilon(1 + \delta). \tag{38}$$

In view of (35), this is equivalent to

$$\left| \frac{1}{n} \sum_{j=0}^{n-1} \varphi(\delta)(\tau^j x) - \Phi(\delta) \right| > \varepsilon(1 + \delta). \tag{39}$$

Let $\mathcal{Q}_n^\delta(\varepsilon)$ denote the measure of the set of genealogies where the sample mean $\frac{1}{n} \sum_{j=0}^{n-1} \varphi(\delta)$ differs from the mean value $\Phi(\delta)$ by more than ε . Analogously to (27), (28) and (29), we find that $\mathcal{Q}_n^\delta(\varepsilon)$ decays exponentially with rate

$$\mathcal{R}(\delta) \equiv \mathcal{R}_\varepsilon(\delta) = \lim_{n \rightarrow \infty} - \frac{1}{n} \log \mathcal{Q}_n^\delta(\varepsilon).$$

In view of (34), the decay rate $\mathcal{R}(\delta)$ is given by

$$\mathcal{R}(\delta) \equiv \min \{k_{\varphi(\delta)}(\Phi(\delta) - (1 + \delta)\varepsilon), \\ k_{\varphi(\delta)}(\Phi(\delta) + (1 + \delta)\varepsilon)\}. \tag{40}$$

Using (33), the definition of $k_{\varphi(\delta)}$, we obtain

$$k_{\varphi(\delta)}(\Phi(\delta) - (1 + \delta)\varepsilon) \\ = h_{\tilde{\mu}(\delta)}(\tau) + \Phi(\delta) - \left(\sup \left\{ h_v(\tau) : v\tau\text{-invariant}, \right. \right. \\ \left. \left. \int \varphi(\delta) dv = \Phi(\delta) - (1 + \delta)\varepsilon \right\} + \Phi(\delta) - (1 + \delta)\varepsilon \right) \\ = h_{\tilde{\mu}(\delta)}(\tau) + (1 + \delta)\varepsilon - \sup \left\{ h_v(\tau) : v\tau\text{-invariant}, \right. \\ \left. \int \varphi dv = \Phi - \varepsilon \right\}. \tag{41}$$

The last term $\sup\{\dots\}$ is independent of δ since

$$\int \varphi(\delta) dv = \Phi(\delta) - (1 + \delta)\varepsilon \Leftrightarrow \int \varphi dv = \Phi - \varepsilon.$$

Analogously,

$$k_{\varphi(\delta)}(\Phi(\delta) + (1 + \delta)\varepsilon) \\ = h_{\tilde{\mu}(\delta)}(\tau) - (1 + \delta)\varepsilon - \sup \left\{ h_v(\tau) : v\tau\text{-invariant}, \right. \\ \left. \int \varphi dv = \Phi + \varepsilon \right\}. \tag{42}$$

Combining (40)–(42) applied with $\delta = \delta_1$ and 0, we obtain with $\Delta\mathcal{R} = \mathcal{R}(\delta_1) - \mathcal{R}(0)$ and $\Delta H = h_{\tilde{\mu}(\delta_1)}(\tau) - h_{\tilde{\mu}}(\tau)$

$$\Delta H - \delta\varepsilon \leq \Delta\mathcal{R} \leq \Delta H + \delta\varepsilon$$

and hence the desired result

$$\Delta H \Delta\mathcal{R} > 0$$

for sufficiently small ε .

Remark. It should be evident to the reader that the argument invoked to prove the fluctuation theorem does not appeal to the specific demographic constraints which

define the Leslie model. The argument should therefore apply to general non-linear dynamical systems described by the difference equation (2), provided that the system converges to a unique steady state in which condition (4) holds. Accordingly, the fluctuation theorem should also apply to demographic systems structured in terms of size, and to certain classes of ecological systems defined by non-negative transition matrices and characterizing dynamical systems defined by Eq. (2).

4. Numerical examples

We give a numerical example in order to illustrate the large deviation results. Let us consider the Leslie matrix

$$A = \begin{pmatrix} \frac{3}{4} & \frac{1}{2} \\ \frac{1}{2} & 0 \end{pmatrix}$$

and corresponding perturbations with $\delta = \pm 0.2$. Then r , Φ and H assume the following values:

δ	0	-0.2	0.2
$r(\delta)$	0	0.091	-0.889
$\Phi(\delta)$	-0.450	-0.370	-0.525
$H(\delta)$	0.450	0.461	0.436

Fig. 4 displays the corresponding rate functions $k_{\varphi(\delta)}$. These functions are convex functions of ε . The decay rate is given by the degree of convexity: The narrower the shape of the rate function, the larger are the values of $k_{\varphi(\delta)}(\Phi + \varepsilon)$ for ε close to 0, and, by (34), the faster is the decay rate \mathcal{R} of genealogies with large deviation from their expected behavior.

Since $k_{\varphi(\delta)}$ has the highest degree of convexity for $\delta = -0.2$ and the smallest one for $\delta = 0.2$, we expect from (29) that for most genealogies, $P_n(\varphi)(x)$, the deviation of the sample mean from the normalized average defined in (26), assumes smaller values in the case $\delta = -0.2$ than for $\delta = 0$, whereas for $\delta = 0.2$ it should assume larger values. We tested this by evaluating numerically $P_{1000}(\varphi)(x)$ and $P_{2000}(\varphi)(x)$ for a sample of 500 randomly chosen genealogies in either case. The results are shown in Figs. 5 and 6, respectively.

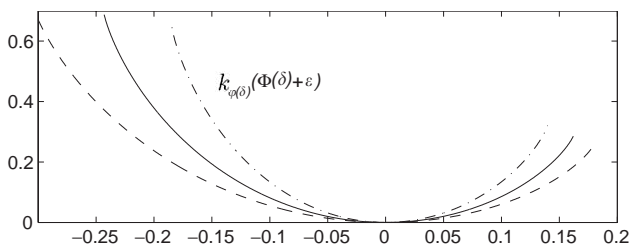


Fig. 4. Rate functions $k_{\varphi(\delta)}(\Phi(\delta) + \varepsilon)$ for $\delta = 0$ (solid), $\delta = -0.2$ (dashdot), and $\delta = 0.2$ (dashed).

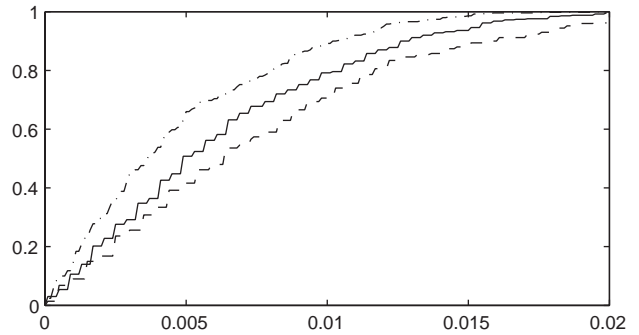


Fig. 5. Distribution function of $P_{1000}(\varphi)(x)$ with $\delta = 0$ (solid), $\delta = -0.2$ (dashdot), and $\delta = 0.2$ (dashed). The value at ε is the relative number of genealogies x with $P_{1000}(\varphi)(x) \leq \varepsilon$.

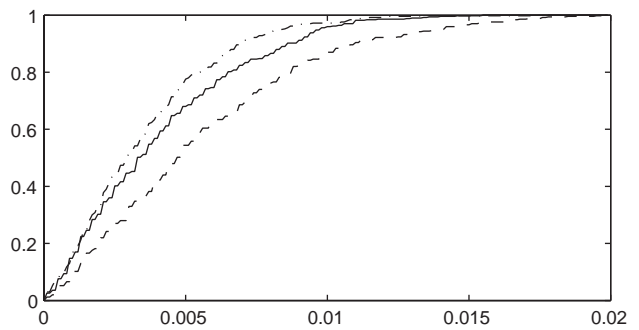


Fig. 6. Relative number of genealogies x with $P_{2000}(\varphi)(x) \leq \varepsilon$ with $\delta = 0$ (solid), $\delta = -0.2$ (dashdot), and $\delta = 0.2$ (dashed).

The curves show that for any ε between 0 and 0.02 the relative number of genealogies x with $P_n(\varphi)(x) < \varepsilon$ is larger the smaller the value δ . This means that the smallest fluctuation is achieved for small δ , the case where entropy assumes its largest value.

5. Evolution of demographic stability

The fluctuation theorem has an important implication for evolutionary dynamics. In earlier studies, Demetrius (1992), for deterministic models, and Arnold et al. (1994) for random matrix models, we studied the evolutionary changes in entropy under mutation and natural selection (directionality theory) and derived a set of principles relating ecological constraints with evolutionary changes in entropy. We will now appeal to the fluctuation theorem to derive equivalent principles relating ecological factors with evolutionary changes in stability.

There exists a large body of work, which goes back to studies by MacArthur (1962), that analyses the evolutionary dynamics of populations with *non-overlapping* generations—the *r-K* model—and postulates certain relations between ecological constraints and evolutionary trends in stability (see for example Mueller and Joshi, 2000). We will contrast directionality theory with

the r - K model. We will show that directionality theory, which pertains to populations with *overlapping* generations, subsumes the r - K model and thus provides a more coherent framework for analyzing the trends in stability observed in natural populations.

5.1. Directionality theory

Directionality theory integrates Mendelian genetics with demography to study changes in entropy in populations subject to different classes of ecological constraints, Demetrius (1992, 2000, 2001). The theory distinguishes between constraints defined in terms of the ecological forces the population experiences throughout its evolutionary history. These constraints can be analytically expressed, see (20), in terms of the reproductive potential Φ given by

$$\Phi = \frac{\sum p_j \log V_j}{\sum j p_j} \quad (43)$$

Here

$$\Phi = r - H,$$

where r is the population growth rate ($r \geq 0$), and H the entropy, which we will assume is positive.

The condition $\Phi < 0$ implies $r < H$ and defines what we will call *bounded growth*. This property refers to populations which are either stationary ($r = 0$), or are characterized by an exponential growth rate, which is bounded by entropy. This constraint is typical of ecological regimes described by limited but constant resources.

The condition $\Phi > 0$ implies $r > H$ and defines *unbounded growth*. Populations with this property are described by an exponential growth rate which exceeds entropy. The corresponding ecological regimes are defined by ample but only temporarily available resources.

Directionality theory considers evolution as a two step dynamical system involving (a) an invasion process—the invasion of a mutant in an incumbent population (a local event); (b) a selective process—the establishment of a mutant and its interaction with the incumbent population, subject to the existing ecological constraints (a global event). These two processes can be delineated as follows.

(a) The local event—this implicates two dynamical systems described by the interaction between the ancestral genotype A_1A_1 , and the mutant A_1A_2 . The outcome of this event, which occurs on a short time scale, is the invasion or extinction of the mutant allele.

(b) The global event—this will involve interaction between three dynamical systems defined by genotypes A_1A_1 , A_1A_2 and A_2A_2 ; the type A_2A_2 being generated by the Mendelian process, that is random mating between the types A_1A_1 and A_1A_2 .

The invasion dynamics: Studies of the local event in terms of diffusion processes, Demetrius and Gundlach (1999), Demetrius (2001), show that the condition for the invasion of a mutant allele is determined by entropy. The invasion criteria can be expressed in terms of constraints on the reproductive potential Φ and constraints on the population size, denoted N .

The constraint on population size includes both the reproductive potential Φ , defined by (43), and a new function of the distribution p_j and the net-reproduction variable V_j , which we call the correlation index and denote by γ (see Demetrius, 2001). Population size is said to be large, if $N > \gamma/\Phi$, and small if $N < \gamma/\Phi$.

The invasion-extinction conditions can be described in terms of the following series of implications:

- (A) *Bounded growth* ($\Phi < 0$):
 - (i) If $\Delta H > 0$, then mutant invades almost surely (a.s.),
 - (ii) If $\Delta H < 0$, then the mutant becomes extinct (a.s.).
- (B) *Unbounded growth* ($\Phi > 0$), *large population size* ($N > \gamma/\Phi$):
 - (i) If $\Delta H < 0$, then mutant invades (a.s.),
 - (ii) If $\Delta H > 0$, then the mutant becomes extinct (a.s.).
- (C) *Unbounded growth* ($\Phi > 0$), *large population size* ($N < \gamma/\Phi$):
 - (i) If $\Delta H < 0$, then mutant invades with a probability which is an increasing function of population size,
 - (ii) If $\Delta H > 0$, then the mutant becomes extinct with a probability which is an increasing function of size.

The selection dynamics: Studies of the global event which involves the interaction of the three genotypes subject to the existing ecological constraints, show that if ΔH denotes the change in entropy, induced by the invasion of a mutant type A_1A_2 , and $\tilde{\Delta H}$, the change in entropy which occurs as the population is driven to a new steady state described by the interaction of the three genotypes, we have (Demetrius, 1992)

$$\Delta H \tilde{\Delta H} > 0. \quad (44)$$

The invasion-extinction criteria can be integrated with (44) to derive correlations between ecological conditions, and the change in entropy as one population replaces another in the mutation-selection process. These correlations constitute the directionality principles for entropy, which we qualitatively annotate as follows:

we have

- (Ia) *Bounded growth constraints:* a uni-directional increase in entropy.

- (Ib) *Unbounded growth constraints (large population size)*: a uni-directional decrease in entropy.
- (Ic) *Unbounded growth constraints (small population size)*: random, non-directional change in entropy.

The directionality principle (Ia), (Ib), (Ic) represents changes in entropy as the population evolves from one steady state to the next under the mutation-selection process. These theorem pertain to *global* changes in the genotypic and phenotypic composition of the population. Hence the theorems are different in character from the fundamental theorem of natural selection (Fisher, 1980).

The fundamental theorem asserts that the mean fitness is equal to the genetic variance in fitness, which implies that the mean fitness increases. The mean fitness in this case describes the average viability of the genotypes within the population. Fisher’s theorem thus describes *local* changes in genotypic composition under viability selection and is of little consequence in understanding the long term changes in population composition under different ecological constraints.

We will integrate the directionality principles for entropy with the fluctuation theorem in order to analyze the influence of ecological constraints on evolutionary changes in demographic stability. Before we proceed to this new development we will illustrate certain empirical aspects of the directionality theory.

5.2. Demographic stability—evolutionary changes

We can now appeal to the directionality principles, together with the fluctuation theorem to predict evolutionary changes in demographic stability. The correspondence between ecological constraints and trends in demographic stability which the fluctuation theorem entails can be described in the following table.

If we restrict the analysis to large populations, we can appeal to Table 1 to predict two patterns of dependencies between ecological norms and trends in demographic stability. We have

- (IIa) Under bounded growth conditions, a situation typically induced by limited but constant resources, evolution will result in a uni-directional increase in demographic stability.

Table 1
Relation between ecological constraints and trends in demographic stability

Ecological constraints	Directional trends
Bounded growth	Increase in stability
Unbounded growth, large population size	Decrease in stability
Unbounded growth, small population size	Random, non-directional change in stability

- (IIb) Under unbounded growth conditions, a circumstance typically generated by ample but temporarily unavailable resources, evolution will result in a uni-directional decrease in demographic stability.

We will now contrast (II) with the related claims based on classical models of evolution such as *r-K* selection.

5.3. The *r-K* selection model

The correspondence between ecological norms and directional trends in stability expressed by Table 1 bears on certain hypotheses regarding the evolution of stability postulated by the *r-K* selection theory (MacArthur and Wilson, 1967).

The *r-K* theory, in its analytic incarnation, as distinct from its more qualitative claims, is concerned with the evolutionary dynamics of populations with non-overlapping generations. The theory revolves around the classification of populations in terms of ecological constraints defined by the effect of density on population dynamics. We have:

(A) *Density-independent growth*: This describes a population that grows exponentially at the rate *r* which is independent of population size.

(B) *Density-dependent growth*: This condition defines a population during its stationary phase when size is equal to the carrying capacity of the environment.

The MacArthur–Wilson model distinguishes between *r*-selected and *K*-selected populations and postulates, based on a variety of simple models, that evolution in *K*-selected systems will lead to an increase in stability (see Mueller and Joshi, 2000, Chapter 2 for an analysis of this literature).

As the comparative studies (documented in Mueller and Joshi) indicate, this stability postulate provides some qualitative insight into the relation between ecological constraints and demographic stability in laboratory populations. However, the *r-K* models fail to provide quantitative explanations of trends in life-history and the evolution of stability. This failure resides in the restrictive assumptions which underlie the *r-K* model.

The model embodies two main tenets:

(A) Under density-independent conditions, evolution acts to increase *r*.

(B) Under density-dependent conditions, evolution acts to increase *K*.

These two claims however only pertain to populations with non-overlapping generations. Claim (A), for example, derives from the proposition that the condition for invasion of a mutant allele under density-independent conditions is given by the population growth rate *r*. However, in the case of structured populations, the invasion condition only holds when size is effectively infinite (Demetrius and Gundlach, 1999). Claim (B)

issues from the hypothesis that selective advantage under density-dependent constraints is determined by the carrying capacity K . However, as the analysis in Charlesworth (1994) indicates, this hypothesis in the case of structured populations is only valid when the effect of density on the population dynamics is restricted to certain age categories.

Populations such as *Lucilia cuprina*, *Tribolium confusum* and *Drosophila melanogaster*, the species studied in Mueller and Joshi, are structured systems defined by a high degree of variability in age-specific fecundity and mortality. In view of this demographic heterogeneity, studies of the evolution of stability based on the r - K model become invalid to quantitatively explain the trends in population composition documented by Nicholson (1957), (Lucilia), King and Dawson (1972), (Tribolium), Mueller and Huynh (1994) (Drosophila).

5.4. Directionality theory and r - K selection

The limitations which define the r - K model do not attend directionality theory. Directionality theory is concerned with the evolution of structured populations. It classifies populations in terms of ecological constraints bounded growth ($\Phi < 0$, $0 \leq r \leq H$), and unbounded growth ($\Phi > 0$, $r > H$). It is a stochastic theory which analyses the evolution of life-history variation under these two constraints and shows that evolutionarily stable states can be characterized in terms of extremal states of entropy. The r - K model is concerned with populations without demographic variability. It classifies populations in terms of two ecological constraints: stationary growth ($r = 0$) and exponential growth ($r > 0$). It is a deterministic theory which analyses the dynamics of evolution under these constraints and shows that evolutionary stable states can be characterized by states which maximize the parameters K and r respectively under the different ecological conditions.

The quantity Φ , the reproductive potential is an index of the demographic variability of the population. Here

$$\Phi = r - H.$$

Hence when $\Phi = 0$, a condition which can be used to describe demographic homogeneity or absence of age structure, the quantities r and H coincide. The r - K model, which defines demographically homogeneous populations can therefore be considered the singular limit ($\Phi \rightarrow 0$) of directionality theory. Directionality theory thus provides a more general framework for understanding the dynamics of life-history and the evolution of stability in natural populations.

The contrast between the two theories and their predictions are expressed in Table 2.

Table 2
Directionality theory and the r - K model: a contrast

Evolutionary property	Directionality theory	r - K model
<i>Ecological constraint</i>	Bounded growth ($\Phi < 0$), unbounded growth ($\Phi > 0$)	Stationary growth ($r = 0$), exponential growth ($r > 0$)
<i>Measure of fitness</i>	Entropy H	Growth rate r
<i>Evolutionarily stable states</i>	Extremal states of entropy maximal entropy ($\Phi < 0$), minimal entropy ($\Phi > 0$)	Maximal values for K ($r = 0$), maximal values for growth rate ($r > 0$)

6. Conclusion

The notion that complex demographic systems are stable has emerged as a unifying thesis as a result of qualitative arguments and numerical analysis of simple models during the last three decades. Complexity was roughly defined as the degree of iteroparity of the population. Stability was even more roughly understood as the ability to recover from a perturbation or as the average level of fluctuations in population numbers. This article has provided a precise analytical structure to these notions and used this as a basis for elucidating the complexity-stability hypothesis in structured populations. In this new model complexity is characterized by entropy, a precise index of the degree of iteroparity of the population. Stability is formalized in terms of the rate of decay of fluctuations in population numbers. This article has appealed to new mathematical methods to establish a fluctuation theorem: changes in entropy are positively correlated with changes in fluctuation decay rate. The implications of the fluctuation theorem towards an understanding of the evolution of demographic stability has also been analyzed. By integrating the fluctuation theorem with directionality theorems which predict changes in entropy under different ecological constraints, we establish the following principles:

- (1) A uni-directional increase in stability in populations subject to bounded growth constraints,
- (2) A uni-directional decrease in stability in large populations subject to unbounded growth constraints,
- (3) Random, non-directional changes in stability in small populations subject to unbounded growth constraints.

The fluctuation theorem and the directionality principles for demographic stability as expressed by (1)–(3) underscore the general significance of entropy as a unifying concept in demographic and ecological studies.

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