

A unifying framework for chaos and stochastic stability in discrete population models

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Abstract. In this paper we propose a general framework for discrete time one-dimensional Markov population models which is based on two fundamental premises in population dynamics. We show that this framework incorporates both earlier population models, like the Ricker and Hassell models, and experimental observations concerning the structure of density dependence. The two fundamental premises of population dynamics are sufficient to guarantee that the model will exhibit chaotic behaviour for high values of the natural growth and the density-dependent feedback, and this observation is independent of the particular structure of the model. We also study these models when the environment of the population varies stochastically and address the question under what conditions we can find an invariant probability distribution for the population under consideration. The sufficient conditions for this stochastic stability that we derive are of some interest, since studying certain statistical characteristics of these stochastic population processes may only be possible if the process converges to such an invariant distribution.

Key words: Markov processes – Population dynamics – Chaos – Invariant measures – Recurrence

1 Introduction

One of the most fundamental recent discoveries in theoretical ecology is the possibility of extremely complex dynamics in even the simplest single-species population models [10]. The phenomena were labelled ‘chaotic’ by applied mathematicians but since ecologists failed to observe them in natural populations [5], interest in chaotic dynamics in ecology has only recently revived. New methods in time-series analysis and the theory of chaos itself have been responsible for this. There is now a rather extensive theory on chaos in population models and several tests to check whether a sample obtained from

such a model is indeed chaotic, with the estimation of so-called Lyapunov exponents as one of the most famous examples. For details see the excellent overview by Hastings et al. [6]. As is correctly pointed out in their paper, one of the most important shifts in the theoretical approach to population models is eliminating the assumption that the processes we observe in nature are mere transitions to stable equilibria of some underlying model, and thus insensitive to initial population properties in the long run. In chaotic systems populations which are 'almost the same' in the beginning may show very different behaviour in the long run and it is exactly this sensitive dependence on initial conditions which makes them harder to study. Methods like Lyapunov exponent estimation try to measure this sensitivity and thus provide a method to demonstrate the existence of chaotic dynamics in a population process.

However, most of these methods simply use time-series analysis without any underlying model structure, or just look at one particular model with one particular set of parameter values obtained from field data. Both strategies avoid the more fundamental question if ecological population models are *intrinsically* chaotic or whether just some of the samples obtained are chaotic. It has been observed already that the dynamic behaviour of certain time-series models depend critically on the parameter values used in the model [13], thus making it impossible to analyse those samples which can be modelled by a set of parameter values which are 'close' in the parameter space but predict fundamentally different behaviour. Of course, in practice all estimated parameter values will contain measurement errors.

This observation is particularly important since in most models some parameters, especially the ones which describe the influence of an environment on the population, vary around a certain fixed value in a stochastic way. This poses another, related problem since large scale stochastic simulations have to be used to study these variations but it is not clear on beforehand (and in some cases indeed not true) that these simulation results are valid, unless some 'stochastic stability' conditions are met. While chaotic processes can be characterised as processes which are predictable on a small time scale (since they are deterministic) but unpredictable on a larger time scale (since they are extremely sensitive to initial values), stochastically stable processes can be characterised as processes which are unpredictable on every time scale, but whose statistical properties converge to stationary values which can then be found by appropriate measurements. Therefore certain simulation studies, as carried out extensively by many ecologists, can only be validated when it is rigorously proven that the underlying models are stochastically stable. Otherwise, simulations are used to obtain constant estimates for properties which are not constant in time at all. Some of these questions for stochastic population models have been addressed earlier [2, 3] but stochastic stability has not been treated there, and the results are only valid for one particular model due to Ricker [14].

In this paper we try to show that both chaos and stochastic stability are intrinsic characteristics of population models by providing a framework for these models which is the most general possible considering two fundamental

first principles of population models. This framework will be presented in Sect. 3, after discussing some earlier population models in the next section. We then show in Sect. 4 that every model which satisfies these two first principles will show chaotic behaviour if the natural growth and the density-dependent feedback are strong enough, *irrespective of the particular model under consideration*. This proves that within our framework, chaos in discrete population models is a consequence of the first principles in ecology and not of a certain particular model structure or parameter value. In Sect. 5 we introduce the stochastic extension of our framework and in Sect. 6 we then derive the sufficient conditions for these stochastic models to be stochastically stable, thus showing in which cases measurement and estimation of statistical properties in stochastic ecological models can be guaranteed to be possible. In Sect. 7 we discuss the speed of convergence of the distribution functions in stochastic models. Some numerical examples illustrating our results are given in Sect. 8 and we end with some conclusions.

2 Earlier population models

In [4] Hassell has introduced a systematic approach to the development of so-called density-dependent population models for a single species of the form

$$N_{t+1} = g(N_t)$$

Here N_t represents the population size at time t and g is a known function which is usually assumed to be continuous. Hassell argued that these population models should be based on two fundamental premises:

- (P1) The population should have the *potential* to increase exponentially for small populations
- (P2) There should be a density-dependent feedback which reduces the *actual* rate of increase as the population grows

Ecologists usually look at the ‘mortality’ as a measure of this density-dependent feedback, which is characterised by the following *density dependence function*:

$$\ln N_t \rightarrow \ln \frac{N_t}{N_{t+1}} \quad (2.1)$$

In experimental data [4] it is often found that there is a pronounced density-dependence for large N_t which becomes negligible as N_t decreases, and that the density-dependence for large N_t is characterised either by a fixed slope b (in so called *contest models*) or that this slope increases rapidly with increasing N_t (in *scramble models*). A simple linear contest model describing this situation is for example

$$\ln \frac{N_t}{N_{t+1}} = -\ln r + b \ln N_t \quad (2.2)$$

with $r > 1$ and $b > 1$, resulting in

$$N_{t+1} = rN_t^{(1-b)}$$

Clearly this model is not very realistic for small populations since it predicts that

$$\lim_{N_t \rightarrow 0} N_{t+1} = \infty$$

which means that for very small populations there is an infinite capacity to grow. A simple correction, as proposed in [16] is:

$$N_{t+1} = \begin{cases} r\lambda N_t^{(1-b)} & N_t > N_c \\ \lambda N_t & N_t \leq N_c, \end{cases} \quad (2.3)$$

with $\lambda > 1$ a constant and N_c a critical population value. This means that there is either density-dependence as before for populations which are larger than the critical population, or exponential growth for populations which are smaller than the critical population. However, this model is not smooth at N_c and has some other properties which are unsatisfactory from an ecological point of view [4].

Two famous examples exist of models which 'smoothen' this model. The first one is the *Hassell model* [4]:

$$N_{t+1} = \frac{rN_t}{(1 + N_t)^b}$$

with $r > 1$ and $b > 1$. It is clear that for this model

$$N_{t+1} \approx \begin{cases} rN_t & N_t \approx 0 \\ rN_t^{(1-b)} & N_t \gg 0 \end{cases}$$

and it can thus indeed be interpreted as a smoothed version of model (2.3). Note that the density dependence function is given by

$$\ln \frac{N_t}{N_{t+1}} = -\ln r + b \ln(1 + N_t)$$

which means that the density dependence relation (2.1) will be approximately linear with fixed slope b for large N_t . As mentioned before, we also need *scramble* models in which this slope increases rapidly as the population N_t increases. An example of such a model is due to *Ricker* [14]:

$$N_{t+1} = rN_t e^{-bN_t}$$

It satisfies

$$\ln \frac{N_t}{N_{t+1}} = -\ln r + b e^{\ln N_t}$$

so the density dependence increases exponentially when N_t goes to infinity. Remark that in all these models r represents the exponential growth factor for very small populations, the *natural* growth in ideal circumstances, and b the density-dependent feedback because of limited environmental conditions.

3 A general deterministic population model

In order to smoothen the model (2.3) we propose a more general one:

$$\ln \frac{N_t}{N_{t+1}} = -\ln r + b \ln f(N_t) \tag{3.1}$$

with $r > 1, b > 0$ and in which the function $f: [0, \infty[\rightarrow \mathbb{R}$ is called the density function. We require it to satisfy:

- (A1) $f: [0, \infty[\rightarrow \mathbb{R}$ is strictly positive and continuously differentiable on its domain.
- (A2) $f(0) = 1$
- (A3) The function $L: [0, \infty[\rightarrow \mathbb{R}$ defined by $L(x) = x f'(x)/f(x)$ is strictly increasing.

Condition (A1) guarantees that the transitions are indeed smooth. Condition (A2) makes sure that the model satisfies the first fundamental assumption in ecological models (P1): for small populations exponential growth should be possible

$$N_t \approx 0 \Rightarrow N_{t+1} \approx rN_t$$

Remark that it can always be satisfied by choosing suitable r and b , as long as $r > 1, b > 0$. The last condition (A3) represents the second fundamental assumption in population models (P2). It guarantees that for $b > 0$ the density dependence increases for increasing population size since the slope of the density is:

$$\begin{aligned} \frac{d \ln N_t/N_{t+1}}{d \ln N_t} &= \frac{d b \ln f(N_t)}{d \ln N_t} = b \frac{d \ln f(e^{\ln N_t})}{d \ln N_t} \\ &= \frac{b}{f(e^{\ln N_t})} f'(e^{\ln N_t}) e^{\ln N_t} \\ &= b \frac{N_t f'(N_t)}{f(N_t)} = b L(N_t) \end{aligned}$$

As mentioned in the preceding section, models with $\lim_{x \rightarrow \infty} L(x) < \infty$ are usually called *contest models* while models where L has no finite limit are called *scramble models*. We will see that there is an important difference between the two types when we consider stochastic perturbations of the models.

Note that the Hassell model and the Ricker model are both special cases of our general framework, with $f(x) = 1 + x$ and $f(x) = e^{-x}$ respectively. The first one is a typical contest model and the second one a typical scramble model. Also remark that the linear model (2.2) does not belong to our class of models since it violates the second condition: it does not permit exponential growth for small population sizes.

Our general model can be rewritten in the transition form

$$N_{t+1} = F_{r,b}(N_t) := rN_t [f(N_t)]^{-b} \quad (3.2)$$

which clearly shows the capacity for exponential growth (with exponential growth factor $r > 1$) and the density-dependent feedback that reduces growth (and of which the intensity is characterised by the positive parameter b). The model (3.1) together with the conditions on f can thus be seen as a general population model for non overlapping generations which unifies models like the Hassell and Ricker models, taking into account the premises of ecological population models and the experimental observations on density-dependence (see for example [4]).

In the following lemma some elementary but useful properties of the functions f satisfying (A1)–(A3) and $F_{r,b}$ are derived, that will be needed later on.

Lemma 3.1. *All f satisfying (A1)–(A3) and $F_{r,b}$ as defined in equation (3.2) derived from these satisfy:*

1. f is strictly increasing and $f(x) \geq 1$ for all $x \geq 0$.
2. There exists a $\hat{b} > 0$ such that for all $b > \hat{b}$, the function $F_{r,b}(x)$ has a unique maximal value $F_{r,b}(a)$ in $x = a$. The point a does not depend on r .
3. For all $x_0 > 0$ and $x \geq x_0$:

$$f(x) \geq f(x_0) \cdot \left(\frac{x}{x_0}\right)^{L(x_0)} \quad (3.3)$$

4. If the function L has a finite limit $\bar{L} = \lim_{x \rightarrow \infty} L(x)$ then also for all $x_0 > 0$ and $x \geq x_0$:

$$f(x) \leq f(x_0) \cdot \left(\frac{x}{x_0}\right)^{\bar{L}} \quad (3.4)$$

5. For all $x > 0$:

$$\ln f(e^x) \leq f(1) - 1 + xL(e^x) \quad (3.5)$$

6. For all $x_0 > 0$ and $x > x_0$:

$$\ln f(e^x) \geq \ln f(x_0) + xL(x_0) - L(x_0) \ln x_0 \quad (3.6)$$

7. If the function L has a finite limit $\bar{L} = \lim_{x \rightarrow \infty} L(x)$ then

$$\lim_{x \rightarrow \infty} x^{-1} \ln f(e^x) = \bar{L}$$

Proof. 1. Since $L(0) = 0$ and $L(x)$ is strictly increasing, we have $L(x) > 0$ for $x > 0$ and since f is strictly positive, condition (A3) implies that f' is strictly positive. Therefore $f(x) \geq f(0) = 1$.

2. Since

$$F'(x) = rf(x)^{-b} \left[1 - bx \frac{f'(x)}{f(x)} \right] = rf(x)^{-b} [1 - bL(x)]$$

a critical point a must satisfy $L(a) = \frac{1}{b}$, and must be a maximum. Since L is strictly increasing because of (A3) and independent of r , taking $\hat{b} > 1/L(1)$ gives the result.

3. & 4. We have

$$\int_{x_0}^x \frac{f'(s)}{f(s)} ds = \int_{x_0}^x \frac{L(s)}{s} ds$$

for all $x_0 > 0$ by definition, and for $x \geq x_0$ condition (A3) implies

$$L(x_0) \leq L(x) \leq \bar{L}$$

so the results follow easily.

5. Since $\ln f(0) = 0$ we have

$$\ln f(e^x) = \int_0^{e^x} \frac{f'(s)}{f(s)} ds = \int_0^1 \frac{f'(s)}{f(s)} ds + \int_1^{e^x} \frac{f'(s)}{f(s)} ds \tag{3.7}$$

Because of the first part of the lemma we find

$$\int_0^1 \frac{f'(s)}{f(s)} ds \leq \int_0^1 f'(s) ds = f(1) - f(0) = f(1) - 1$$

and for the second integral

$$\int_1^{e^x} \frac{f'(s)}{f(s)} ds = \int_1^{e^x} \frac{L(s)}{s} ds = \int_0^x L(e^\tau) d\tau \leq xL(e^x) \tag{3.8}$$

where we have used condition (A3) in deriving the last inequality.

6. Follows immediately from 3. by the substitution $x = e^y$ after taking the logarithm of both sides.

7. We use de l'Hospital's rule:

$$\lim_{x \rightarrow \infty} \ln f(e^x)/x = \lim_{x \rightarrow \infty} f'(e^x)e^x/f(e^x) = \lim_{x \rightarrow \infty} L(e^x) = \bar{L} \quad \square$$

Corollary 3.1. *Every population model of the form (3.1), with $b > 0$ and f satisfying conditions (A1)–(A3), has a unique equilibrium population.*

Proof. An equilibrium population N^* satisfies $N^* = F(N^*)$ or $f(N^*) = r^{1/b} > 1$ and since the lemma implies that f is strictly increasing with $f(0) = 1$ and $\lim_{x \rightarrow \infty} f(x) = \infty$, this shows that there exists a unique N^* satisfying this equation. \square

4 Chaos in deterministic population models

It has been established for a long time that very simple Markovian population models can exhibit extremely complex behaviour, which is labelled chaotic by mathematicians [10, 11]. A number of definitions are available for chaos in dynamic systems and for many population models it has been proven that these definitions apply. An interesting problem in the theory of population

dynamics is therefore the question if the concept of chaos depends on the precise details of the model under consideration, or that it represents a structural property. More precisely: if we have two population models of the form

$$N_{t+1} = g(N_t)$$

(with N_t the population at time t) and the functions g have roughly the same shape, we want them to be *both* chaotic or *both* not chaotic: we want chaos to be an intrinsic property which does not depend on small variations in the model. We will show that this can indeed be proven for the most popular definition of chaos in ecology.

Definition 4.1. *A population model $N_{t+1} = g(N_t)$ is called chaotic if it has periodic cycles of all integer periods:*

$$(\forall k \in \mathbb{N}^*) (\exists p \in \mathbb{R}^+) \quad N_0 = p \Rightarrow N_k = p, \quad N_i \neq p \quad (1 \leq i \leq k - 1)$$

and there exists an uncountable subset $M \subset \mathbb{R}^+$ such that

1. M is invariant: $N_t \in M \Rightarrow N_{t+1} \in M$
2. There exists a $\delta > 0$ such that for all $N_0, N'_0 \in M$ with $N_0 \neq N'_0$ we have

$$\limsup_{t \rightarrow \infty} |N_t - N'_t| \geq \delta$$

$$\liminf_{t \rightarrow \infty} |N_t - N'_t| = 0$$

In fact, this is only one of the many possible definitions of chaos. For a discussion on this particular one and its advantages over other definitions like the one by Devaney [1] when interpreted from an ecological point of view, see [17, 18]. The surprising result for our class of models is that they will always be chaotic if the parameters r and b are chosen large enough.

Theorem 4.1. *For every population model of the form (3.1) with a density f satisfying assumptions (A1)–(A3), there exists a $\bar{b} > 0$ such that for $b > \bar{b}$ and $r > \bar{r}(b)$ the model is chaotic.*

Proof. The famous result in [9] states that we only have to prove that \bar{b} and $\bar{r}(b)$ exist such that for $b > \bar{b}$ and $r > \bar{r}(b)$ there exists a point q with

$$F^3(q) < q < F(q) < F^2(q) \tag{4.1}$$

Because of Lemma 3.1 we know that we can find a \hat{b} such that for $b > \hat{b}$ the function F has a unique maximal value $F(a)$ with a independent of r . We take $\bar{b} > \max\{1, \hat{b}, 3/L(1)\}$. Now

$$F(x) = rx[f(x)]^{-b} \leq rx \tag{4.2}$$

because of the first part of Lemma 3.1, so the inverse $F^{-1}(x)$, which is well-defined on $[0, a[$ since $F'(x) > 0$ on this interval, satisfies $F^{-1}(x) \geq x/r$ there. If we take $r > \tilde{r} = f(a)^b$ we have $F(a) > a$ and since $F(0) = 0 < a$ the Intermediate Value Theorem guarantees that there exists a q between 0 and a such that $F(q) = a$. Thus, $q = F^{-1}(a)$ and therefore $a/r \leq q$. But

$q < a = F(q)$ and since $F(a)$ was the unique maximum of F , we also have $F(q) < F(a) = F^2(q)$. Thus

$$\frac{a}{r} \leq q < F(q) < F^2(q)$$

and we only have to prove that $F^2(a) < a/r$ since then

$$F^3(q) = F^2(a) < \frac{a}{r} \leq q$$

and equation (4.1) is satisfied, proving the theorem. Remark that the first and third part of of Lemma 3.1 imply (substituting $x_0 = 1$) that

$$f(x) \geq x^{L(1)} \quad (x \geq 1)$$

so if we choose $\bar{r}(b) > 1/a f(a)^b$ then $f(F(a)) \geq F(a)^{L(1)}$. But then

$$\begin{aligned} F^2(a) &= rF(a)[f(F(a))]^{-b} \\ &\leq r(raf(a)^{-b})(raf(a)^{-b})^{-bL(1)} \\ &\leq \frac{a}{r} r^{3-bL(1)} a^{-bL(1)} f(a)^{L(1)b^2-b} \end{aligned}$$

We took $b > \bar{b} > 3/L(1)$ and since a is independent of r we can now choose

$$\bar{r}(b) > \max \left\{ \bar{r}, \frac{1}{a} f(a)^b, f(a)^{(L(1)b^2-b)/(L(1)b-3)} a^{(-bL(1))/(bL(1)-3)} \right\}$$

to make $F^2(a) < a/r$ for $r > \bar{r}(b)$. This proves the theorem. □

We may thus conclude that our general model not only unifies the two main principles of ecology and experimental observations, but also guarantees that chaotic behaviour occurs in this model when natural reproduction and environmental feedback are strong enough.

5 Population models with a stochastic environment

We have seen that the general population model (3.1) has two free parameters once the function f has been specified: a *natural growth* parameter $r > 1$ which is the exponential growth factor in an ideal environment, and an environmental parameter b which represents the rate of density-dependent feedback of the environment. We now want to consider population models in which the environment (that is, the parameter b) varies *stochastically*. That is, we now take

$$N_{t+1} = F_{r, \zeta_t}(N_t) = \frac{rN_t}{f(N_t)^{\zeta_t}} \tag{5.1}$$

in which $N_0 > 0$ can be chosen freely and $\{\xi_t | t \in \mathbb{N}\}$ is a set of independent identically distributed random variables with a distribution function which satisfies some mild conditions that will be specified later on. Remark that this implies that $\{N_t | t \in \mathbb{N}\}$ is a stochastic Markov process. We will denote the probability space for this process by (Ω, \mathcal{F}, P) with Ω the sample space, \mathcal{F} an appropriate σ -field and P the probability measure. We use the notation $\mathbb{P}(A) = P(\{\omega | A(\omega)\})$ and take the symbol $X \sim \pi$ to state that the stochastic variable X has probability distribution π . The symbol \mathbb{E} denotes the usual expectation operator. The indicator function of a set A will be denoted by $\mathbf{1}_A$; it has the value one on A and the value zero outside A .

We will now address the question under what conditions there exists an invariant distribution π , that is, a distribution satisfying

$$N_t \sim \pi \Rightarrow N_{t+1} \sim \pi$$

It is easy to see that an initial distribution of this kind does not change in time and it is therefore important when we are interested in the limiting behaviour of our stochastic population process. The invariant distribution represents a 'stochastic equilibrium' and if the probability distribution of the process converges to a stationary distribution, this distribution has to be invariant. Moreover, studying certain statistical properties of the distribution function of the population only makes sense if the distribution is stationary in time.

We will now state some preliminary results on discrete time Markov processes on a continuous state space that we will need in the sequel. All results are stated without proofs. These can be found in standard text books about the theory of Markov processes, for example [15] or the references in [2, 3]. We are interested in transition probabilities

$$\mathbb{P}(N_t \in A | N_0 = x)$$

for $x \in]0, \infty[$ and A a Borel-set. When the distribution of the noise $\{\xi_t | t \in \mathbb{N}\}$ has a positive density everywhere on \mathbb{R}^+ , we have

$$\mathbb{P}(N_t \in A | N_0 = x) = \int_A p_t(\tau | x) d\tau$$

with $p_t(\tau | x)$ the t -step transition density which is strictly positive for all values of x and $\tau \in]0, x t^d[$. This implies that the process is *Lebesgue-irreducible*: every set in the state space with positive Lebesgue-measure can be reached from any initial value N_0 . Furthermore, we may conclude that the process is *aperiodic*: there are no cyclic subsets in the state space. For g a bounded measurable function on the state space, the mapping

$$g \rightarrow \mathbb{E}[g(N_1) | N_0 = x]$$

is called the *transition probability operator* of the process. Under our assumptions, the transition probability operator maps bounded continuous functions to bounded continuous functions.

An irreducible Markov process is called *recurrent* if the expectation of the number of returns to A is infinite:

$$\sum_{t=1}^{\infty} \mathbb{P}(N_t \in A | N_0 = x) = \infty$$

for all sets A with positive Lebesgue-measure. Otherwise the process is called *transient*. Every recurrent process has a σ -finite invariant measure π , satisfying

$$\pi(A) = \int_{\mathbb{R}^+} \mathbb{P}(N_t \in A | N_0 = x) \pi(dx)$$

for any Borel set A . If the measure π is finite:

$$\int_{\mathbb{R}^+} \pi(dx) < \infty$$

and we can therefore make it a probability measure by normalising it, the process is called *positively recurrent*, otherwise it is called *null-recurrent*. In the latter case there exists at least one set A with positive Lebesgue-measure such that

$$\lim_{n \rightarrow \infty} \frac{1}{n} \sum_{t=1}^n \mathbb{P}(N_t \in A | N_0 = x) = 0$$

A further consequence is that the process returns to A so rarely that the expectation of the *first return time*, defined by

$$T_A = \min \{t > 0 | N_t \in A\}, \quad (N_0 \in A)$$

is infinite. If the process $\{N_t | t \in \mathbb{N}\}$ is irreducible and positively recurrent then the invariant measure π is unique and $\pi(A) > 0$ for all A with positive Lebesgue-measure. In this case T_A has finite expectation.

It is clear from these results that it is interesting from a biological point of view to know if a certain biological process is positively recurrent or not: if we are interested in an invariant probability measure, we must first prove positive recurrence. We will use the following theorem to obtain results for our class of stochastic population models (see [12, 15]):

Theorem 5.1. *Suppose that a Markov process $\{X_t | t \in \mathbb{N}\}$ is Lebesgue-irreducible and that its one step transition probability maps continuous functions to continuous functions. If there exists a compact set K , an $\varepsilon > 0$, $C > 0$ and a function V such that*

1. $(\forall x \in \mathbb{R}) \quad V(x) \geq 0$
2. $(\forall x \in K^c) \quad \mathbb{E}[V(X_1) | X_0 = x] - V(x) < -\varepsilon$
3. $(\forall x \in K) \quad \mathbb{E}[V(X_1) | X_0 = x] \leq C$

then the process $\{X_t | t \in \mathbb{N}\}$ is positively recurrent.

The conditions of this theorem are called *mean drift conditions* and they roughly state that the process $V(X_t)$ is a supermartingale outside some compact set, with an expectation which decreases uniformly. The function V is often called a *Stochastic Lyapunov Function*. Note that the Lyapunov function is not required to be continuous.

6 Sufficient conditions for stationarity

Using the results of the last section we will now give sufficient conditions for the stochastic population models to have an invariant probability measure. We will assume, as stated earlier, that the model has the form

$$N_{t+1} = F_{r,\zeta_t}(N_t) = \frac{rN_t}{f(N_t)^{\zeta_t}} \tag{6.1}$$

and that the following conditions are satisfied:

- (B1) $N_0 > 0$ (initial population not trivial) and $r > 1$ (there is natural growth)
- (B2) $\{\zeta_t | t \in \mathbb{N}\}$ are independent identically distributed stochastic variables with finite first and second order moments
- (B3) the random variables $\{\zeta_t | t \in \mathbb{N}\}$ have an absolutely continuous distribution, with a probability density which is positive on the whole \mathbb{R}^+

Under these assumptions, the transition probability operator maps continuous functions to continuous functions. Indeed, if g is a bounded continuous function on \mathbb{R}^+ and ϕ is the distribution of the noise ζ then

$$\mathbb{E}[g(N_1) | N_0 = x] = \int_{\mathbb{R}} g(rxf(x)^{-\zeta})\phi(d\zeta)$$

and this is continuous in x by Lebesgue’s dominated convergence theorem, since f is continuous.

Our result is split into two separate theorems, one for the contest models and one for the scramble models, since the analysis for these two cases is different.

Theorem 6.1. *Consider the stochastic process given by (6.1) satisfying conditions (B1)–(B3) and with the function f satisfying conditions (A1)–(A3). If*

$$\lim_{x \rightarrow \infty} L(x) = \bar{L} < \infty$$

and

$$\mathbb{E}((1 - \bar{L}\zeta_t)\mathbf{1}_{\{\zeta_t \leq 1/\bar{L}\}}) < 1 \tag{6.2}$$

then there exists a unique invariant probability distribution π on \mathbb{R}^+ for this process.

Proof. Define the process $Y_t = \ln N_t$, then we have that $\{Y_t | t \in \mathbb{N}\}$ is positively recurrent if and only if $\{N_t | t \in \mathbb{N}\}$ is positively recurrent, and obviously

$$Y_{t+1} = Y_t + \ln r - \zeta_t \ln f(e^{Y_t}) \tag{6.3}$$

Since the probability density is positive on the whole \mathbb{R}^+ and $\ln r > 0$ the process is irreducible. We will therefore prove that the function $V: \mathbb{R} \rightarrow \mathbb{R}^+$ defined by

$$V(y) = \begin{cases} y & y \geq 0 \\ -ay & y < 0 \end{cases}$$

with $a > 0$ a suitably chosen constant that we will specify later on, is a Lyapunov function for the process $\{Y_t\}$. We introduce the functions

$$B(y) = \frac{y + \ln r}{\ln f(e^y)}$$

and

$$p(y) = \mathbb{P}(\zeta_t \leq B(y)) = \mathbb{P}(Y_{t+1} \geq 0 | Y_t = y)$$

Because of Lemma 3.1 we have

$$\lim_{y \rightarrow \infty} B(y) = 1/\bar{L} \tag{6.4}$$

It is also easy to establish that we must have

$$\lim_{y \rightarrow -\infty} p(y) = 0 \tag{6.5}$$

Evaluating the expected growth of V in a point y we find

$$\begin{aligned} \mathbb{E}[V(Y_1) | Y_0 = y] - V(y) &= \mathbb{E}(y + \ln r - \zeta_t \ln f(e^y)) \mathbf{1}_{\{\zeta_t \leq B(y)\}} \\ &\quad + \mathbb{E}(-ay - a \ln r + a \zeta_t \ln f(e^y)) \mathbf{1}_{\{\zeta_t > B(y)\}} - V(y) \end{aligned}$$

Rearranging terms gives

$$\begin{aligned} \mathbb{E}[V(Y_1) | Y_0 = y] - V(y) &= (y + \ln r)p(y) - (\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t \leq B(y)\}}) \ln f(e^y) \\ &\quad + (-ay - a \ln r)(1 - p(y)) \\ &\quad + a(\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}}) \ln f(e^y) - V(y) \end{aligned} \tag{6.6}$$

Now for $y \ll 0$ the first term will become equal to or smaller than zero because of (6.5), the second and the fourth term both go to zero since $\ln f(e^y) \rightarrow 0$ as $y \rightarrow -\infty$ and the expectations have upper bounds which do not depend on y . The third term is asymptotically equal to $-ay - a \ln r$ and the last term is equal to $-(-ay) = ay$. Therefore we have

$$\mathbb{E}[V(Y_1) | Y_0 = y] - V(y) < -\frac{1}{2} a \ln r, \quad (y \ll 0) \tag{6.7}$$

For $y \gg 0$ we find, using equation (6.6) and the fact that in this case $V(y) = y$, that

$$\begin{aligned} \mathbb{E}[V(Y_1)|Y_0 = y] - V(y) &= ay \left(p(y) - 1 + \frac{\ln f(e^y)}{y} \mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}} \right) \\ &\quad + y \left(p(y) - 1 - \frac{\ln f(e^y)}{y} \mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t \leq B(y)\}} \right) \\ &\quad + p(y) \ln r - a(1 - p(y)) \ln r \end{aligned}$$

The last two terms have an upper bound which is independent of y . Because of dominated convergence and Lemma 3.1 the bracketed expression in the second term will converge as $y \rightarrow \infty$:

$$p(y) - 1 - \frac{\ln f(e^y)}{y} \mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t \leq B(y)\}} \xrightarrow{y \rightarrow \infty} \mathbb{E}(1 - \bar{L}\zeta_t) \mathbf{1}_{\{\zeta_t \leq 1/\bar{L}\}} - 1$$

which implies, because of (6.2) that for y big enough, the second term will be smaller than $-v|y|$ for some $v > 0$. Analogously, the bracketed expression in the first term converges according to the dominated convergence theorem:

$$p(y) - 1 + \frac{\ln f(e^y)}{y} \mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}} \xrightarrow{y \rightarrow \infty} -\mathbb{P}(\zeta_t > 1/\bar{L}) + \bar{L}\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > 1/\bar{L}\}}$$

so for y sufficiently large it will become smaller than the positive value $D := \bar{L}\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > 1/\bar{L}\}}$. Therefore, if we take $a < \frac{1}{2}v/D$, the first term will become smaller than $vy/2$, and therefore we find for the total in (6.6):

$$\mathbb{E}[V(Y_1)|Y_0 = y] - V(y) < \hat{C} - \frac{1}{2}vy \tag{6.8}$$

for y big enough, with \hat{C} a constant which is independent of y . Taking (6.7) and (6.8) together we see that there exist positive y_1, y_2 such that if we take $K = [-y_1, y_2]$ we have for $y \in \mathbb{R} \setminus K$:

$$\mathbb{E}[V(Y_1)|Y_0 = y] - V(y) < -\varepsilon$$

with

$$\varepsilon = \min \left\{ \frac{1}{2}vy_2 - \hat{C}, \frac{1}{2}a \ln r \right\}$$

This shows that the conditions of Theorem 5.1 are satisfied since it is easy to see, using (6.6), that for every $y \in K$ we have

$$\mathbb{E}[V(Y_1)|Y_0 = y] \leq y_2 + \ln r + (1 + a) |\mathbb{E}\zeta_t| \ln f(e^{y_2}) + ay_1 := C$$

The result now follows from Theorem 5.1. □

We have thus found a sufficient condition for the existence of a stationary distribution in contest models. Remark that this condition will automatically be satisfied if the probability density of the environment ζ_t is taken small enough (or even zero) for negative values since then

$$\mathbb{E}((1 - \bar{L}\zeta_t) \mathbf{1}_{\{\zeta_t \leq 1/\bar{L}\}}) \approx \mathbb{E}((1 - \bar{L}\zeta_t) \mathbf{1}_{\{0 \leq \zeta_t \leq 1/\bar{L}\}}) < 1$$

The following example illustrates this.

Example 6.1: contest models with Gaussian distributed environments.

Suppose we have a stochastic contest model where the $\{\zeta_t | t \in \mathbb{N}\}$ are independent Gaussian random variables with mean μ and variance σ^2 . Then the process N_t as defined in (6.1) has a unique invariant probability measure when

$$\mu > \frac{1}{\bar{L}}, \quad \sigma < \frac{\sqrt{2\pi}}{\bar{L}}$$

Indeed, evaluating the conditional expectation in (6.2) gives:

$$\frac{1}{\sigma\sqrt{2\pi}} \int_{-\infty}^{1/\bar{L}} (1 - \bar{L}x) e^{-1/2((x - \mu)/\sigma)^2} dx \leq \frac{\bar{L}}{\sigma\sqrt{2\pi}} \int_{-\infty}^{1/\bar{L}} \left(\frac{1}{\bar{L}} - x\right) e^{-1/2((x - L^{-1})/\sigma)^2} dx$$

Introducing a new integration variable $s = 1/\bar{L} - x$ we find that the conditional expectation is smaller than

$$\frac{\bar{L}}{\sigma\sqrt{2\pi}} \int_0^{\infty} s e^{-1/2(s/\sigma)^2} ds = \frac{\sigma\bar{L}}{\sqrt{2\pi}} < 1$$

which proves that there exists indeed an invariant probability measure for this case, since the other requirements of the theorem are trivially satisfied for Gaussian distributed random variables. \square

Having established a sufficient condition for stationarity when L has a finite limit, we now turn to the scramble models, where L diverges to infinity. The following theorem is an extension of results in [2], where a proof is given for the specific case of the Ricker model.

Theorem 6.2. Consider the stochastic process (6.1) satisfying conditions (B1)–(B2) and with the function f satisfying conditions (A1)–(A3). If

$$\lim_{x \rightarrow \infty} L(x) = \infty$$

and the $\{\zeta_t | t \in \mathbb{N}\}$ have a probability density function which is positive on $]0, \infty[$, zero on $]-\infty, 0[$, but with possibly an atom at the origin satisfying

$$\mathbb{P}(\zeta_t = 0) < \left(\limsup_{x \rightarrow \infty} \frac{L(rx)}{L(x)} \right)^{-1} \tag{6.9}$$

then there exists a unique invariant probability measure π on \mathbb{R}^+ for this process.

Proof. We use the Lyapunov function

$$V(y) = \begin{cases} yL(e^y) & y \geq 0 \\ -ay & y < 0 \end{cases}$$

for the process $Y_t := \ln N_t$. Here $a > 0$ will be specified later on. We have

$$\begin{aligned} \mathbb{E}[V(Y_1) | Y_0 = y] - V(y) &= \mathbb{E}(y + \ln r - \zeta_t \ln f(e^y)) L(e^{y + \ln r - \zeta_t \ln f(e^y)}) \mathbf{1}_{\{\zeta_t \leq B(y)\}} \\ &+ \mathbb{E}(-ay - a \ln r + a\zeta_t \ln f(e^y)) \mathbf{1}_{\{\zeta_t > B(y)\}} - V(y) \end{aligned} \tag{6.10}$$

For $y \ll 0$ this will become smaller than $-\frac{1}{2}a \ln r$ for $y < -y_1$ with $y_1 > 0$ large enough, since $\zeta_t \geq 0$, $L > 0$ and $\ln f(e^y) \rightarrow 0$ as $y \rightarrow -\infty$ together imply that the above expression is asymptotically equivalent to

$$(-ay - a \ln r)(1 - p(y)) - V(y) \approx -ay - a \ln r - (-ay)$$

as y goes to $-\infty$. For $y \gg 0$ we find that (6.10) is smaller than

$$(y + \ln r)L(e^{y+\ln r})p(y) - a(y + \ln r)(1 - p(y)) + a|\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}}|[f(1) - 1 + yL(e^y)] - yL(e^y)$$

because of (3.5). Rearranging gives

$$yL(e^y) \left[p(y) \frac{L(re^y)}{L(e^y)} \left(1 + \frac{\ln r}{y} \right) - 1 \right] + ay[p(y) - 1 + |\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}}|L(e^y)] + a[(f(1) - 1)|\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > B(y)\}}| + \ln r(p(y) - 1)]$$

Since $\lim_{x \rightarrow \infty} L(x) = \infty$ we have that $\lim_{y \rightarrow \infty} B(y) = 0$ so

$$\lim_{y \rightarrow \infty} p(y) = \lim_{y \rightarrow \infty} \mathbb{P}(\zeta_t \leq B(y)) = \mathbb{P}(\zeta_t = 0)$$

so for $y \geq y_2$, with $y_2 > 0$ large enough we have, because of (6.9)

$$yL(e^y) \left[p(y) \frac{L(re^y)}{L(e^y)} \left(1 + \frac{\ln r}{y} \right) - 1 \right] < -vyL(e^y)$$

for a certain positive v and choosing

$$a < \frac{v}{2(1 + |\mathbb{E}\zeta_t \mathbf{1}_{\{\zeta_t > 0\}}|)}$$

gives

$$\mathbb{E}[V(Y_1)|Y_0 = y] - V(y) < \hat{C} - \frac{1}{2}vyL(e^y)$$

with \hat{C} a constant which is independent of y . So again, if we take $K = [-y_1, y_2]$ the conditions of Theorem 5.1 are satisfied outside K and on K we find

$$\begin{aligned} \mathbb{E}[V(Y_1)|Y_0 = y] &= \mathbb{E}(y + \ln r - \zeta_t \ln f(e^y)) L(e^{y+\ln r - \zeta_t \ln f(e^y)}) \mathbf{1}_{\{\zeta_t \leq B(y)\}} \\ &\quad - \mathbb{E}(ay + a \ln r - a \zeta_t \ln f(e^y)) \mathbf{1}_{\{\zeta_t > B(y)\}} \\ &\leq (y_2 + \ln r)L(re^{y_2}) + ay_1 + ay_2 \mathbb{E}\zeta_t \ln f(e^{y_2}) \end{aligned}$$

and thus the theorem has been proven. □

Remark that there is a fundamental difference between the class of stochastic processes we use in these two results: in the second one we assume that ζ_t can *only* attain nonnegative values. Also note that all conditions given here have been proved to be sufficient, but not necessary. However, simulations results like those presented in Sect. 8 of this paper suggest that they are indeed necessary as well. A rigorous proof of this statement is currently the subject of further research.

7 Stochastic stability

Now that we have found sufficient conditions for the existence of an invariant probability measure for the stochastic population models, we will address the question of stochastic stability. That is, we would like to know under what conditions an arbitrary initial probability distribution on the state space converges to this invariant probability distribution and what can be said about the speed of convergence. This is of some importance, because if we cannot guarantee that an arbitrary initial population will converge to a stationary random variable in time, some attempts to measure statistical properties of the population over time may be useless. Moreover, we can only compute the invariant distribution numerically by iterating an arbitrary initial distribution and hoping that this converges to the invariant one.

Since we want to prove a stronger result than simple pointwise convergence of the distributions, we introduce the following *total variation norm* for signed measures ν on \mathbb{R}^+ :

$$\|\nu\| = \sup_{A \in \mathcal{B}(\mathbb{R}^+)} \nu(A) - \inf_{A \in \mathcal{B}(\mathbb{R}^+)} \nu(A)$$

with $\mathcal{B}(\mathbb{R}^+)$ the Borel sets in \mathbb{R}^+ . If we define P_x^t to be the probability measure of N_t given the initial condition $N_0 = x$, and π the stationary probability measure, we can now state precisely the property we would like to establish:

Definition 7.1. *The Markov process $\{N_t | t \in \mathbb{N}\}$ with invariant probability distribution π is called **ergodic** if for every $x \in \mathbb{R}^+$*

$$\lim_{t \rightarrow \infty} \|P_x^t - \pi\| = 0$$

*and **geometrically ergodic** if there exists a $\rho > 1$ such that for every $x \in \mathbb{R}^+$*

$$\sum_{t=1}^{\infty} \rho^t \|P_x^t - \pi\| < \infty$$

Remark that the last inequality implies that the total variation norm converges as $o(\rho^{-t})$. Therefore, establishing geometric ergodicity means that the distribution function converges exponentially, in norm, to the stationary distribution function π . This implies that numerical computations concerning the stationary distribution of geometrically ergodic models will be more robust than computations involving models which are only ergodic. We will need the following lemmas which are special cases of results proven in [12]:

Lemma 7.1. *Suppose that the irreducible Markov process $\{N_t | t \in \mathbb{N}\}$ admits a stationary probability distribution and is **Harris recurrent**, that is, it visits every Borel set in its domain infinitely often:*

$$(\forall A \in \mathcal{B}(\mathbb{R}^+)) \quad (\forall N_0 \in A) \quad \mathbb{P} \left(\sum_{t=1}^{\infty} \mathbf{1}_{\{N_t \in A\}} = \infty \right) = 1$$

Then the process is ergodic.

Lemma 7.2. *Suppose there exists a compact set K , constants $C < \infty$ and $\beta \in]0, 1[$, and a function V on \mathbb{R}^+ such that*

1. $(\forall x \geq 0) \quad V(x) \geq 1$
2. $(\forall x \in K^c) \quad \mathbb{E}[V(N_{t+1})|N_t = x] - V(x) \leq -\beta V(x)$
3. $(\forall x \in K) \quad \mathbb{E}[V(N_{t+1})|N_t = x] \leq C$

then the process $\{N_t|t \in \mathbb{N}\}$ is geometrically ergodic.

Lemma 7.3. *If a Markov process $\{N_t|t \in \mathbb{N}\}$ is geometrically ergodic, then there exists a $\kappa > 1$ such that for every compact set H*

$$\sup_{x \in H} \mathbb{E}[\kappa^{T_H}|N_0 = x] < \infty$$

Since conditions (B1)–(B3) imply already that every positive Borel set will be visited infinitely often, we immediately have from Lemma 7.1:

Corollary 7.1. *All processes (6.1) satisfying conditions (B1)–(B3) and with the function f satisfying conditions (A1)–(A3) which admit a stationary probability measure, are ergodic.*

So in all cases where we have proven that a stationary distribution exists, every initial population will converge to a random variable having this distribution. That is, the population models are stochastically stable. However, the speed of convergence is not necessarily exponential. To prove this, we need the following lemma, which is a generalisation of an earlier result in [2]. It states that if the logarithmic process Y_t starts in an initial condition y which is small enough, the number of steps to return to the origin is almost $|y|/(1 + \ln r)$ with a probability that is arbitrarily close to one:

Lemma 7.4. *Let the conditions (B1) and (B2) be satisfied and define the process Y_t as in equation (6.3) with f satisfying conditions (A1) and (A2). Then for arbitrary $\delta, c \in]0, 1[$, there exists a $Q > 0$ such that for all $Y_0 = y < -Q$:*

$$\mathbb{P}\left(\min\{t > 0 | Y_t > 0\} \geq (1 - c) \frac{|y|}{1 + \ln r}\right) > 1 - \delta$$

Proof. Take $\delta, c \in]0, 1[$ and denote $\mathbb{E}\zeta_t = \mu$ and $\mathbb{E}(\zeta_t - \mathbb{E}\zeta_t)^2 = \sigma^2$. First remark that (A1) implies that f is right-differentiable in zero, so

$$\lim_{y \rightarrow -\infty} \frac{\ln f(e^{cy})}{e^{cy}} = \lim_{x \rightarrow 0} \frac{\ln f(x) - \ln f(0)}{x - 0} = \lim_{x \rightarrow 0} \frac{f'(x)}{f(x)} = f'(0)$$

and we therefore have, for y smaller than some fixed negative value $-\hat{Q}$

$$0 < (|y| \sigma - \mu) \ln f(e^{cy}) < 1 \tag{7.1}$$

Constructing the following sets in probability space

$$\hat{B}_K = \bigcap_{t=0}^K \{\omega \in \Omega \mid \zeta_t(\omega) \geq -|y|\sigma + \mu\} \tag{7.2}$$

we find, using Chebyshev’s inequality, that

$$P(\hat{B}_K) \geq \left(1 - \frac{1}{y^2}\right)^{K+1}$$

We now take K the smallest integer which is larger than $(1 - c)|y|/(1 + \ln r)$. We then have that

$$\left(1 - \frac{1}{y^2}\right)^{K+1} \geq \left(1 - \frac{1}{y^2}\right)^{2+(1-c)|y|/(1+\ln r)}$$

and since the right hand side converges to 1 as $y \rightarrow -\infty$, there exists a $Q > \hat{Q}$ so large that

$$y < -Q \Rightarrow P(\hat{B}_K) > 1 - \delta \tag{7.3}$$

and we may choose this Q such that

$$Q > (1 + \ln r)/c \tag{7.4}$$

Conditioning on the event \hat{B}_K and with initial condition $Y_0 = y < -Q$ we have that

$$Y_t \leq y + t(\ln r + 1) \quad (t = 0, 1, 2 \dots K)$$

We prove this with induction. It is clearly true for $t = 0$ and if it is true for a certain time $t < K$ then we have for time $t + 1$, since we condition on (7.2):

$$Y_{t+1} \leq Y_t + \ln r + (|y|\sigma - \mu) \ln f(e^{Y_t}) \tag{7.5}$$

Because of the induction hypothesis and our choice of K we then have

$$Y_t \leq y + t(\ln r + 1) \leq y + (K - 1)(\ln r + 1) \leq y + (1 - c)|y| = cy$$

But since f is strictly increasing (see Lemma 3.1) this implies that $f(e^{Y_t}) \leq f(e^{cy})$ and together with (7.5) and (7.1) this implies that the induction hypothesis is true for $t + 1$. We may thus conclude that for $t = 0, 1, 2 \dots K$ we have

$$\begin{aligned} Y_t \leq y + K(\ln r + 1) &\leq y + \ln r + 1 + (1 - c)|y| = cy + \ln r + 1 \\ &\leq -cQ + \ln r + 1 < 0 \end{aligned}$$

where we used (7.4) to obtain the last step. This shows that, conditioned on \hat{B}_K , we have that $\min\{t > 0 \mid Y_t > 0\} > K$. The probability of the event \hat{B}_K is larger than $1 - \delta$ because of equation (7.3), and this proves the lemma. \square

This lemma now enables us to prove that contest models may be ergodic without being geometrically ergodic:

Theorem 7.1. Consider the stochastic process (6.1) satisfying conditions (B1)–(B3) and with the function f satisfying conditions (A1)–(A3). If

$$\lim_{x \rightarrow \infty} L(x) = \bar{L} < \infty$$

and

$$\mathbb{P}(\zeta_t \leq 0) > 0$$

then the population process is **not** geometrically ergodic.

Proof. Suppose that there exists an invariant probability measure π and choose an arbitrary $\kappa > 1$. We will show that $\mathbb{E}\kappa^{T_H} = \infty$ for the set $H := [\sqrt{r}, r]$, and the result then follows from Lemma 7.3. For arbitrary $k > 2$ take $\gamma = 1/(k + 1) \in]0, 1/3[$ and call $\rho = \min\{\bar{L}^{-1}, ((\ln r)/\ln f(1))\}$. Denote $\mathbb{P}(\zeta \leq \gamma\rho) = p_\gamma \geq p_0 > 0$. Let Q be such that the conclusion of Lemma 7.4 is satisfied for $c = \delta = \frac{1}{2}$, and choose a C such that

$$L(1)C - 1 > \max\left\{\frac{6|\ln p_0|(1 + \ln r)}{\ln r \cdot \ln \kappa}, \frac{3}{2}\left(\frac{Q}{\ln r} + 1\right)\right\} \tag{7.6}$$

We take the initial condition $N_0 \in H = [\sqrt{r}, r]$ and condition on the event

$$B_k = \{\omega | \zeta_0(\omega) \dots \zeta_{k-1}(\omega) \leq \gamma\rho, \zeta_k(\omega) > C\}$$

with probability $P(B_k) = p_\gamma^k(1 - p_{C/\rho})$. Then we have for $t = 0 \dots k - 1$, using $f(x) \leq f(1)x^{\bar{L}}$ and the definition of ρ , that

$$N_{t+1} = \frac{r N_t}{f(N_t)^{\zeta_t}} \geq \frac{r N_t}{f(1)^{\gamma\rho} N_t^{\bar{L}\gamma\rho}} \geq r^{1-\gamma} N_t^{1-\gamma} \geq r^{1-\gamma} \sqrt{r}^{1-\gamma} > r^{2/3} \sqrt{r}^{2/3} = r$$

so the process does not return to $H = [\sqrt{r}, r]$ in the first k steps and since $N_{t+1} \geq r^{1-\gamma} N_t^{1-\gamma}$ and $N_0 > 1$

$$\begin{aligned} N_k &\geq r^{(1-\gamma) + (1-\gamma)^2 + \dots + (1-\gamma)^k} N_0^{(1-\gamma)^k} \\ &> r^{(1-\gamma) + (1-\gamma)^2 + \dots + (1-\gamma)^k} \end{aligned} \tag{7.7}$$

and at time $k + 1$ we have, since $x \geq 1 \Rightarrow f(x) \geq f(1)x^{L(1)}$

$$\begin{aligned} N_{k+1} &= r N_k f(N_k)^{-\zeta_k} \leq r N_k^{1-L(1)C} f(1)^{-C} \\ &< f(1)^{-C} \cdot r^{1-(L(1)C-1)\sum_{i=1}^k (1-\gamma)^i} \end{aligned}$$

where the last inequality follows from $L(1)C - 1 > 0$ and (7.7). We have $f(1)^{-C} < 1$ so

$$\ln N_{k+1} < \ln r \left[1 - (L(1)C - 1) \sum_{i=1}^k (1 - \gamma)^i \right] \leq \ln r \left[1 - (L(1)C - 1) \frac{2}{3} \right] \leq -Q$$

and because of our choice of Q we thus have, with probability larger than $\frac{1}{2}$, that the number of steps it takes to get back at H is at least

$$\frac{|\ln N_{k+1}|}{2(1 + \ln r)} \geq \left(-1 + (L(1)C - 1) \sum_{i=1}^k (1 - \gamma)^i \right) \cdot \frac{\ln r}{2(1 + \ln r)}$$

implying

$$\begin{aligned} \mathbb{E} \kappa^{T_H} &\geq \frac{1}{2} p_\gamma^k (1 - p_{C/\rho}) \cdot \kappa^{[-1 + (L(1)C - 1) \sum_{i=1}^k (1 - \gamma)^i] \cdot \ln r / (2 + \ln r)} \\ &\geq \frac{1}{2} (1 - p_{C/\rho}) \exp \left[-k |\ln p_\gamma| + \frac{\ln r \cdot \ln \kappa}{2(1 + \ln r)} \left(-1 + (L(1)C - 1) \sum_{i=1}^k (1 - \gamma)^i \right) \right] \end{aligned}$$

Using (7.6) and since $p_\gamma \geq p_0 > 0$, we conclude that

$$\begin{aligned} \mathbb{E} \kappa^{T_H} &\geq \frac{1}{2} (1 - p_{C/\rho}) \exp \left[-k |\ln p_0| + \frac{\ln r \cdot \ln \kappa}{2(1 + \ln r)} \left(-1 + \frac{6|\ln p_0|(1 + \ln r)}{\ln r \cdot \ln \kappa} \sum_{i=1}^k (1 - \gamma)^i \right) \right] \\ &\geq \frac{1}{2} (1 - p_{C/\rho}) e^{-\ln r \cdot \ln \kappa / (2(1 + \ln r))} \exp \left[|\ln p_0| \left(-k + 3 \sum_{i=1}^k (1 - \gamma)^i \right) \right] \end{aligned}$$

The right hand side can be made arbitrarily large by choosing k large enough since we took $\gamma = 1/(k + 1)$ and

$$-k + 3 \sum_{i=1}^k (1 - \gamma)^i = -k + 3 \left(\frac{1 - (1 - (1/k + 1))^{k+1}}{1/(k + 1)} - 1 \right) \stackrel{k \rightarrow \infty}{\approx} (2 - 3e^{-1})k - 3e^{-1}$$

This shows that $\mathbb{E} \kappa^{T_H} = \infty$ which proves the result. □

Apparently, contest models do not admit geometrical ergodicity when the stochastic environment is not purely adversary. However, when the stochastics are purely adversary and bounded, stochastic contest models may indeed be geometrically ergodic:

Theorem 7.2. *Consider the stochastic process (6.1) satisfying condition (B1), with the function f satisfying conditions (A1)–(A3) and $\lim_{x \rightarrow \infty} L(x) = \bar{L} < \infty$. Assume that the stochastic process ζ_t satisfies condition (B2), is absolute continuous with a density which is square integrable and positive on $]0, \hat{\zeta}]$ for a certain $\hat{\zeta} > 1/\bar{L}$, zero on $] - \infty, 0[\cup]\hat{\zeta}, \infty [$, and with possibly an atom at the origin satisfying $\mathbb{P}(\zeta = 0) < r^{-n}$ for a certain $n \in \mathbb{N}^+$. Then the process is geometrically ergodic.*

Proof. First remark that one may establish that $\hat{\zeta} > 1/\bar{L}$ implies that the process is irreducible. We can thus take the Lyapunov function

$$V(x) = \begin{cases} x^{-c} & 0 \leq x < 1 \\ x^n & x \geq 1 \end{cases}$$

with $c > 0$ to be specified later. Let f_ζ be the probability density of ζ_t and define $p_0 = \mathbb{P}(\zeta = 0)$. Because of the condition in the theorem we can take an

$\varepsilon \in]0, 1[$ such that $p_0 r^n < 1 - \varepsilon$. Take the interval $K = [\delta, x_0]$ where x_0 satisfies

$$\ln f(x_0) > \frac{1}{2n} \left(\frac{\|f_\zeta\|_2 (1 - p_0) r^n}{(1 - \varepsilon - p_0 r^n)} \right)^2, \quad x_0 > 1 \tag{7.8}$$

with

$$\|f_\zeta\|_2 = \sqrt{\int_0^\infty f_\zeta(s)^2 ds}$$

and $\delta > 0$ will be specified later. Since around $x = 0$

$$\Delta V(x) := \mathbb{E}[V(N_{t+1}) | N_t = x] - V(x) \approx (rx)^{-c} - x^{-c} = \left(\frac{1}{r^c} - 1 \right) V(x)$$

we can find a δ such that for $x \leq \delta$

$$\Delta V(x) < -\frac{1}{2} \left(1 - \frac{1}{r^c} \right) V(x)$$

so the geometrical ergodicity condition for V is satisfied for $[0, \delta[\subset K^C$. For $]x_0, \infty[\subset K^C$ we find:

$$\begin{aligned} \Delta V(x) &= \mathbb{E} \left[\frac{rx}{f(x)^\zeta} \right]^n \mathbf{1}_{\{\zeta < (\ln r + \ln x)/(\ln f(x))\}} + \mathbb{E} \left[\frac{f(x)^\zeta}{rx} \right]^c \mathbf{1}_{\{\zeta > (\ln r + \ln x)/(\ln f(x))\}} - x^n \\ &\leq x^n \left[p_0 r^n + (1 - p_0) \int_0^{(\ln r + \ln x)/(\ln f(x))} \frac{r^n}{f(x)^{ns}} f_\zeta(s) ds \right. \\ &\quad \left. + (1 - p_0) \int_{(\ln r + \ln x)/(\ln f(x))}^{\hat{\zeta}} C_1 x^{c\bar{L}s - c - n} f_\zeta(s) ds - 1 \right] \end{aligned} \tag{7.9}$$

with $C_1 = f(1)^{c\hat{\zeta}} r^{-c}$, where we have used that $f(x) \leq f(1)x^{\bar{L}}$ for $x \geq 1$. Now the third term in this expression is smaller than

$$\begin{aligned} x^n \left[(1 - p_0) C_1 x^{c(\bar{L}\hat{\zeta} - 1) - n} \int_0^{\hat{\zeta}} f_\zeta(s) ds \right] &= x^n [(1 - p_0) C_1 x^{c(\bar{L}\hat{\zeta} - 1) - n}] \\ &< x^n [(1 - p_0) C_1 x^{-n/2}] \end{aligned}$$

if we take

$$c < \frac{n}{2(\bar{L}\hat{\zeta} - 1)}$$

which is possible since we demanded that $\bar{L}\hat{\zeta} > 1$. So the term inside the bracket will converge to zero when $x \rightarrow \infty$. Since $x \geq x_0$ we find that the other terms in (7.9) are smaller than

$$\begin{aligned} x^n \left[p_0 r^n + (1 - p_0) \int_0^{(\ln r + \ln x)/\ln f(x)} \frac{r^n}{f(x)^{ns}} f_\zeta(s) ds - 1 \right] \\ \leq x^n \left[p_0 r^n + (1 - p_0) \int_0^\infty \frac{r^n}{f(x)^{ns}} f_\zeta(s) ds - 1 \right] \end{aligned}$$

$$\begin{aligned} &\leq x^n \left[p_0 r^n + (1 - p_0) r^n \int_0^\infty \frac{1}{f(x_0)^{ns}} f_\zeta(s) ds - 1 \right] \\ &\leq x^n \left[p_0 r^n + (1 - p_0) r^n \sqrt{\int_0^\infty \frac{1}{f(x_0)^{2ns}} ds} \sqrt{\int_0^\infty f_\zeta(s)^2 ds} - 1 \right] \\ &= x^n \left[p_0 r^n + (1 - p_0) r^n \sqrt{\frac{1}{2n \ln f(x_0)}} \|f_\zeta\|_2 - 1 + \frac{1}{2} \varepsilon \right] - x^n \frac{1}{2} \varepsilon \end{aligned}$$

Using equation (7.8) and since $x > 1$ this gives

$$\begin{aligned} &\leq x^n \left[p_0 r^n + (1 - p_0) r^n \|f_\zeta\|_2 \frac{1 - \varepsilon - p_0 r^n}{(1 - p_0) r^n \|f_\zeta\|_2} - 1 + \frac{1}{2} \varepsilon \right] - 1^n \frac{1}{2} \varepsilon \\ &\leq x^n \left(-\frac{1}{2} \varepsilon \right) - \frac{1}{2} \varepsilon \end{aligned}$$

Therefore, if we choose $\beta = \min\{\frac{1}{2}\varepsilon, \frac{1}{2}(1 - r^{-c})\} \in]0, 1[$ and x_0 big enough we have that $\Delta V(x) \leq -\beta V(x)$ on K^c and $V(x)$ trivially bounded on K , which proves the result. \square

We must therefore conclude that although in all cases where an invariant distribution exists, it is stochastically stable, we can only guarantee it to be exponentially stable for contest models with bounded environmental stochastics. As mentioned earlier this means in practice that computations for some stochastic population models may be quite sensitive to small numerical errors. Analogous results for scramble models are not yet known, and a subject of further research.

8 Examples of applications

We will now illustrate our results by some numerical examples.

Example 8.1: stochastic stability of a contest model.

We consider a stochastic perturbation of the Hassell model. We take the environmental parameters identically independently distributed Gaussian random variables with mean 3 and variance 1, and a natural growth rate $r = 2$:

$$N_{t+1} = \frac{rN_t}{(1 + N_t)^{\zeta_t}}, \quad r = 2, \quad \zeta_t \sim \text{i.i.d. } N(3, 1)$$

For this model we have

$$f(x) = 1 + x \Rightarrow L(x) = \frac{x}{x + 1} \Rightarrow \bar{L} = \lim_{x \rightarrow \infty} L(x) = 1$$

So for this particular choice of the environmental random variables, condition (6.2) for the existence of an invariant distribution becomes

$$\mathbb{E}(1 - \bar{L} \zeta_t) \mathbf{1}_{\{\zeta_t \leq 1/\bar{L}\}} = \frac{1}{1 \cdot \sqrt{2\pi}} \int_{-\infty}^1 (1 - 1 \cdot \tau) e^{-(\tau - 3)^2/2} d\tau \approx 0.0084 \ll 1$$

and therefore the distribution of the stochastic process $\{N_t\}$ should converge to a stationary distribution π . Figure 1a shows the distribution of N_t for $t = 1, 2, \dots, 5$ when we take the initial condition $N_0 = 1$, and Fig. 1b when $N_0 = 0.5$. We see that the distribution converges indeed to the same stationary distribution in both cases. Remark that convergence seems to be geometrically fast, although strictly speaking we have only proven it to be so for models for which $\mathbb{P}(\zeta_t < 0) = 0$ and where the values of ζ_t are bounded. However, for this model we have $\mathbb{P}(\zeta_t < 0) = \mathbb{P}(\zeta_t > 6) \approx 0.001$ which explains the ‘almost geometrically’ fast convergence.

Taking the same stochastic perturbation model but now with environmental variables which have zero mean:

$$N_{t+1} = \frac{rN_t}{(1 + N_t)^{\zeta_t}} \quad r = 2, \quad \zeta_t \sim \text{i.i.d. } N(0, 1)$$

we find

$$\mathbb{E}(1 - \bar{L}\zeta_t)\mathbf{1}_{\{\zeta_t \leq 1/\bar{L}\}} = \frac{1}{1 \cdot \sqrt{2\pi}} \int_{-\infty}^1 (1 - 1 \cdot \tau)e^{-\tau^2/2} d\tau \approx 1.083 > 1$$

so we cannot guarantee that the system is stochastically stable. We can indeed see that it is not, looking at the distribution functions in Fig. 2. The initial distribution ‘wanders off’ in the positive direction, and it will eventually spread out over the entire positive axis, while converging pointwise to zero in every single point. These two examples clearly show the importance of our conditions for stochastic stability in the analysis of populations in stochastic environments.

Example 8.2: stochastic stability of a scramble model.

We now take a look at a typical stochastic perturbation of a scramble model:

$$N_{t+1} = rN_t e^{-N_t \zeta_t}, \quad r = 2, \quad \begin{aligned} \mathbb{P}(\zeta_t = 0) &= p_0 \\ \mathbb{P}(\zeta_t = |Z_t|) &= 1 - p_0 \end{aligned} \quad Z_t \sim \text{i.i.d. } N(3, \frac{1}{2})$$

For the Ricker model we have

$$f(x) = e^x \Rightarrow L(x) = x$$

and according to Theorem 6.2 this means that a stationary distribution exists if

$$p_0 < \left(\limsup_{x \rightarrow \infty} \frac{L(rx)}{L(x)} \right)^{-1} = \left(\limsup_{x \rightarrow \infty} \frac{rx}{x} \right)^{-1} = \frac{1}{r} = 0.5$$

First the distributions for $p_0 = 0.2$ were calculated; after seven iterations the distribution function showed no significant changes any more and the stationary distribution of Fig. 3a was obtained. Remark that peaks are found at distances which differ by a factor r due to the atom at zero in the environment which implies a population growth with factor r .

For $p_0 = 0.8$ we find the distribution functions of Fig. 3b. The distribution spreads on the entire positive axis, with peaks travelling to infinity due to

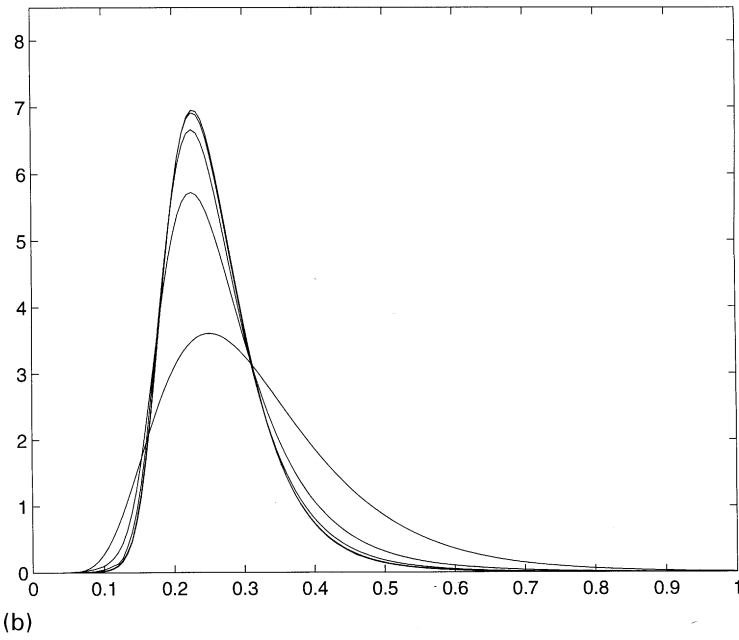
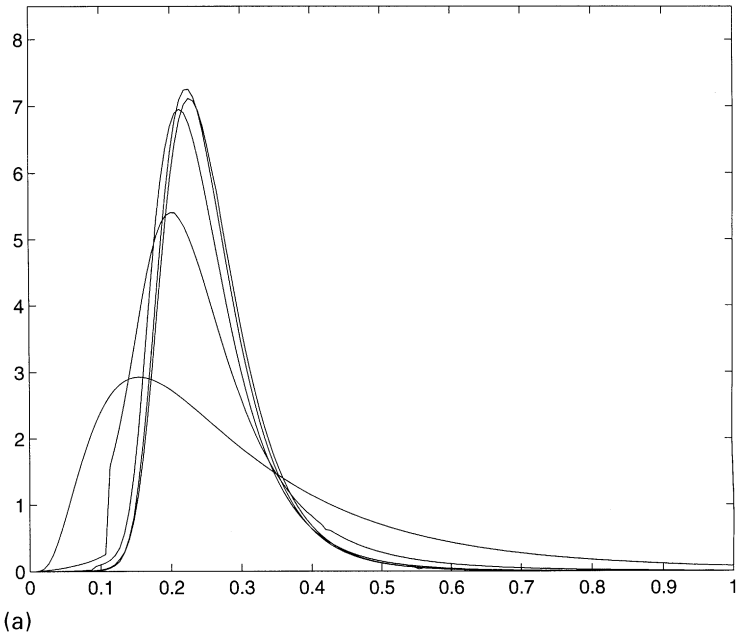


Fig. 1. Hassell model, $r = 2$, $b \sim N(3, 1)$. **a** $N_0 = 1.0$, **b** $N_0 = 0.5$

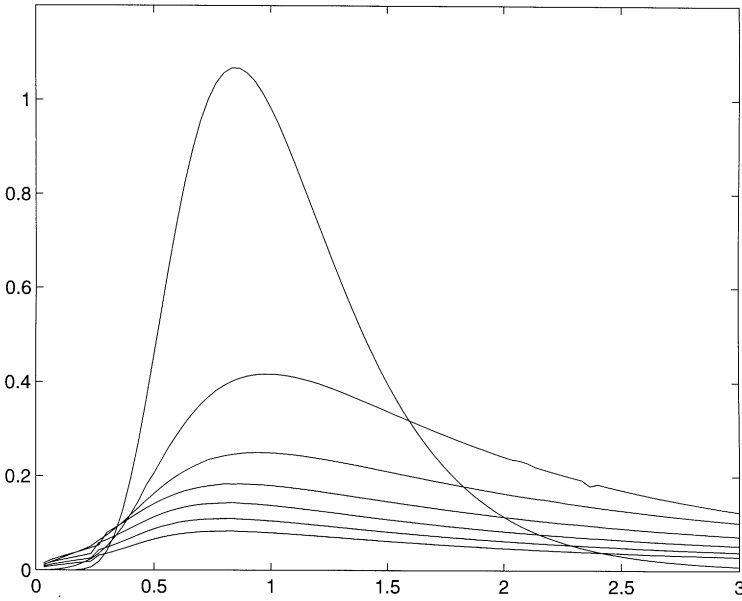


Fig. 2. Hassell model, $r = 2$, $b \sim N(0, 1)$, $N_0 = 0.5$

multiplication by r in every iteration, while the distribution converges to zero in every single point. We thus see how the conditions of Theorem 6.2 can be used in scramble models that allow pure natural growth.

Example 8.3: chaos in scramble and contest models.

As shown in Sect. 6, contest and scramble models may show very different behaviour when perturbed stochastically. However, we already mentioned in the introduction that two models may be very ‘close’ while showing fundamentally different dynamic behaviour. In fact, a scramble model can be very similar to a contest models and still show very different dynamics in the deterministic case. Consider the following two models:

$$\begin{cases} N_{t+1} = 22.23 N_t (1 + 0.28 N_t)^{-20} \\ N_0 = 0.5990 \end{cases} \quad \begin{cases} M_{t+1} = 20 M_t e^{-5M_t} \\ M_0 = 0.5990 \end{cases} \quad (8.1)$$

One may easily show that these models have the same unstable equilibrium in $N^* = M^* \approx 0.59915$ and that the one step dynamics are very close, as shown in Fig. 4a. It is clear that even very accurate data obtained from field studies cannot be expected to discriminate significantly between the two models.

But the long term dynamics of this process will differ considerably, as can be seen in Fig. 4b. Remark that we use the same initial condition for both processes, which is very close to the unstable equilibrium. After some time, the process N_t will spend more time around the equilibrium value than M_t , which oscillates more evenly between high and low values, as can clearly be seen after $t = 100$. This example shows that even very accurate field data may not be precise enough to verify statements about the dynamics.

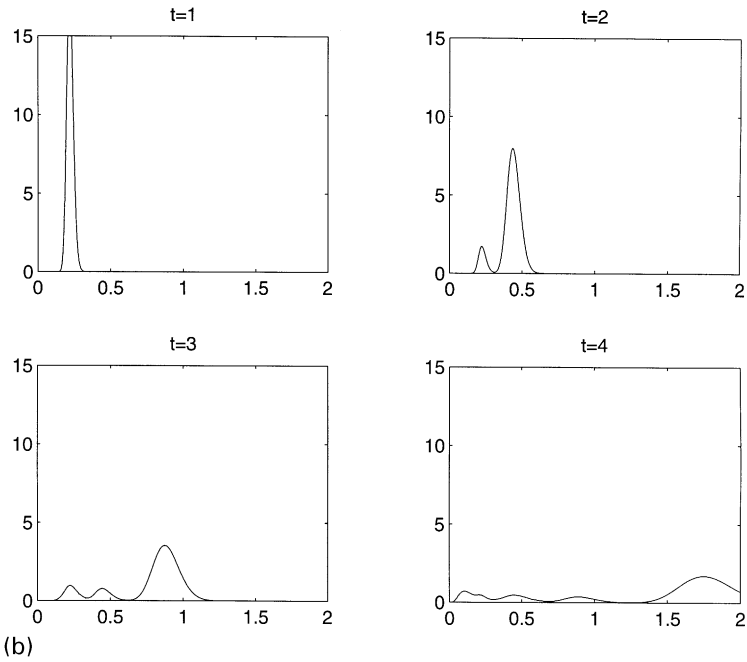
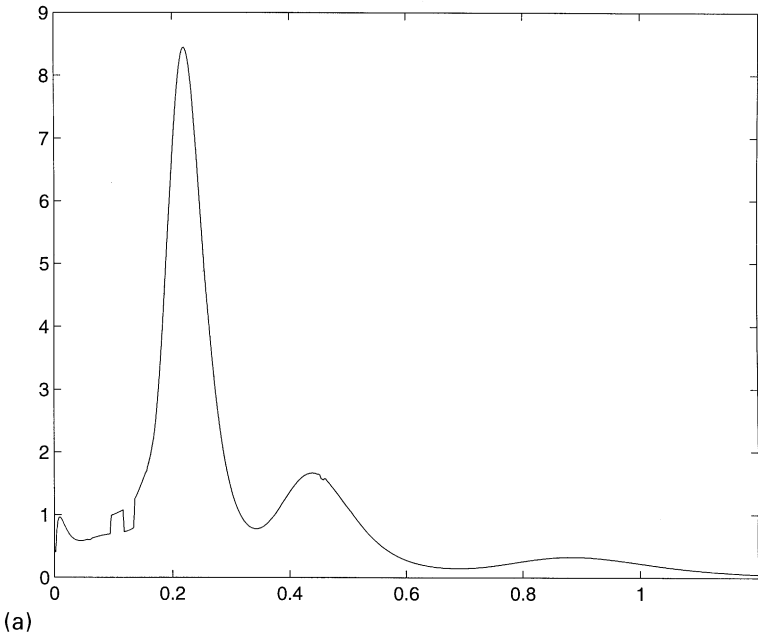
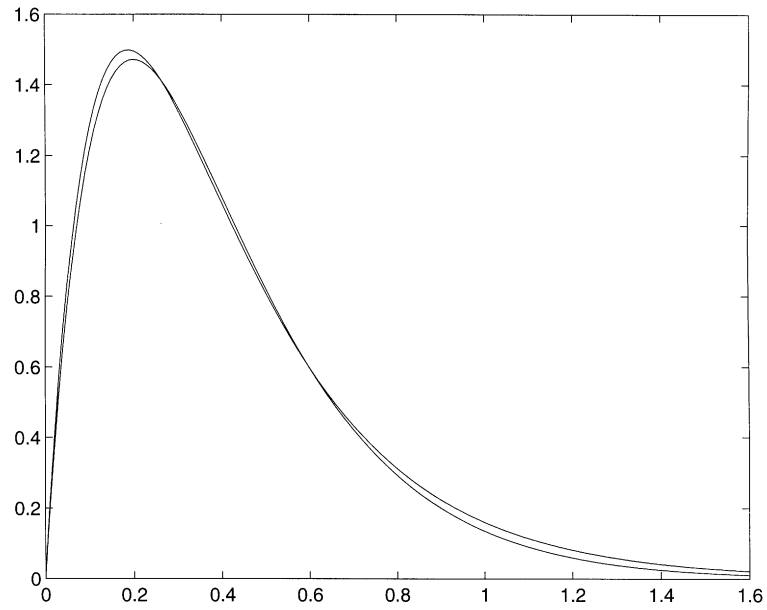
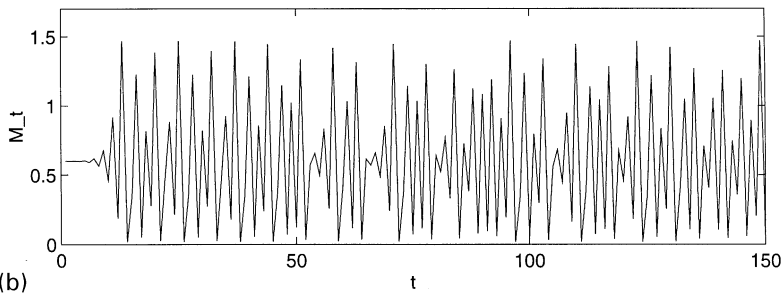
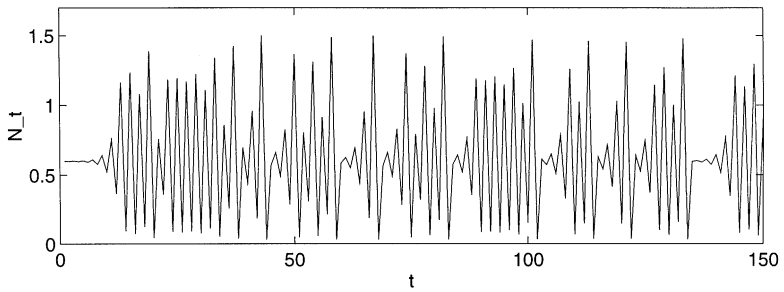


Fig. 3. Distributions for Ricker model, $r = 2$. **a** $p_0 = 0.2 < \frac{1}{r}$, $t = \infty$, **b** $p_0 = 0.8 > \frac{1}{r}$



(a)



(b)

Fig. 4. The processes N_t and M_t . **a** Transition functions, **b** Dynamics

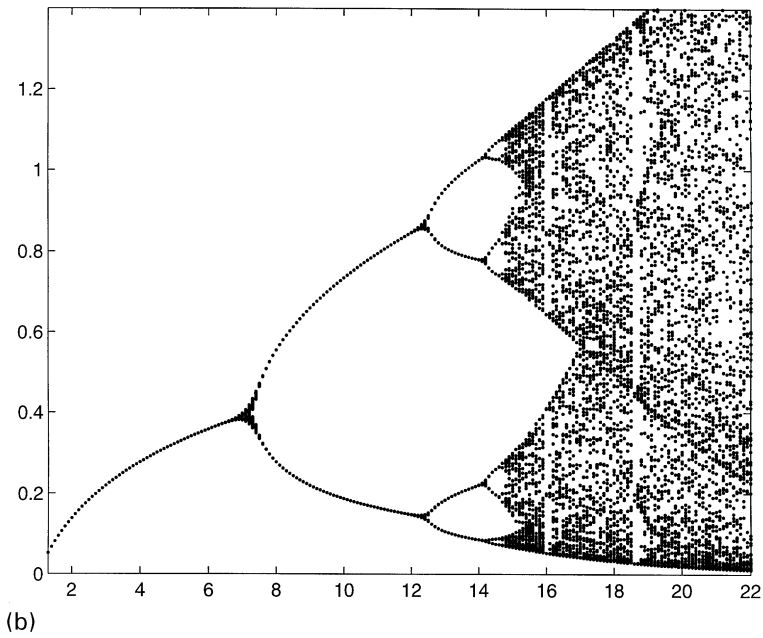
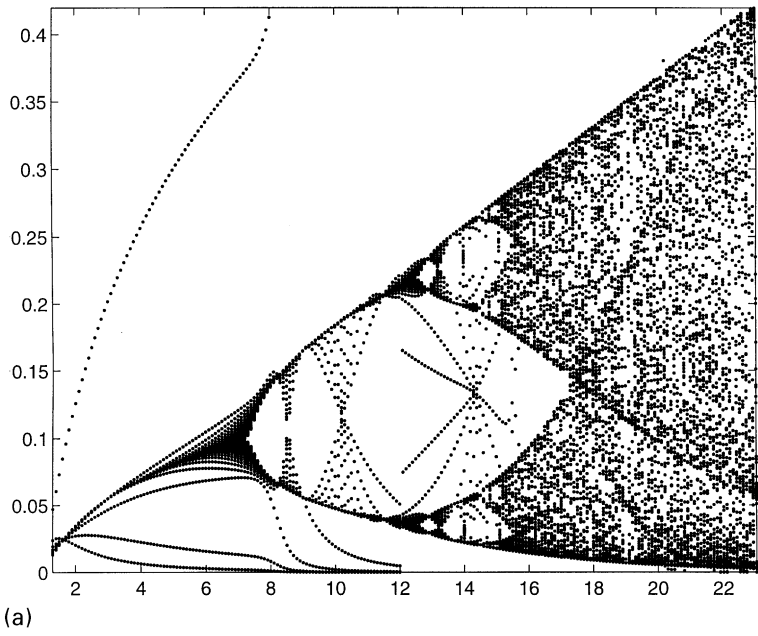


Fig. 5. Bifurcation diagrams in r . **a** N_t ($b = 20$), **b** M_t ($b = 5$)

However, according to Theorem 4.1 we can guarantee, assuming that the growth and environmental parameters are big enough, that both models will be chaotic, without having to analyse in detail their dynamic behaviour. In Figs. 5a, b the bifurcation diagrams in r for both models are shown. We see that for small values of r both models admit stable cycles with periods that are a power of 2, and that for higher values of r chaos occurs after a rapid series of period-doubling bifurcations. Note that the precise structures in the bifurcation diagrams are quite different, but this is unimportant: for the particular values we use above, $r = 22.2$ and $r = 20$ respectively, we are well in the chaotic regions in both cases, enabling us to conclude that the dynamics may be different, but equally complex.

9 Conclusions

In this paper we have addressed two important questions in the study of single species discrete population models. The first one was the question under which conditions a population model may exhibit chaotic behaviour. We have introduced very general population models which take into account the two fundamental premises of population dynamics, and shown that these models will *always* show chaotic behaviour if both the natural growth and environmental feedback are strong enough. This result depends only on the two premises and not on the particular structure of the population model under consideration. We then studied a stochastic perturbation of these models by allowing the environmental parameter to vary stochastically. A sufficient condition was given for the existence and stochastic stability of a stationary probability measure for the resulting stochastic population process. This condition turned out to be satisfied in all cases where the environmental influence was purely adversary, but also if there was a limited possibility of favourable environments.

The most surprising aspect of the results presented here is their very general nature. The two intuitively appealing premises stated in the first paragraph apparently contain sufficient information about the ‘nature’ of the dynamics to prove both chaos in the deterministic models and stability in the stochastic ones. It is interesting to see how the crucial observation in the proof of chaos is the fact that the critical point a of the dynamics does not depend of the natural growth parameter r but is determined uniquely by the function L and the environmental parameter b . It is exactly this separation of natural and environmental influences in the population which enables us to prove that the dynamics will become sufficiently complex. In the stochastic contest models we have something similar. Since for large values of N_t we have, if $\bar{L} < \infty$,

$$N_{t+1} = rN_t f(N_t)^{-\zeta_t} \approx r f(1)^{-\zeta_t} N_t^{1 - \bar{L}\zeta_t}$$

we see again that the growth of N_t can be separated in a multiplicative term and a power term $1 - \bar{L}\zeta_t$ and condition (6.2) for stochastic stability is

therefore a rather natural one. Again, the natural growth is merely a scaling factor and the real nature of the dynamics is determined only by the upper and lower bounds on the dynamics which are provided by the function L . The existence of these bounds is a direct consequence of the second premise of population dynamics, as shown in Lemma 3.1.

Therefore one may state that both the occurrence of chaos in discrete deterministic population models and the possibility of a stable stationary probability distribution in their stochastic perturbations, are a consequence of the ecological principles behind population models, and not of the details of a particular model. Since it is impossible in practice to describe any population exactly with one particular model, this should be a reassuring point for those who use population models to fit experimental data. If it would be possible to show that a small perturbation of a deterministic model could destroy its capacity for chaotic behaviour, then one could never conclude from a particular set of field data that a certain population process might be chaotic. Likewise, if the stability of a stationary distribution of a stochastic population model can be proven for a particular model, but not for a model which is 'close' to this one, then the calculation of mean, variance and other statistical characteristics would be useless from a mathematical point of view. In this way the framework provided here can be used not only as a theoretically interesting generalisation, but also as a rigorous justification for the use of population models to obtain theoretical statements about experimental data.

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