Branching processes

Are: Models for population dynamics, that incorporate inter-individual variation in offspring numbers

Used: To study dynamics of small populations

Give information about:

- **Establishment success**
- **Initial population growth**
- **Development of population structure and size**

Application in adaptive dynamics:

- **Probability of successful invasion of a specific type of mutant**
- **Expected time until invasion success**

BPs in the context of AD

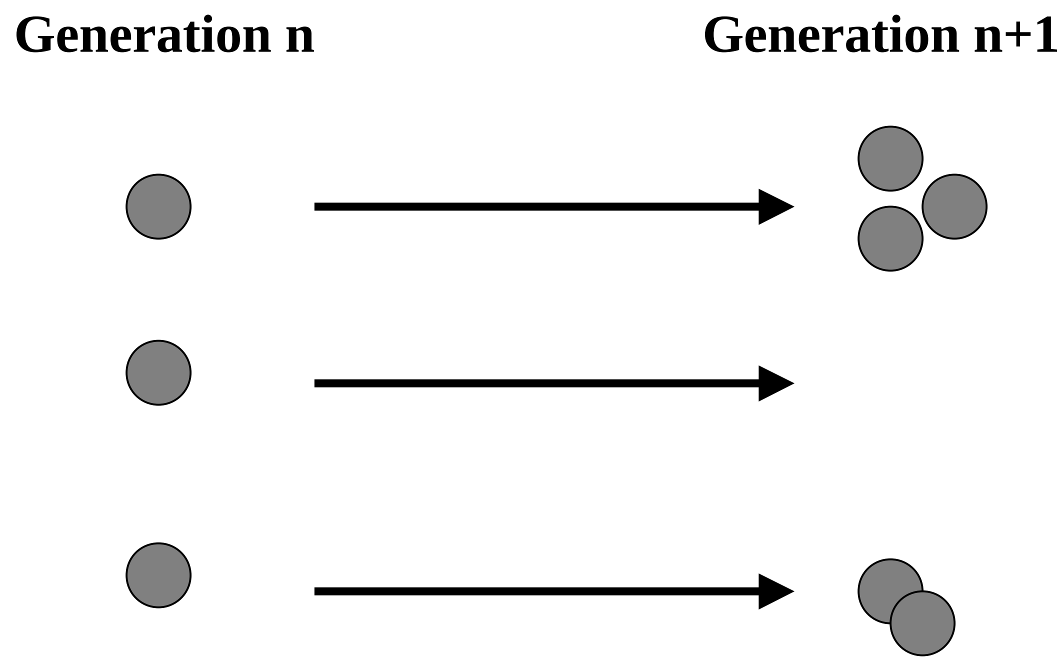
If mutants reproduce independently: classical BPs can be used

If mutants do not affect the resident dynamics: Resident population determines environment of BP

- **constant: ordinary BP**
- **changing: inhomogeneous BP**
    - **deterministic: e.g.periodic or monotone changes in resident density**
    - **random: e.g. through external factors or demographic stochasticity of residents**
    - **chaotic: model as random?**

If mutants do affect the resident dynamics or do not reproduce independently: BP with population size dependence. Not much results yet.

The archetypal branching process (Galton-Watson):

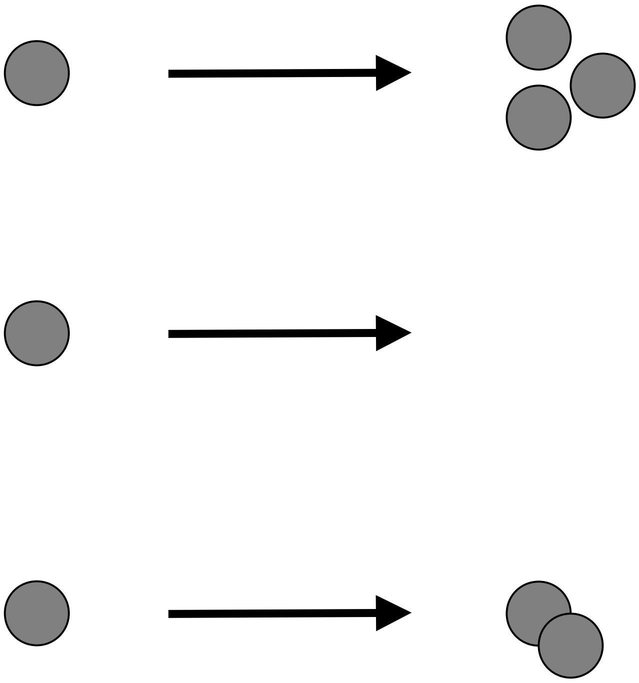


- •Discrete reproduction periods (‘generations’; no overlap or parents equivalent to offspring)
- •1 type of individuals, with identical offspring distribution
- •They do not affect each other’s reproduction
- •Distributions of offspring numbers do not change in time

Adaptive dynamics context:

Resident sets a fixed background

Time: n **n+1**



$\xi_1 = 3$

$\xi_2 = 0$

$\xi_3 = 2$

population size:

$$z_n \longrightarrow z_{n+1} = \sum_{i=1}^{z_n} \xi_i$$

ξ_i **independent identically distributed r.v.'s**

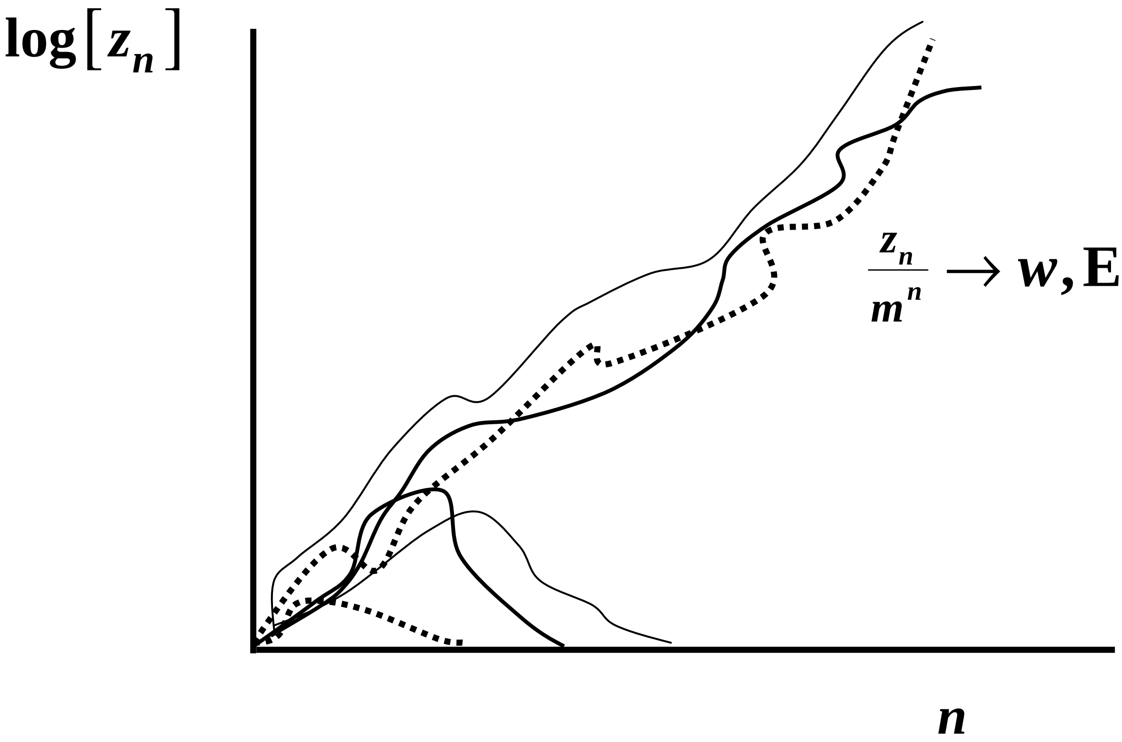
Expected number of offspring per individual:

$$\mathbf{E}[\xi] = m$$

If $\mathbf{Pr}[\xi = 1] < 1$ **then:**

$m > 1 \longleftrightarrow$	**probability of extinction smaller than 1 'supercritical process'**
$m < 1 \longleftrightarrow$	**always extinction, *finite* expected time to extinction 'subcritical process'**
$m = 1 \longleftrightarrow$	**always extinction, *infinite* expected time to extinction 'critical process'**

For supercritical processes there are two possibilities:
Extinction or Exponential growth



$$\frac{z_n}{m^n} \to w, \mathrm{E}[w] = 1$$

Extinction probability:

Q = expected proportion of processes started by 1 individual that goes extinct

Interpretation:

growth up to a 'safe size'
being able to invade a resident population

Adaptive dynamics

Chance per period of birth of a mutant with trait value x : $\mu(x)$

Extinction probability of the mutant BP: $Q(x)$

Chance per period of a successful invasion by that type of mutant: $\mu(x)(1-Q(x))$

Expected time until a successful invasion:

$$\frac{1}{\sum_x \mu(x)(1-Q(x))}$$

Probability trait value z is the lucky first:

$$\frac{\mu(z)(1-Q(z))}{\sum_x \mu(x)(1-Q(x))}$$

How to calculate Q?

Generating function of the offspring distribution:

$$f(s) = \mathbf{E}\left[s^{\xi}\right]$$

$$= \sum_{k=0}^{\infty} \mathbf{Pr}[\xi = k] \cdot s^k, \; s \in [0,1]$$

Then Q is the smallest non-negative root of the equation:

$$Q = f(Q)$$

Example: geometric offspring distribution

$$\mathbf{Pr}[\xi = k] = (1 - p)\,p^k$$

$$f(s) = (1-p)\sum_{k=0}^{\infty} p^k \cdot s^k = \frac{(1-p)}{1-ps}$$

$$Q = \frac{1-p}{1-pQ}$$

BUT:

- **not always possible to find an explicit expression for *Q***
- **sometimes no completely specified offspring distribution**
- **robust results wanted**

Approximations (using only first 2 moments of ξ):

If	Then
$\mathbf{E}[\xi] = 1 + \varepsilon > 1$	$1 - Q \geq \dfrac{2\varepsilon}{\mathbf{E}[\xi(\xi - 1)]}$

If furthermore there is a family of offspring distributions such that

$$\mathbf{E}[\xi(\varepsilon)] = 1 + \varepsilon$$

and there are ε_0 and $\delta > 0$ such that

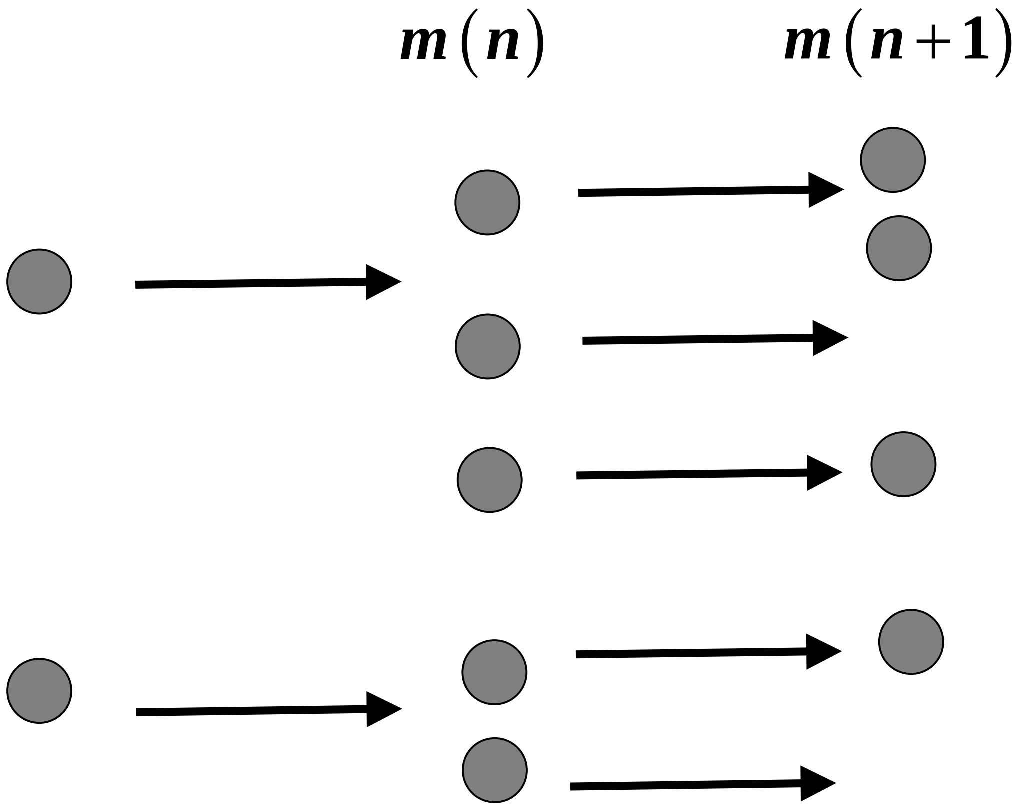
$$\sup_{0 \leq \varepsilon \leq \varepsilon_0} \mathbf{E}\left[\xi(\varepsilon)^{2+\delta}\right] < \infty$$

Then

$$1 - Q = \frac{2\varepsilon}{\mathbf{E}[\xi(\xi - 1)]} + o(\varepsilon) \text{ as } \varepsilon \to 0$$

Inhomogeneous BP

Expected numbers of offspring:



Difference between deterministic and random variation.

Adaptive dynamics: Resident background not fixed (but not affected by mutant).

Deterministic environments

General rules for criticality are not available.
Depends very much on type of variation.

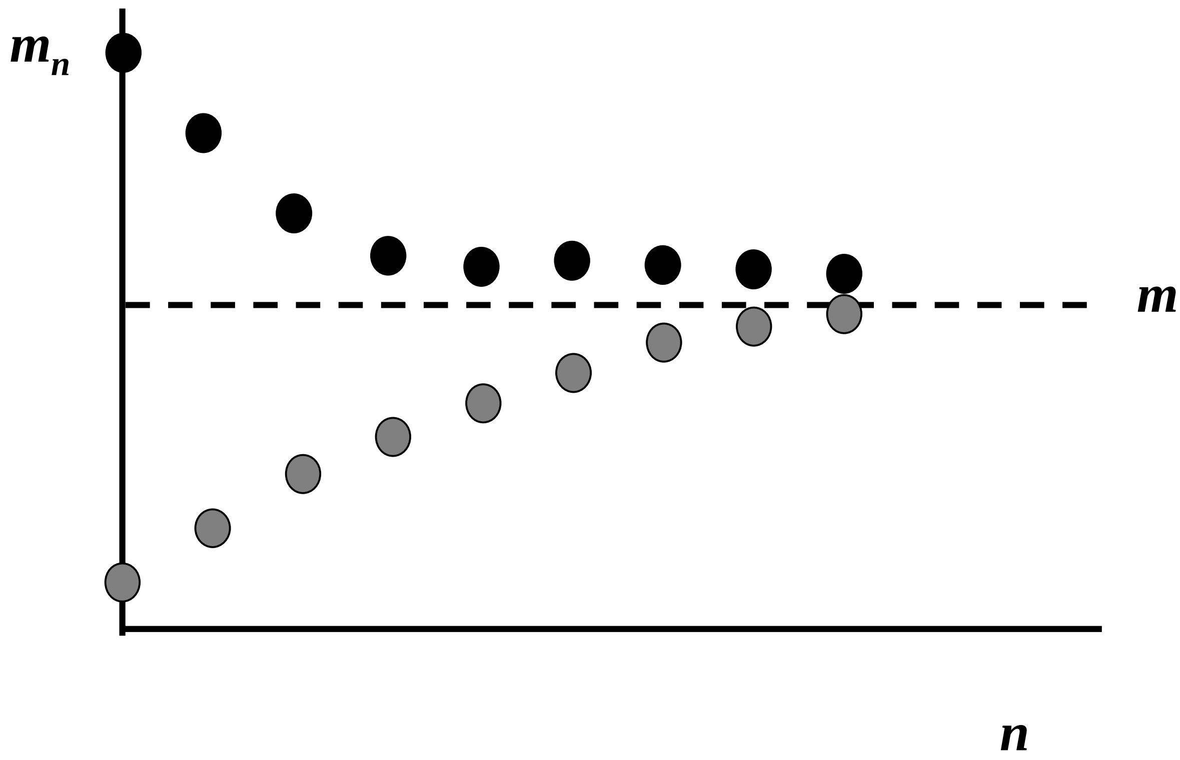
Sufficient condition for Q = 1: $$\lim_{n\to\infty} \prod_{j=1}^{n-1} m_j = 0$$

Specific cases can be worked out. Two examples:
monotonic, periodic

Monotonically changing m_n: $\lim_{n\to\infty} m_n = m$

$m > 1$ **:** $Q < 1$

$m \leq 1$**:** $Q = 1$



Periodic with period $T > 1$:

for all k $\quad m(k) = m(k+T)$

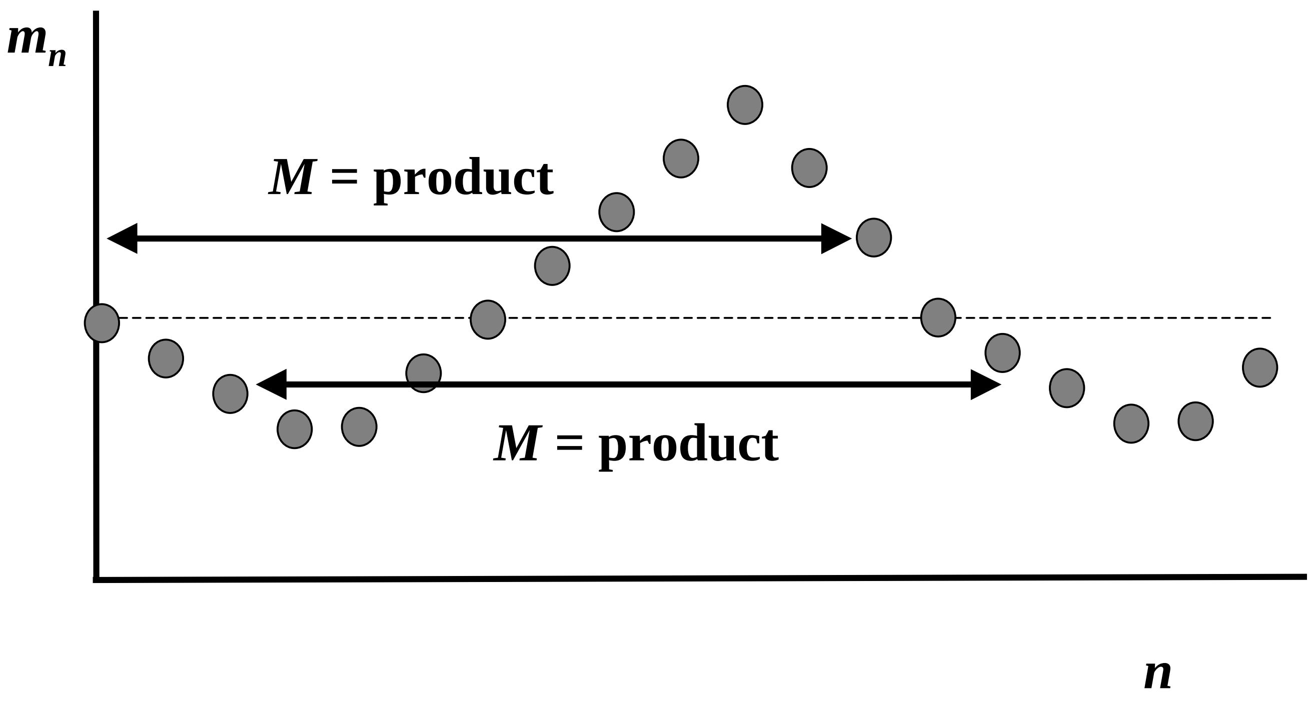
Define:

$$M = m_0 m_1 m_2 m_3 \ldots m_{T-1}$$
$$\left(= m_{k-T} \ldots m_{k-1},\ k = T, T+1, \ldots\right)$$

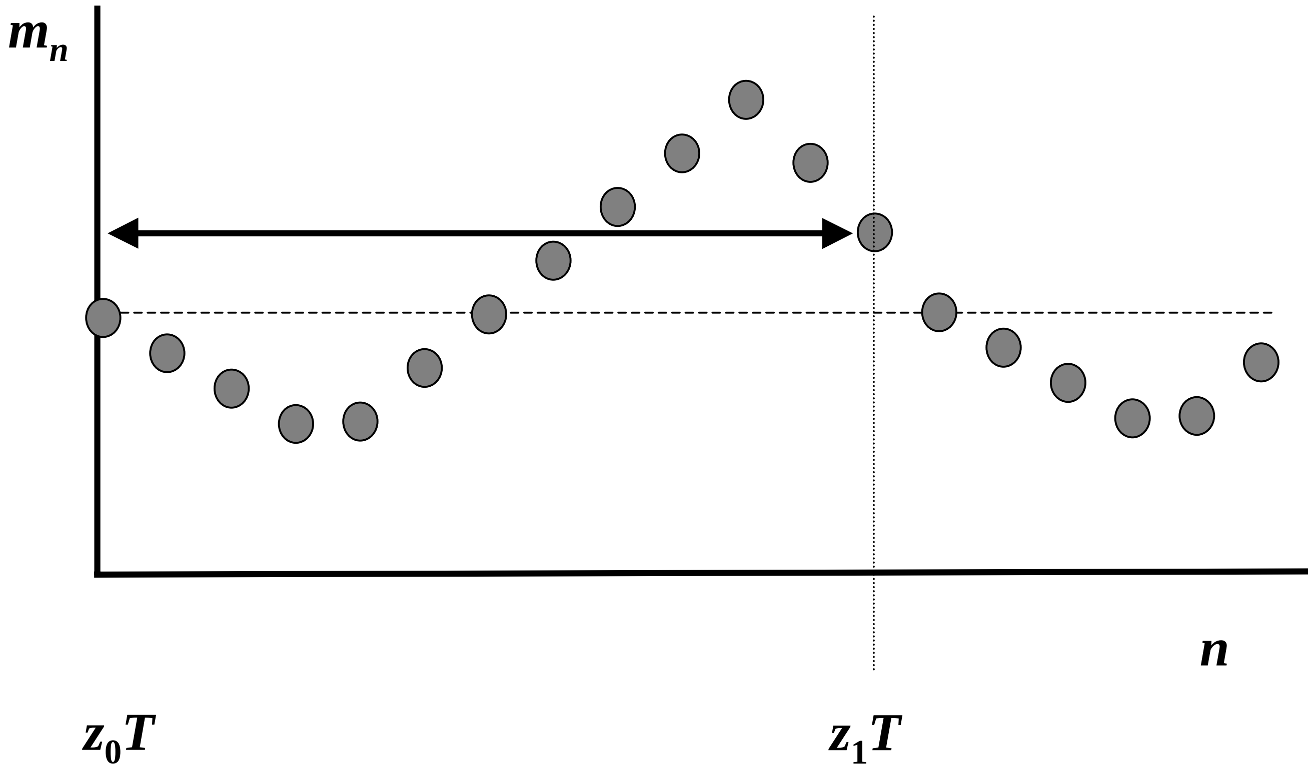
Then:

$M > 1$: $Q < 1$

$M \leq 1$: $Q = 1$



Periodic BPs can be transformed to standard BPs

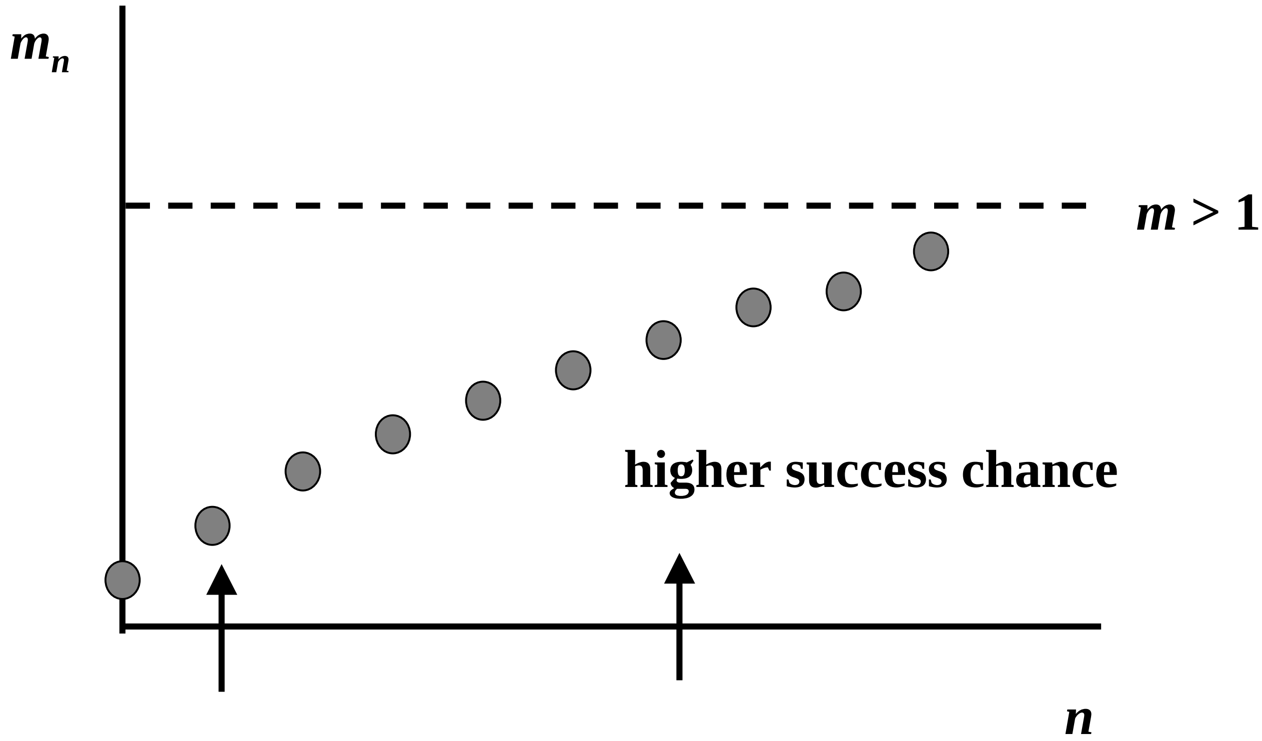


Pr[ξ = k] in transformed process = probability that an individual alive at time 0 has k living descendants at time T-1 in original process.

(for such processes Q can be calculated as before)

BUT *Q* is the extinction chance if an invasion takes place at time 0. The extinction chance of a BP now depends on the time of invasion.

Example:



Calculation of Q_t

Generating function of offspring distribution of individuals in the *k*-th generation:

$$f(k,s) = \mathbf{E}\left[s^{\xi(k)} \right]$$

$$= \sum_{j=0}^{\infty} \mathbf{Pr}\left[\xi(k) = j \right] s^{j}, s \in [0,1]$$

Generating function of population size in the *k*-th generation, given invasion of a single individual at time $t < k$:

$$f_t(k,s) = \mathbf{E}\left[s^{z_k} \middle| z_t = 1 \right]$$

Then

$$Q_t = \lim_{n\to\infty} f_t\left(1, f\left(2, \ldots f\left(n-1, s\right)\ldots\right)\right),$$

(for abitrary $0 \le s < 1$).

Adaptive dynamics

Chance per time unit of birth of a mutant with trait value *x*: $\mu_t(x)$
(also varies in time if dependent on resident population size)

Chance per time unit of a successful invasion by that type of mutant *at time t*:

$$\mu_t(x)(1-Q_t(x))$$

Expected time until a successful invasion:

$$1+\sum_{n=1}^{\infty}\prod_{t=1}^{n}\left(1-\sum_{x}\mu_t(x)(1-Q_t(x))\right)$$

Chance that a mutant with trait value *z* is the first to invade:

$$\sum_{t=0}^{\infty}\mu_t(z)(1-Q_t(z))\prod_{s=0}^{t}\left(1-\sum_{x}\mu_s(x)(1-Q_s(x))\right)$$

Inhomogeneous BP: random environment

Extinction probability now *is a random variable* itself

Different realizations of sequences:	Expected proportion of BPs that dies out:
$m_0^{\ 1}, m_1^{\ 1}, m_2^{\ 1} \ldots$	Q^1
$m_0^{\ 2}, m_1^{\ 2}, m_2^{\ 2} \ldots$	Q^2
$m_0^{\ 3}, m_1^{\ 3}, m_2^{\ 3} \ldots$	Q^3

For stationary ergodic m_t:

$$Q = \Pr\left[\text{extinction} \middle| \Omega_m\right]$$

Ω_m **σ-algebra generated by $m_0, m_1, \ldots$**

heuristic notation: $Q = \Pr\left[\text{extinction} \middle| m_0, m_1, \ldots\right]$

If

$$\left|\mathrm{E}\left[\log(m_t)\right]\right| < \infty$$

$$\mathrm{E}\left[\left|\log\left(1 - \Pr(\xi(t) = 0)\right)\right|\right] < \infty$$

Then

$$\mathrm{E}\left[\log(m_t)\right] < 0 \Leftrightarrow \Pr\left[Q = 1\right] = 1$$

$$\mathrm{E}\left[\log(m_t)\right] > 0 \Leftrightarrow \Pr\left[Q < 1\right] = 1$$

Calculation of distribution and moments of Q

Define: $Q_t = \Pr\left[\text{extinction} \middle| m_t, m_{t+1}, \ldots\right]$

Then $Q_t = f\left(t, Q_{t+1}\right) \quad Q = \lim_{t \to -\infty} Q_t$

E.g. for a Poisson offspring distribution:

$$Q_t = \exp\left[-m_t\left(1 - Q_{t+1}\right)\right]$$

Iteration method:

choose:	simulate:	calculate:	simulate:	etc.
$Q_0{}^1$	$m_0{}^1$	$Q_{-1}{}^1$	$m_{-1}{}^1$	
$Q_0{}^2$	$m_0{}^2$	$Q_{-1}{}^2$	$m_{-1}{}^2$	
$\vdots$	$\vdots$	$\vdots$	$\vdots$	
$Q_0{}^k$	$m_0{}^k$	$Q_{-1}{}^k$	$m_{-1}{}^k$	

Q-values converge to a stationary distribution

(There are also approximations for E[Q], based on the moments of m)

Adaptive dynamics

Chance per time unit of birth of a mutant with trait value x: $\mu_t(x)$
(also varies randomly in time if dependent on resident population size)

Chance of successful invasion by that type of mutant *at time t*

$$\mu_t(x)\left(1-Q_t(x)\right)$$

with μ_t and Q_t *random variables*

Expected time until a successful invasion:

$$1+\sum_{n=1}^{\infty}\mathrm{E}\left[\prod_{t=1}^{n}\left(1-\sum_{x}\mu_t(x)\left(1-Q_t(x)\right)\right)\right]$$

Chance that a mutant with trait value z is the first to invade:

$$\mathrm{E}\left[\sum_{t=0}^{\infty}\mu_t(z)\left(1-Q_t(z)\right)\prod_{s=0}^{t}\left(1-\sum_{x}\mu_s(x)\left(1-Q_s(x)\right)\right)\right]$$

Adaptive dynamics-continued

NB subsequent Q_t are *not independent*.
Their autocorrelation depends on the properties of the environmental sequence.

For independent or positively autocorrelated m_t, the Q_t are positively autocorrelated.
This implies that increasing lags between invasions increases the chance of success.

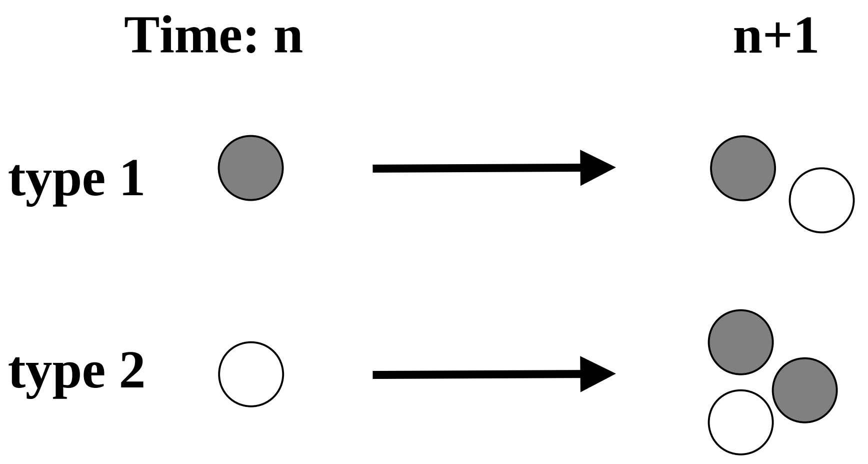
For alternating m_t they can become negatively autocorrelated.
In such environments, increasing lags between invasions is disadvantageous.

What does this imply for the effect of mutation chance on invasion success?

Multitype processes

Several different types of individuals, e.g.:

•male/female
•age (generation overlap)
•location
•genotype (AD: several types of mutant heterozygotes in polymorphic resident population)



$$\left(z_{n1}, z_{n2}\right)^T \longrightarrow \left(z_{(n+1)1}, z_{(n+1)2}\right)^T$$

Numbers of offspring of different individuals independent.
Offspring distributions may depend on parent's type

There are two kinds of multitype processses:

***Indecomposable*: every type of individual can eventually have progeny of any other type. E.g. genotypes in well-mixed populations.**
(These can be periodic, but periodic processes can be transformed to non-periodic ones, so we only consider non-periodic processes.)

***Decomposable*: there are (groups of) types that can not produce types belonging to other groups.**
E.g. females produce male/female offspring; males ‘produce’ only male offspring (themselves).

Expected numbers of offspring are given by the 'mean matrix' *M* with elements:

$$m_{hj} \qquad h=1, ..., d;\ j = 1, ..., d$$

= expected nr of offspring of type *j* that is produced by an individual of type *h*

ρ = dominant eigenvalue (Perron root) of *M*

Extinction with probability one if:

$$\rho < 1$$

or $\rho = 1$ **and each type can eventually have progeny of a type that has a positive chance of having no offspring**

Positive establishment chance if: $\rho > 1$

Extinction probability : $Q = (Q_1, \ldots, Q_d)^T$

Q_h **= extinction probability if initially there is one ancestor of type** h

generating function: $f(s) = (f_1(s), \ldots, f_d(s))^T$

with:

$$f_h(s) = \mathrm{E}_h\left[s_1^{\xi_1}, \ldots, s_d^{\xi_d}\right]$$

$$= \sum_{k_1} \ldots \sum_{k_d} \Pr\left[\xi_{h1} = k_1 \wedge \ldots \wedge \xi_{hd} = k_d\right] \cdot s_1^{k_1} \ldots s_d^{k_d}$$

Then:

$$Q = f(Q), \text{ with } 0 \le Q_h < 1 \text{ for all } h$$

If ρ > 1: there is one such Q

Approximation for slightly supercritical indecomposable processes

Mean matrix ($\varepsilon > 0$):

$$M_\varepsilon = \left(m_{hj}(\varepsilon)\right)_{h,j=1}^{d}$$

with dominant eigenvalue $\rho(\varepsilon) > 1$, $\rho(\varepsilon) \to 1$ as $\varepsilon \to 0$

and suppose that for all ε there is a $n(\varepsilon)$ such

that all entries of $M_\varepsilon^{n(\varepsilon)}$ are positive

(i.e. M_ε is positively regular)

Let $u(\varepsilon)$ be the corresponding left eigenvector (stable state distribution) and $v(\varepsilon)$ the right eigenvector (reproductive value), with:

$$\boldsymbol{u}^T \boldsymbol{v} = |\boldsymbol{u}| = 1$$

and define:

$$B(\varepsilon) = \sum_h \sum_j \sum_k u_h(\varepsilon) v_j(\varepsilon) \mathrm{E}\left[\xi_{hj}\left(\xi_{hk} - \delta_{jk}\right)\right] v_k(\varepsilon)$$

$$\delta_{jk} = 1 \text{ if } j = k, 0 \text{ otherwise}$$

If

$$\liminf_{\varepsilon \to 0} B(\varepsilon) = 0$$

and there is a $\delta > 0$ such that

$$\sup_{i,\varepsilon} \mathbf{E}\left[\left(\xi_{i,1}{}^2 + \ldots + \xi_{i,d}{}^2\right)^{1+\delta}\right] < \infty$$

then, as $\varepsilon \to 0$

$$1 - Q_h(\varepsilon) = \frac{2(\rho(\varepsilon) - 1)}{B(\varepsilon)} v_h(\varepsilon) + o(\varepsilon)$$

Adaptive dynamics

Chance per period of a mutant of type *h*, with trait value (or allele effect) *x*: $\mu_h(x)$

Chance of successful invasion by a mutant with trait value *x*:

$$\sum_h \mu(x)\left(1-Q_h(x)\right)$$

Expected time until a successful invasion:

$$\frac{1}{\sum_h \sum_x \mu_h(x)\left(1-Q_h(x)\right)}$$

Probability value *z* is the first:

$$\frac{\sum_h \mu_h(z)\left(1-Q_h(z)\right)}{\sum_h \sum_x \mu_h(x)\left(1-Q_h(x)\right)}$$

And more...

- Multitype inhomogeneous processes.
- If mutants affect resident population size or other resources, mutant reproduction depends on mutant population size (and maybe history). (Some results by Klebaner, Jagers and Sagitov: can produce slower than exponential growth rates in near-critical processes.)
- Bi-sexual BPs (Alsmeijer)
- Sibling dependence(Olofsson)