Modelling invasions and calculating establishment success chances

Patsy Haccou, Leiden University

3rd Nordic EWM Summer School for
PhD Students in Mathematics
University of Turku, June 22-27, 2009

Biological examples of invaders

- Exotic species
- Biocontrol agents
- Mutants
- Tumour cells
- Insecticide or pesticide resistance genes
- Artificially modified genes
- Pathogens

What kind of models for invasion studies?

Usually initial numbers are small

↓

Fate is largely determined by chance, e.g.
- variation in offspring numbers
- hybridization and backcross chance (in introgresion)
- interaction with resident individuals

↓

Stochastic processes

Some classical population models

discrete time $$x(n+1) = m \cdot x(n)$$

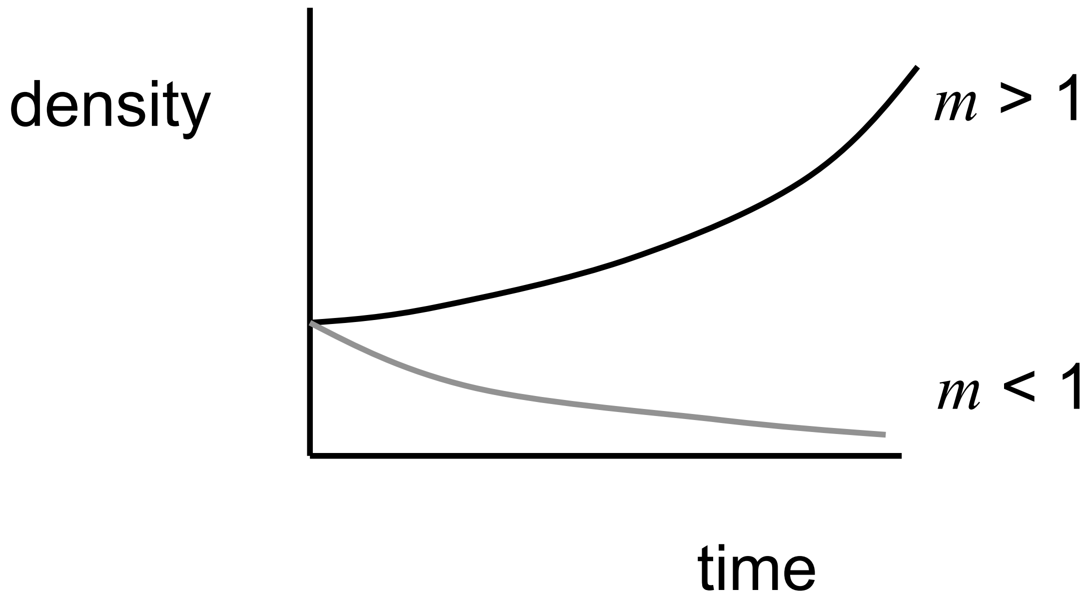
continuous time $$\frac{dx}{dt} = m \cdot x$$

m: (mean) number of offspring per individual

- Deterministic
- x: density, continuous

Predictions

$$x(n+1) = m \cdot x(n) \longrightarrow x(n) = m^n x(0)$$



Implications

$$x(n+1) = m \cdot x(n)$$

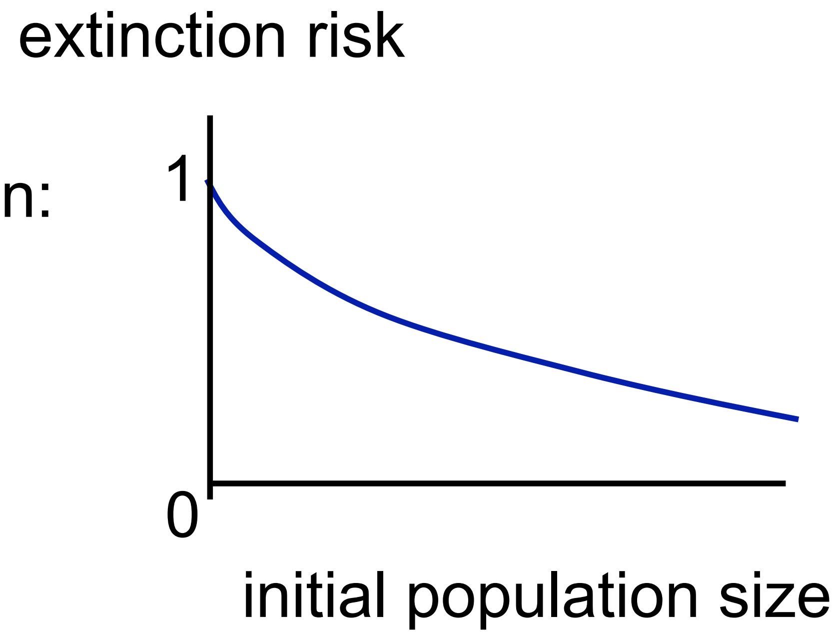
when m < 1: never success, always extinction
when $m \geq$ 1: always establishment, never extinction
independent of initial population size (as long as $x(0) > 0$)

Typical result of deterministic models

Small populations

individuals are discrete entities -> jumps in x
inter-individual variation in offspring
establishment chance depends on population size

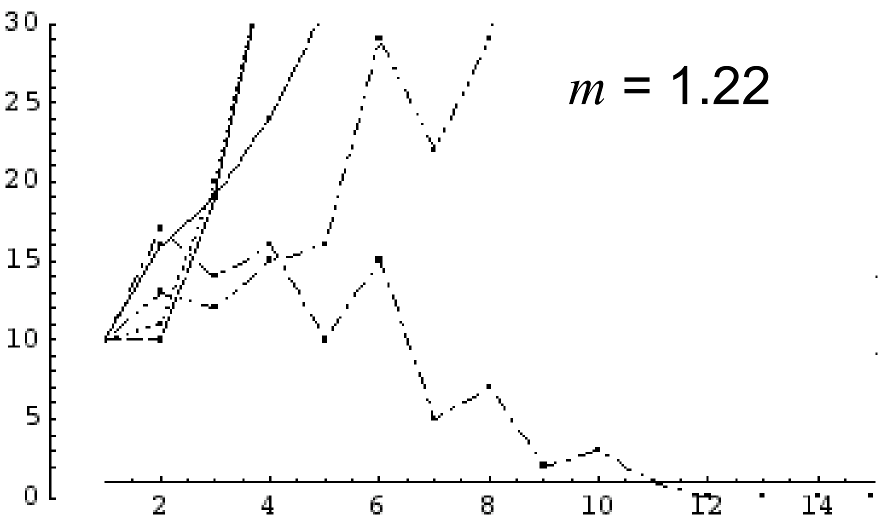
e.g. independent reproduction:
population size = 1: risk Q
population size = 2: Q^2
population size = n : Q^n

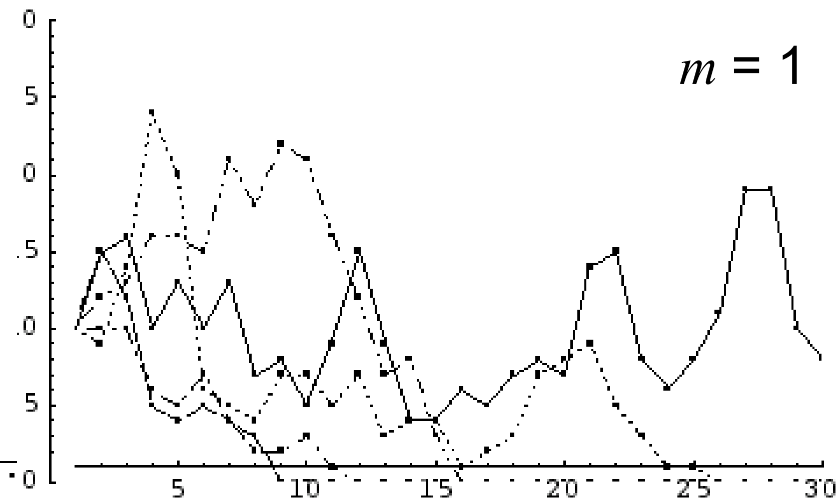


Some results

Populations may be successful or not if $m > 1$
Always die out if $m \leq 1$

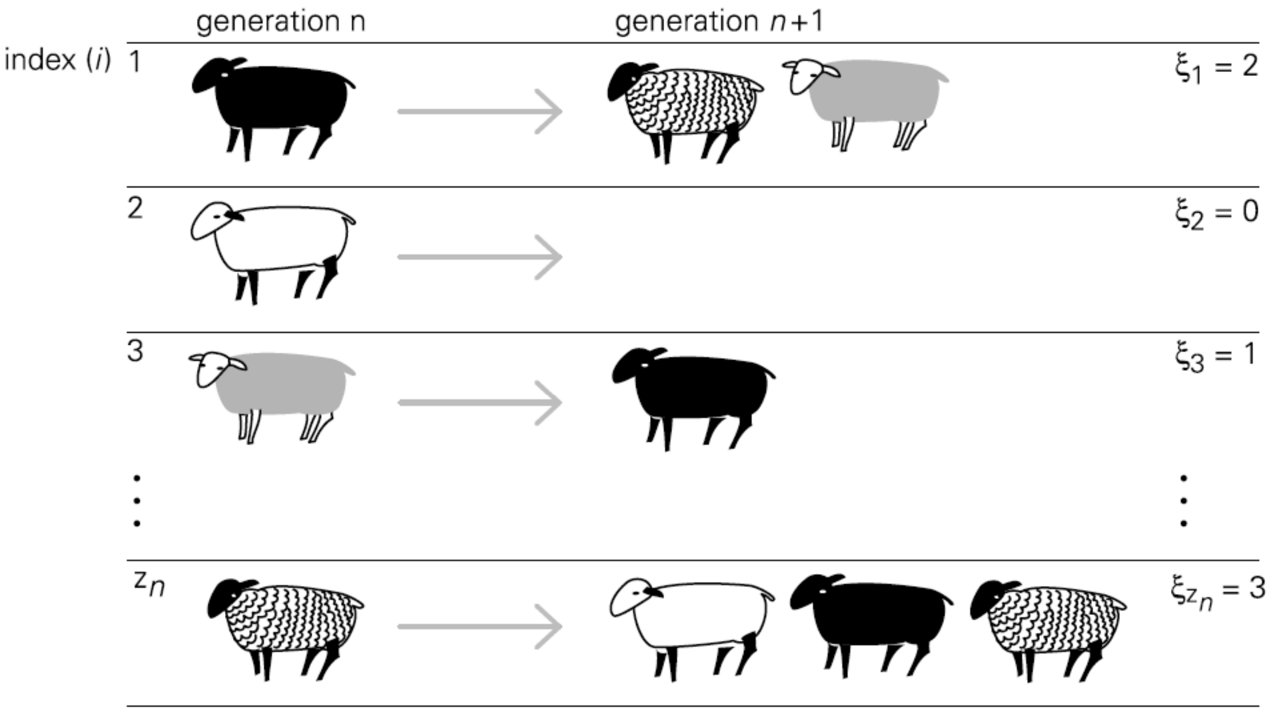
Examples: fate of 5 populations of 10 individuals
(Geometric offspring)





Basic model: branching process (Galton and Watson)

- Independent reproduction
- Nonoverlapping generations
- Identical offspring distributions

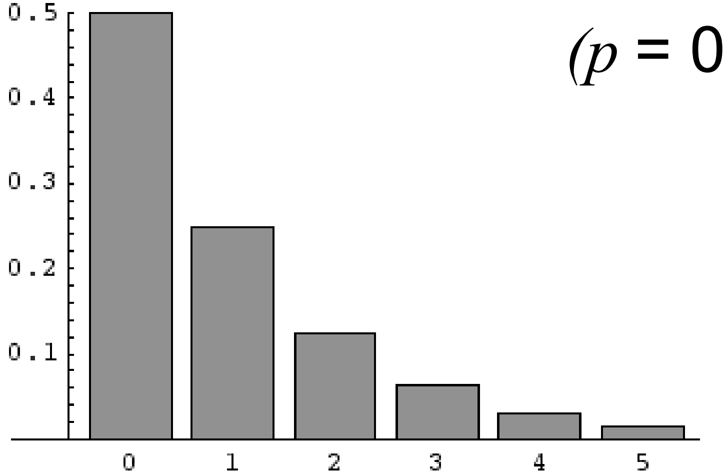


Popular offspring distributions

Geometric

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

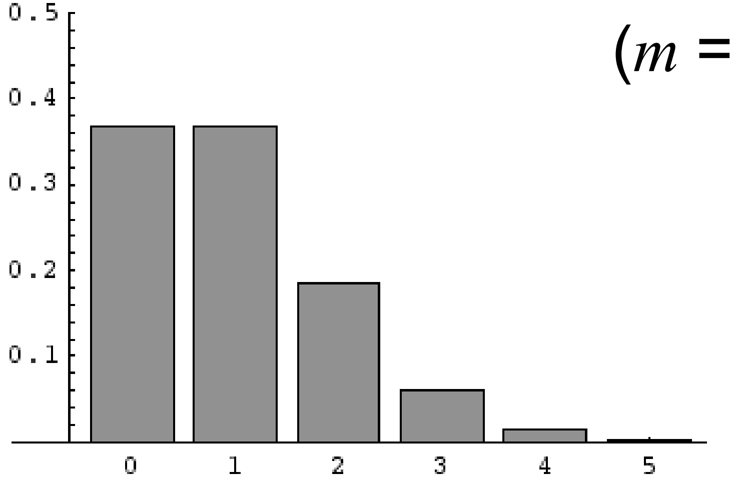
(*p* = 0.5)



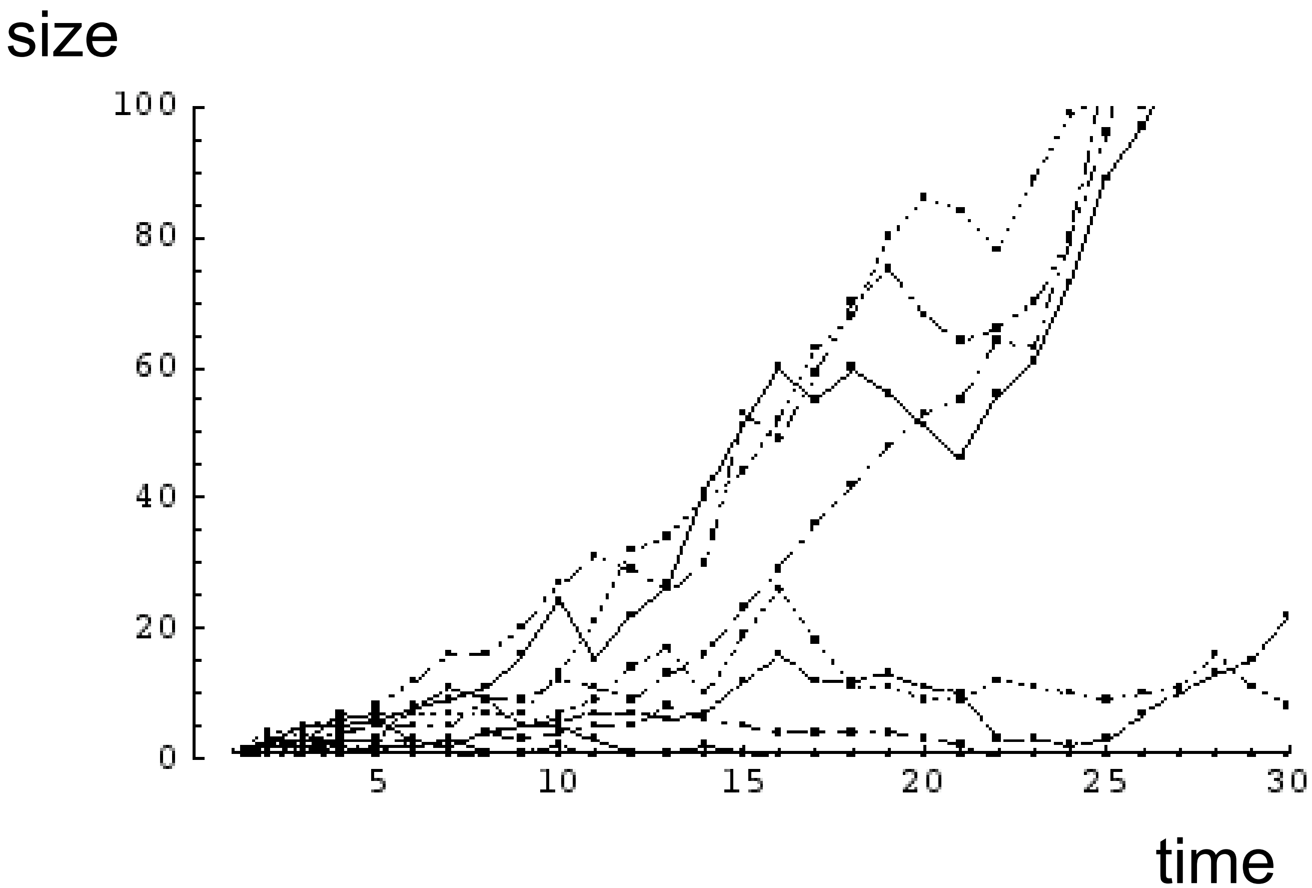
Poisson

$$\Pr[k \text{ offspring}] = e^{-m}\frac{m^k}{k!}$$

(*m* = 1)

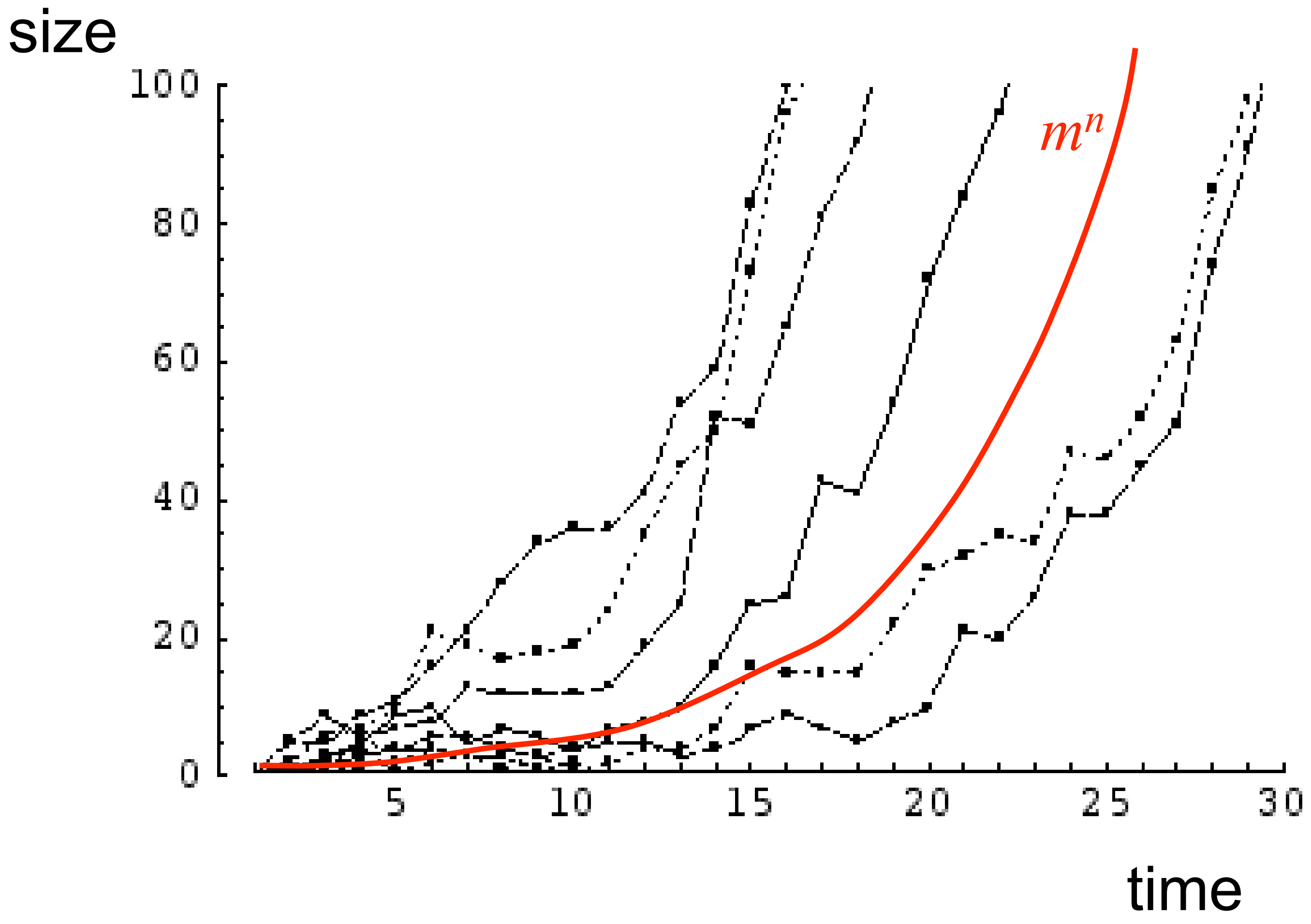


Example: 20 runs



Poisson(1.1) distributed offspring numbers

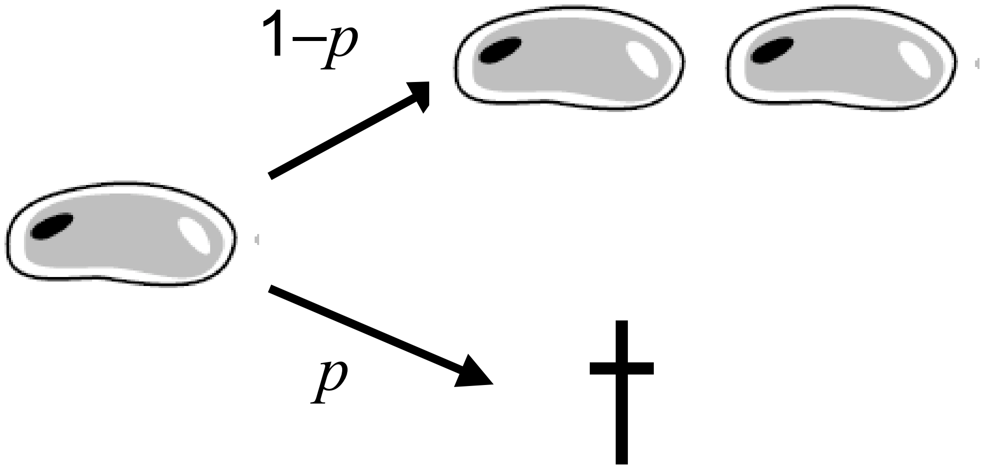
Example: 20 runs



Poisson(1.2) distributed offspring numbers

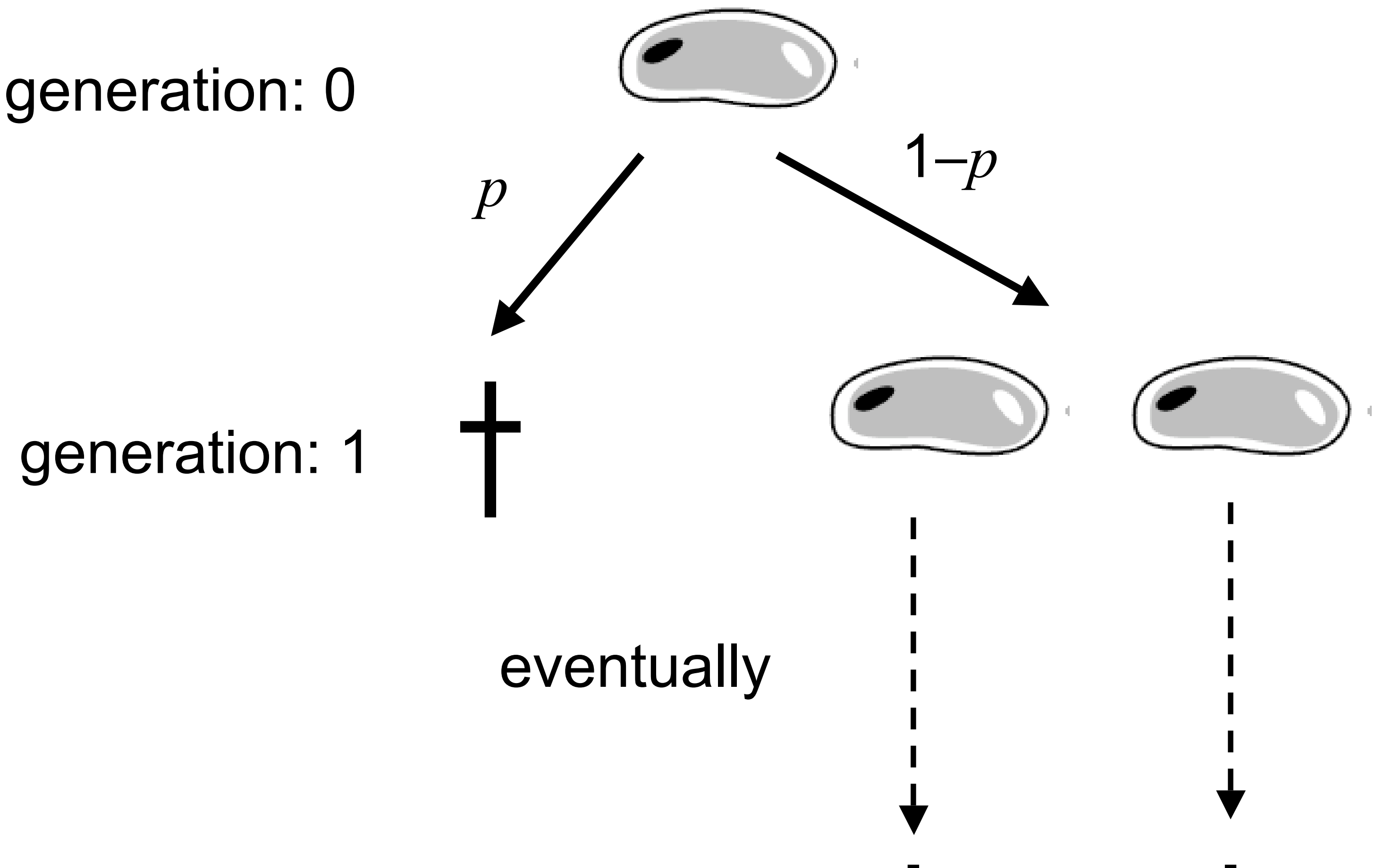
Calculation of extinction probability

Example “splitting process”



Q: probability of extinction if we start with 1 individual

Roads to extinction

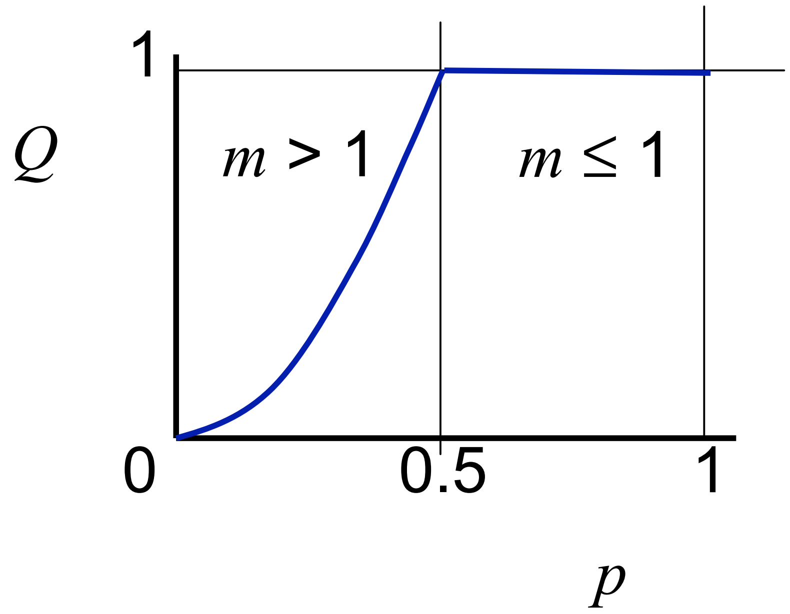


$$Q = p + (1 - p)Q^2$$

Calculation of Q

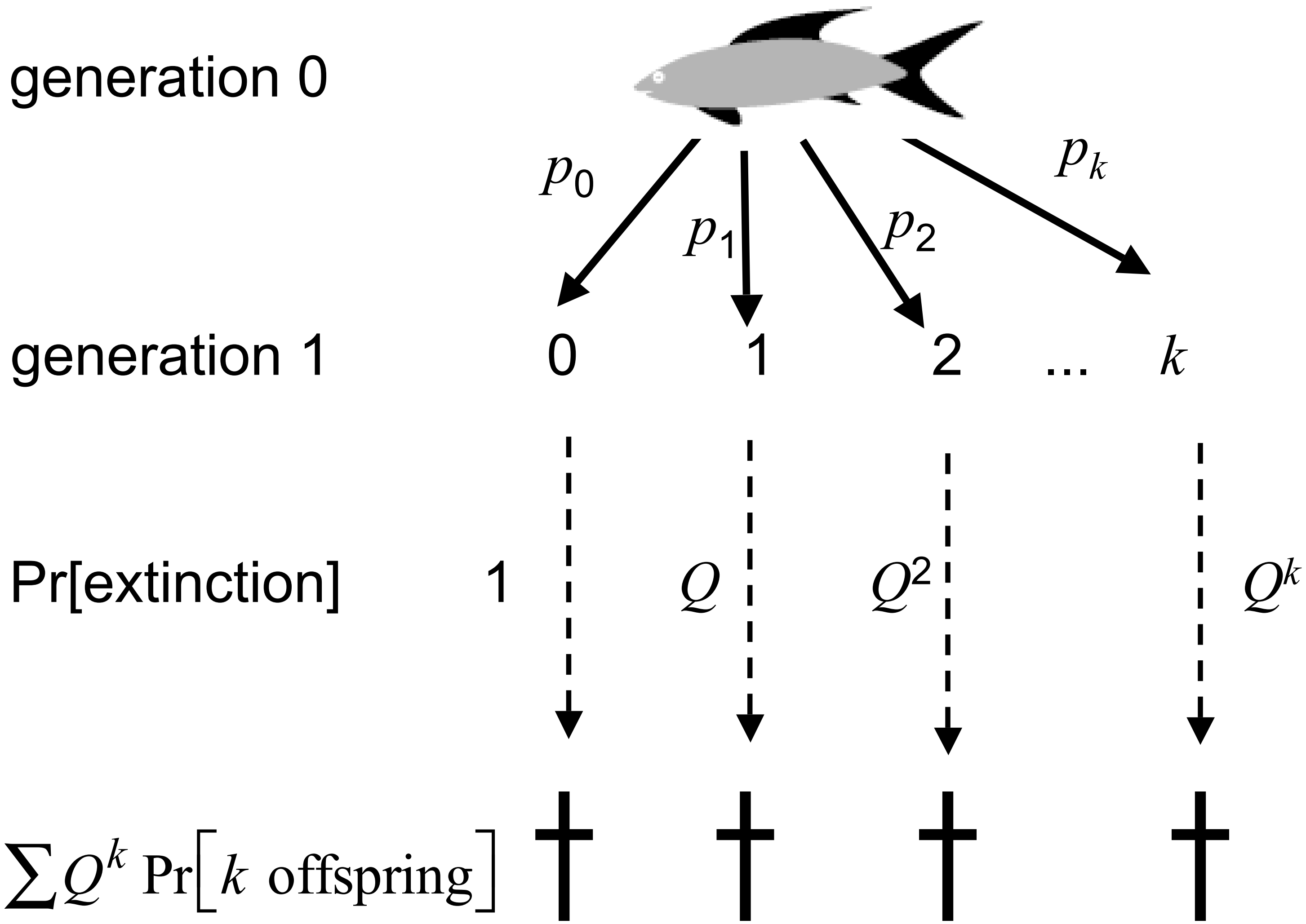
$$Q = p + (1-p)Q^2 \longrightarrow \text{solutions: 1 and } \frac{p}{1-p}$$

smallest root = extinction probability



$$m = 2(1-p)$$

General calculation of Q



$$Q = \sum_k Q^k \Pr\left[k \text{ offspring}\right]$$

Facts about Q

$$f(s) = \sum_k s^k \Pr[\xi = k]$$ probability generating function of offspring distribution

For $s \in [0,1]$:

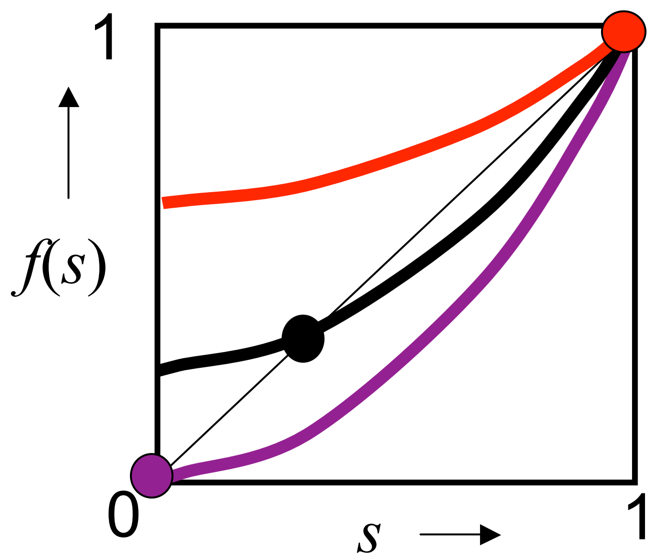
$f(s) \geq 0$

all derivatives of $f(s) \geq 0$

$f(0) = \Pr[\xi=0]$

$f(1) = 1$

$f'(1) = m$



Q is smallest root of: $Q = f(Q)$

$m \leq 1$ $\rightarrow$ certain extinction

$m > 1$ and Pr[0 offspring] > 0 $\rightarrow$ $0<Q<1$

Pr[0 offspring] = 0 $\rightarrow$ $Q = 0$

Some terminology

Subcritical branching process: $m < 1$

Extinction certain, expected extinction time finite

Critical branching process: $m = 1$

Extinction certain, expected extinction time infinite

Supercritical branching process: $m > 1$

Positive establishment chance

Example: Poisson(m) offspring

$$f(Q) = \sum_{k=0}^{\infty} e^{-m} \frac{m^k}{k!} Q^k = e^{-m} e^{mQ}$$

$$\Rightarrow \quad Q = e^{-(1-Q)m}$$

No explicit solution.
Solve numerically or approximate.

Approximation of Q

For slightly supercritical processes: Q close to 1

$$f(Q) = f(1) + f'(1)(Q-1) + \frac{1}{2} f''(1)(Q-1)^2 + O\left((Q-1)^3\right)$$

$$f(s) = \mathrm{E}\left[s^x\right] \Rightarrow f(1) = 1, f'(1) = \mathrm{E}[x], f''(1) = \mathrm{E}\left[x(x-1)\right]$$

$$f(Q) \approx 1 + m(Q-1) + \frac{1}{2}\mathrm{E}\left[x(x-1)\right](Q-1)^2$$

$$(1-Q) \approx \frac{2(m-1)}{\mathrm{E}\left[x(x-1)\right]} \approx \frac{2(m-1)}{\mathrm{Var}[x]}$$

Applications of the GWBP to biology

Main assumptions:

1. All reproductive individuals are equivalent, with identical offspring distributions
2. Individuals do not affect each other’s reproduction
3. Offspring distributions do not change in time

At first sight not so realistic. However......

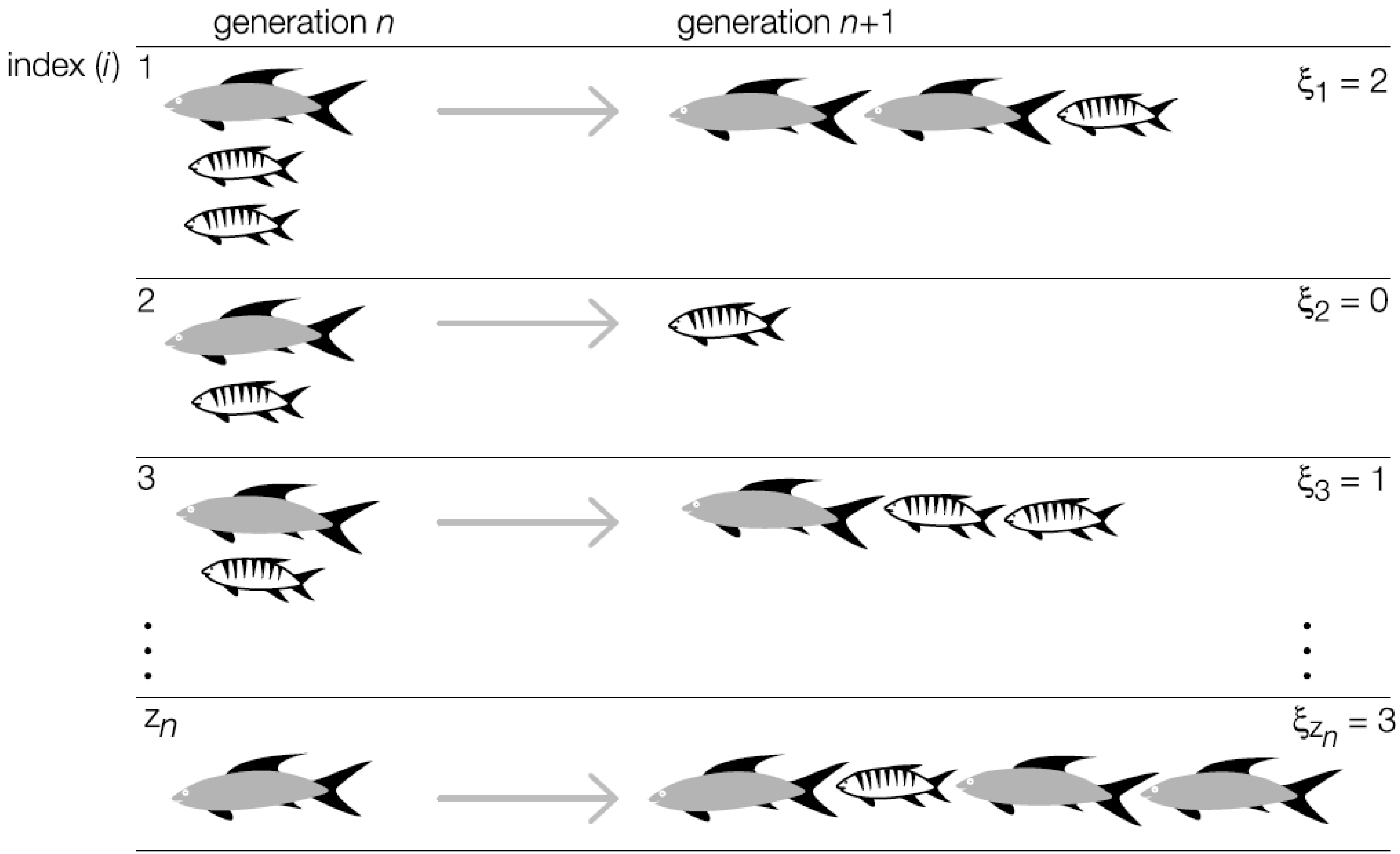
1. All *reproductive* individuals are equivalent

Clonal reproduction: unicellulars, e.g. bacteria, yeast

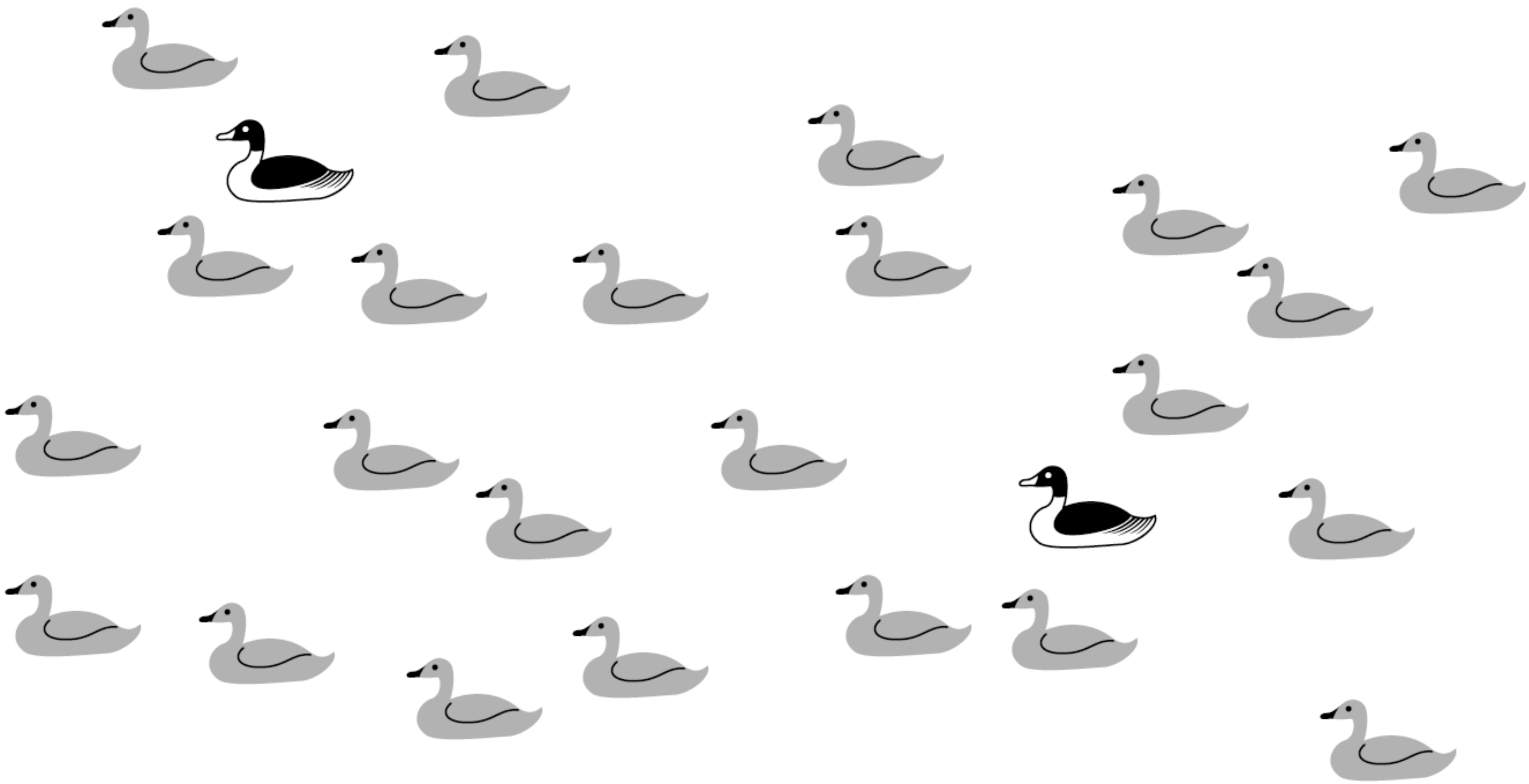
Hermaphrodites, e.g. monoecious plants

Two-sex species: only count females, provided:
enough males available
no genetic difference in reproduction,
e.g. heterozygous mutants in a homozygous resident population

Counting only females

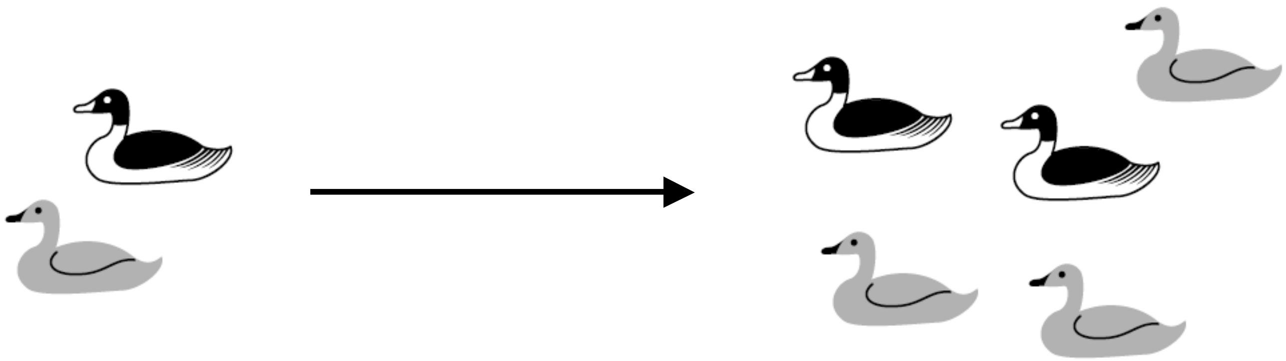


Invasion of mutants:
count only heterozygotes

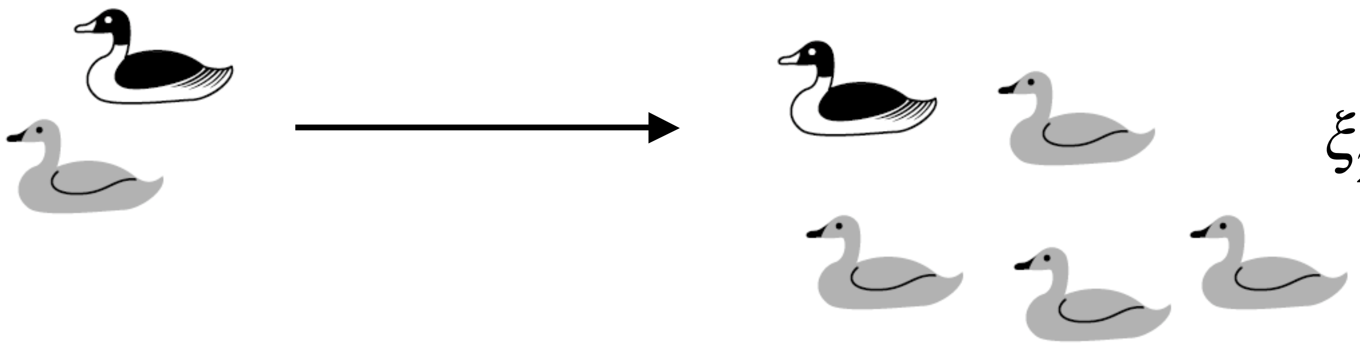


mutant: heterozygote, mates with homozygous resident
-> offspring are heterozygous too

Mutant invasion as a GWBP



$\xi_1 = 2$



$\xi_2 = 1$

2. Individuals do not affect each other's reproduction

Initial growth in environment with abundant resources.

Invasion in a large resident population that keeps the resource supply at a fixed level.
Invaders do not mate and compete with each other, but only with residents.

Example

Resident population large ->
deterministic density-dependent model, e.g.

$$x(n+1) = \frac{ax(n)}{1+bx(n)}$$

$a > 1$: initial per-capita growth
$b > 0$: intra-specific competition

Equilibrium: $\hat{x} = \frac{a-1}{b}$

Invader model GWBP with e.g. $m = \frac{a_m}{1+c\hat{x}} = \frac{a_m}{1+c(a-1)/b}$

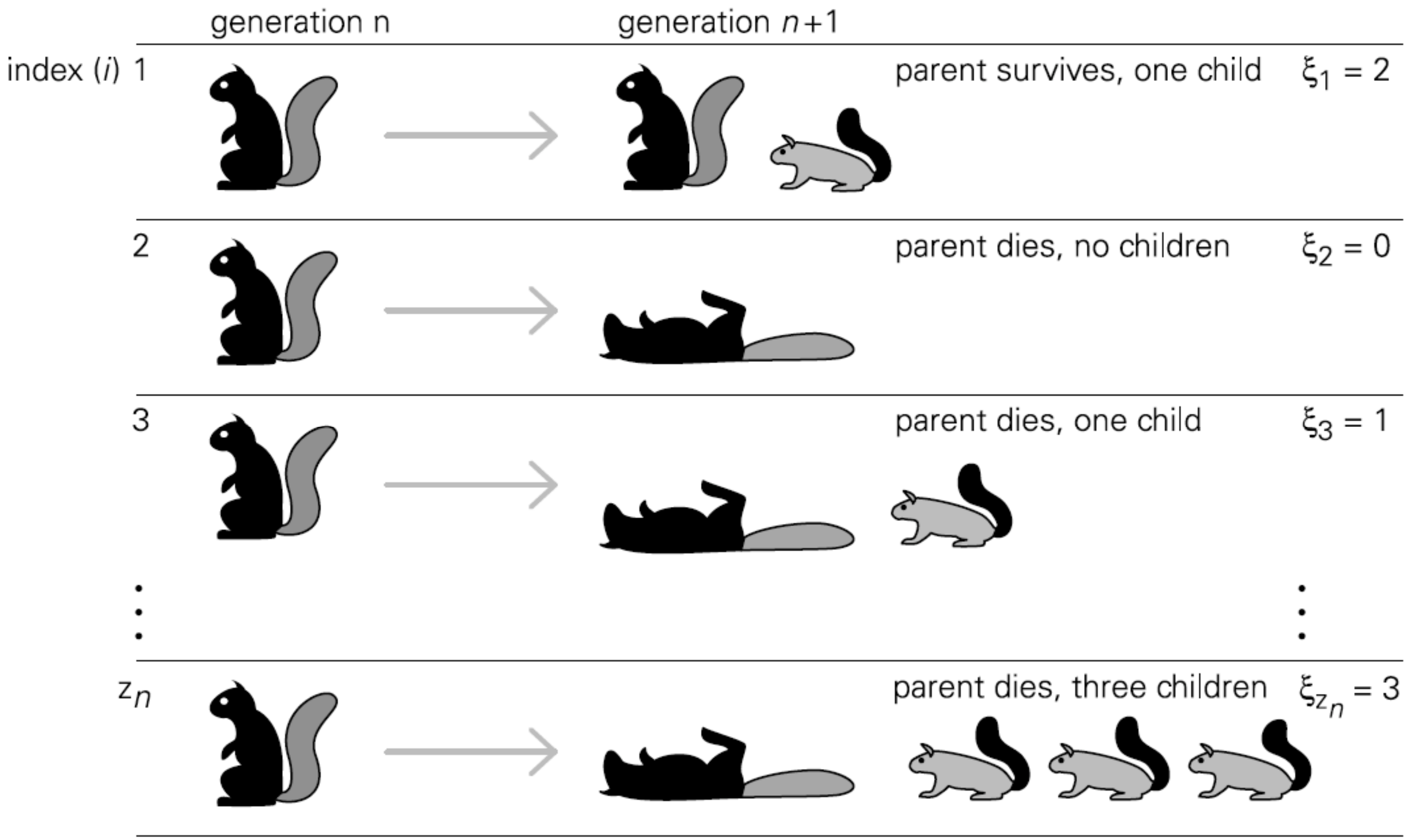
$a_m > 0$: per-capita growth of invader without competition
$c > 0$: inter-specific competition

3. Offspring distributions do not change in time

Non-overlapping generations: reproduction only once in a lifetime.

Repeated reproduction, adults equivalent to juveniles, and constant mortality chance (no age-dependence), e.g. determined by predation risk.

Overlapping generations as a GWBP



From extinction to invasion probability

BP model: Q = extinction probability
-> $1-Q$ = establishment success chance
But: modelpopulations that do not go extinct grow infinitely large

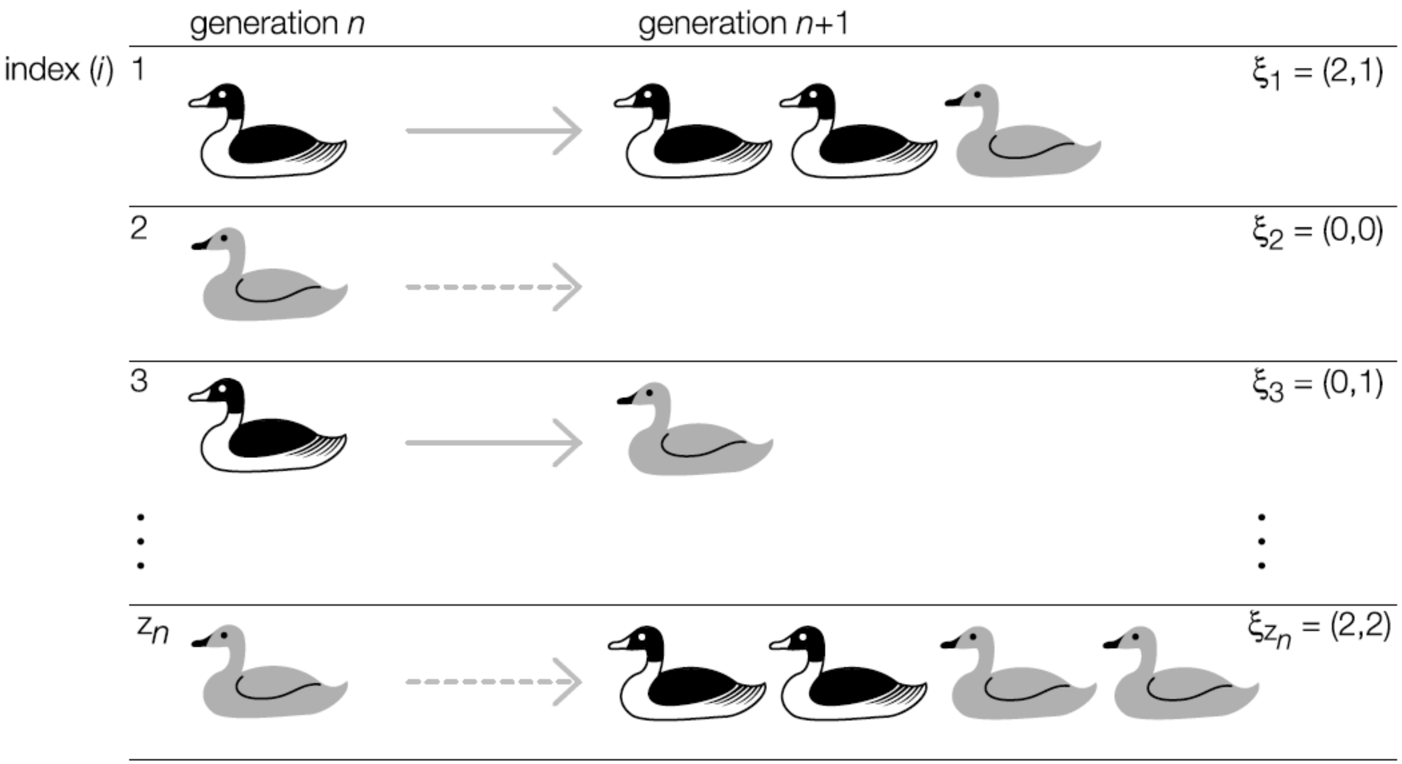
Problems:
(1) Realistically: populations have limited size
(2) At large numbers invaders will affect each other

(1) Numerical analysis reveals: $1-Q$ is a good approximation for the chance to grow up to a large, fixed level.
(2) If $1-Q > 0$ invasion is possible, but invaders might not take over a resident population completely (coexistence). This has to be examined separately.

Generalizations of the GWBP

Multitype processes
Time-inhomogeneous processes
Bisexual BP
Population size -dependent

Generalizations of the GWBP: Multi type processes



Mean matrix

m_{hj} = expected number of offspring of type j produced by 1 individual of type h

$$M = \begin{pmatrix} m_{11} & m_{12} & \cdots & m_{1d} \\ m_{21} & . & . & . \\ \vdots & . & . & \vdots \\ m_{d1} & . & \cdots & m_{dd} \end{pmatrix}$$

Different kinds of multitype processes

Indecomposable: each type can *eventually* produce every other type, e.g.:

$$M = \begin{pmatrix} 0 & 3 \\ 1 & 2 \end{pmatrix}$$

Type 1 produces only type 2 offspring, but can have grandchildren of both types.

Decomposable: absorbing sets, e.g.

$$M = \begin{pmatrix} 2 & 1 \\ 0 & 1 \end{pmatrix}$$

Type 2 can only ever produce type 2

Periodic indecomposable processes

Example:

$$M = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix} \quad = M^3 = M^5 = \ldots = M^{2n+1}, n = 0,1,2,\ldots$$

$$M^2 = \begin{pmatrix} 1 & 0 \\ 0 & 1 \end{pmatrix} = M^4 = M^6 = \ldots M^{2n}$$

transformation to nonperiodic process: only consider process at even n, with mean matrix

$$M' = M^2$$

Extinction of indecomposable multitype processes

ρ: largest eigenvalue of M

$\rho < 1$: Subcritical process: certain extinction in finite time
$\rho = 1$: Critical process: certain extinction, infinite expected time
$\rho > 1$: Supercritical process: extinction probability < 1

Extinction probability depends on initial type.
If no extinction occurs expected numbers of all types grow with rate ρ.

Extinction of decomposable processes

Extinction probability depends on initial type, may be 1 for some types and less for others.

In processes that don't go extinct, some types may go extinct, while others grow, different types can grow at different rates, e.g.

$$M = \begin{pmatrix} 0.1 & 0 \\ 0 & 2 \end{pmatrix}$$

ρ=2, but if first individual has type 1, extinction is certain. If first individual has type 2, the process is supercritical, and non-extinct populations grow at rate 2.

Calculation of extinction probabilities for multitype processes

$$Q_h = \Pr\left[\text{extinction if initial individual has type } h\right]$$

pgf of offspring distribution of type h:

$$f_h\left(s_1,\ldots s_d\right) = \mathrm{E}\left[s_1^{\xi_{h1}} s_2^{\xi_{h2}} \ldots s_d^{\xi_{hd}}\right]$$

ξ_{hj} = number of type j children produced by a parent of type h, then

$$Q_h = f_h\left(Q_1,\ldots,Q_d\right)$$

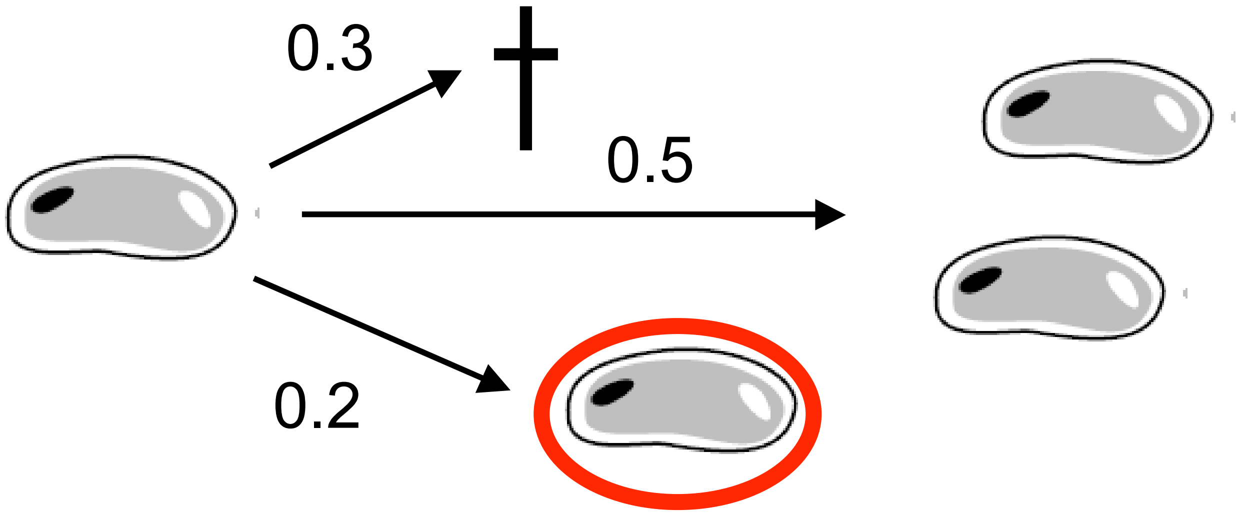
Proof

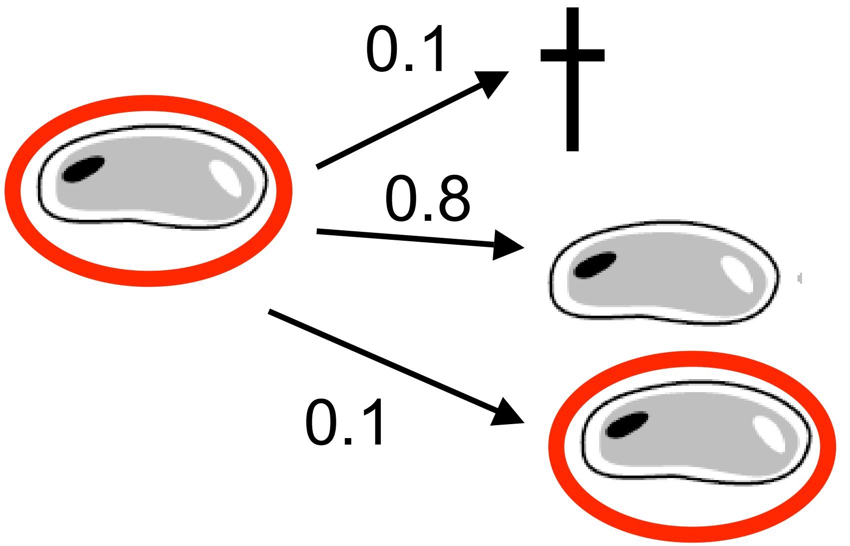
$$\Pr\left[\text{extinct if initial type is } h\right]$$

$$= \sum_{x_1} \dots \sum_{x_d} \Pr\left[\xi_{h1} = x_1, \dots, \xi_{hd} = x_d\right] Q_1^{x_1} Q_2^{x_2} \dots Q_d^{x_d}$$

$$= \mathrm{E}\left[Q_1^{\xi_{h1}} Q_2^{\xi_{h2}} \dots Q_d^{\xi_{hd}}\right]$$

Example: spore formation



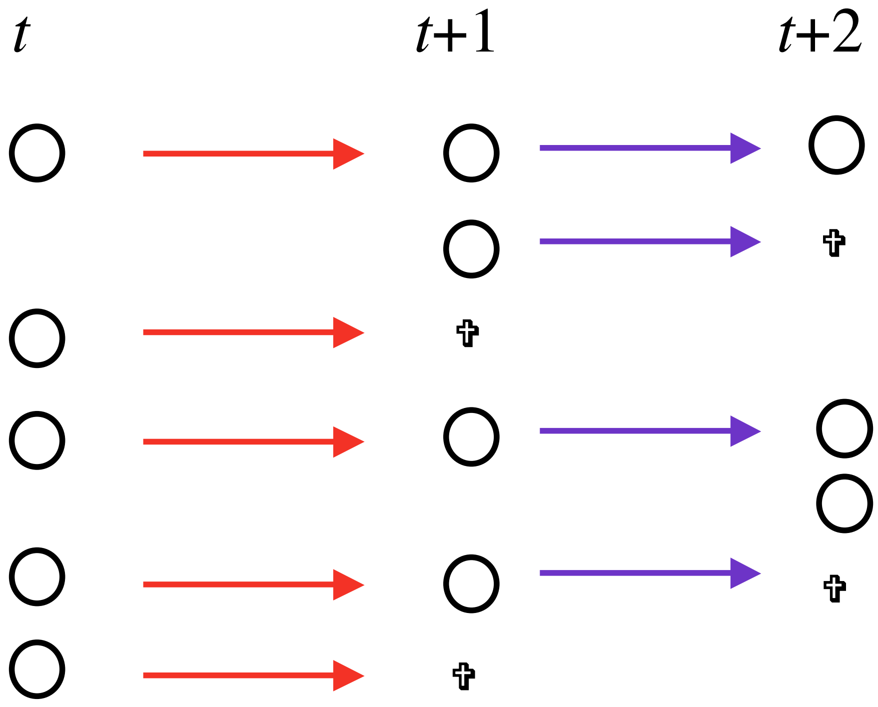


$$Q_1 = 0.3 + 0.5Q_1^2 + 0.2Q_2$$

$$Q_2 = 0.1 + 0.8Q_1 + 0.1Q_2$$

Generalizations of the GWBP: Changing environments

Smith (1968), Smith & Wilkinson (1969): Inhomogeneous BP



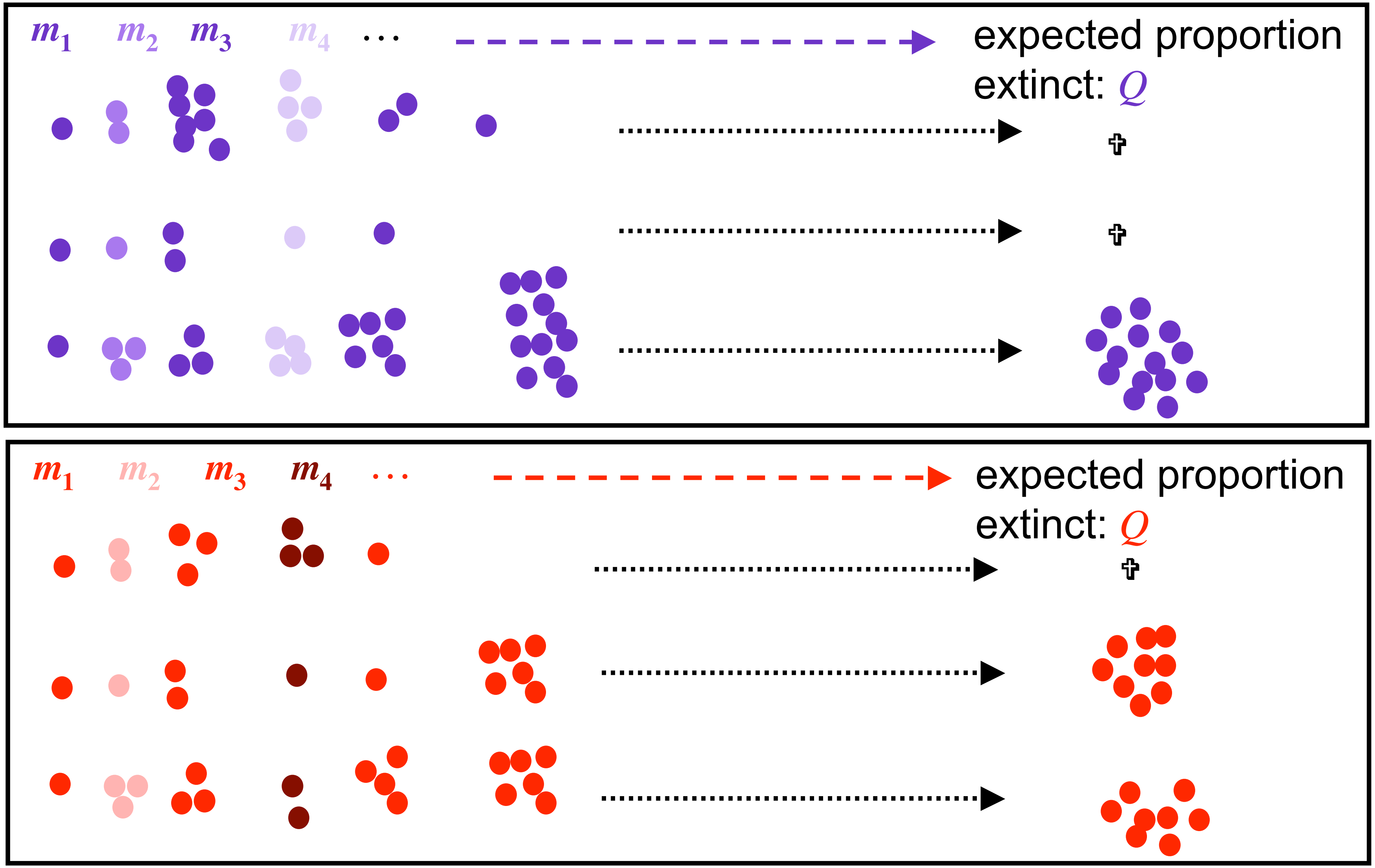
Expected # offspring: m_t m_{t+1}

Extinction of inhomogeneous processes

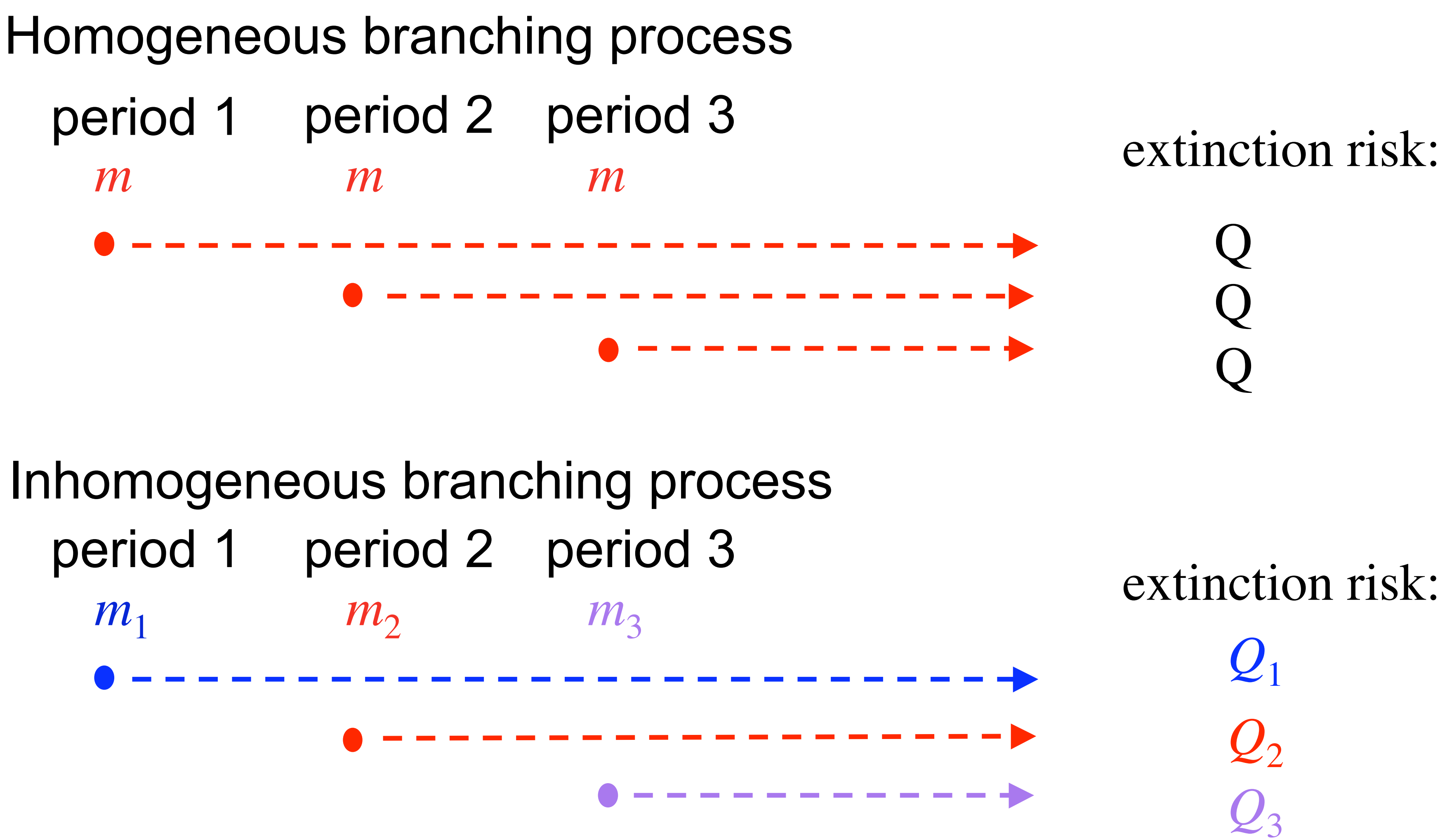
$\mathrm{E}[\log m_t] \leq 0$ Certain extinction: $Q = 1$

$\mathrm{E}[\log m_t] > 0$ Extinction probability Q is a random variable with $\mathrm{E}[Q] < 1$

Q is a random variable: example



Extinction depends on invasion time



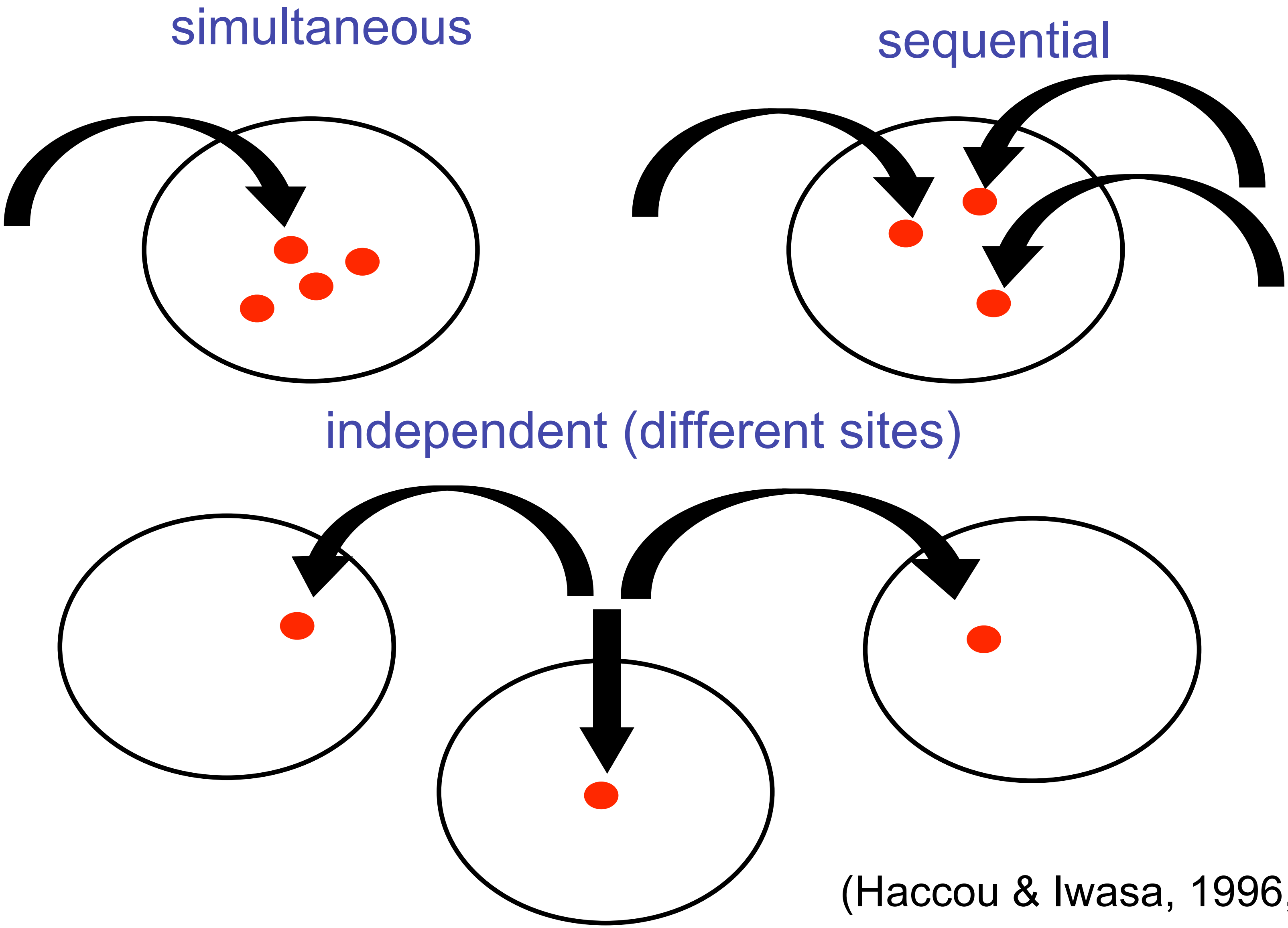
Numerical calculation of Q

Q_t: Pr[1 invader at t fails],
$f_t(s)$: pgf of offspring distribution at t

$$Q_t = \sum_k \Pr\left[\text{invader at } t \text{ has } k \text{ offspring}\right] Q_{t+1}^k$$
$$= f_t\left(Q_{t+1}\right)$$

Backward iteration (i.i.d. m_t values):
Start with array of (arbitrary) Q-values in (0,1)
Simulate random m-values
Calculate Q-values 1 timestep *before*
Continue until distribution is stable

Invasion mode affects establishment



(Haccou & Iwasa, 1996, TPB)

Invasion mode and extinction risk

Simultaneous $$Q_{sim} = \mathrm{E}\left[Q_t^n\right] = \mathrm{E}\left[Q^n\right]$$

Sequential $$Q_{seq} = \mathrm{E}\left[\prod_{t=1}^{n} Q_t\right]$$

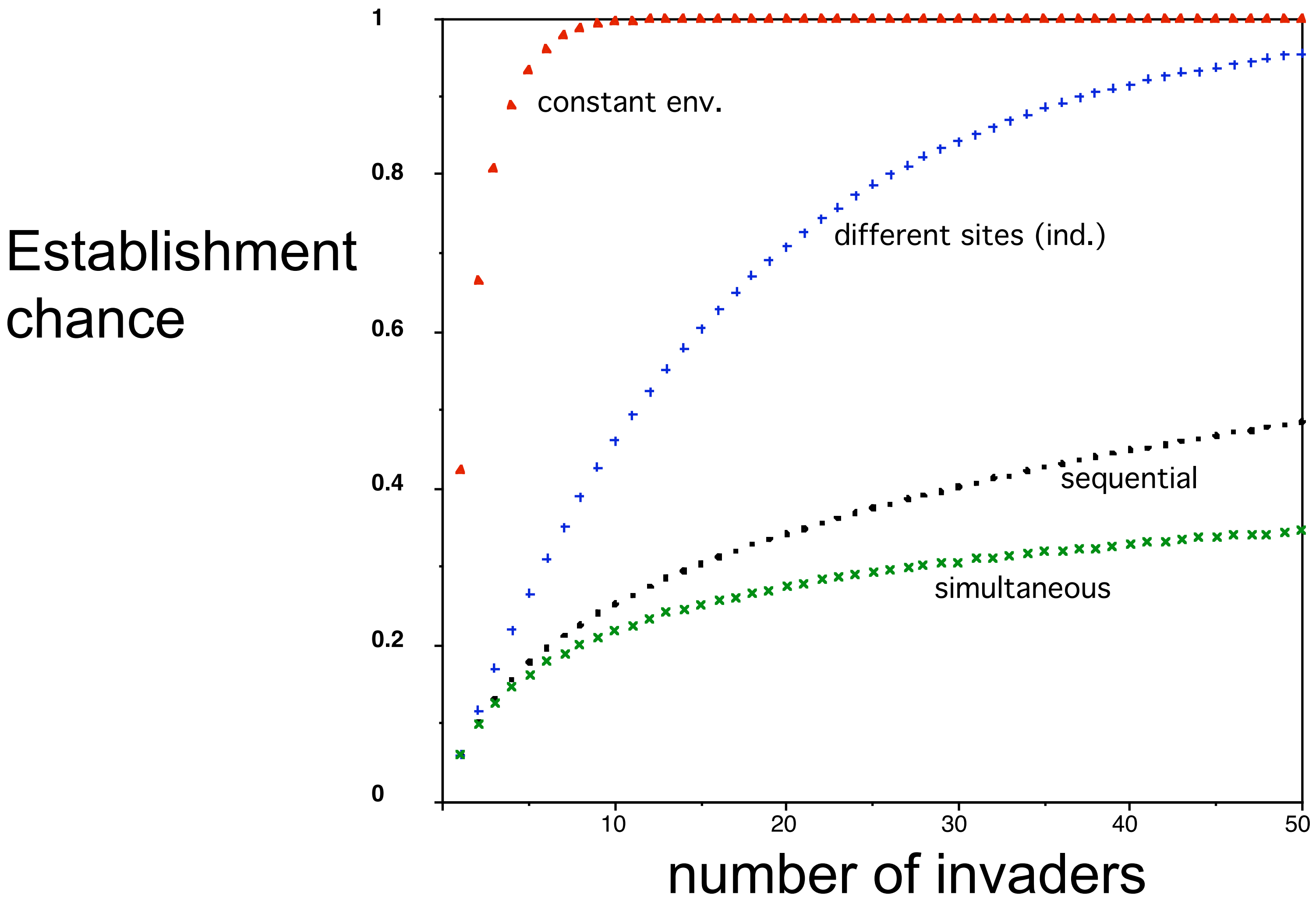
Independent sites $$Q_{ind} = \left(\mathrm{E}\left[Q_t\right]\right)^n = \left(\mathrm{E}\left[Q\right]\right)^n$$

Jensen's inequality: $\left(\mathrm{E}\left[Q\right]\right)^n \le \mathrm{E}\left[Q^n\right]$ $\qquad Q_{ind} \le Q_{sim}$

Hölder's inequality: $\mathrm{E}\left[\prod_{t=1}^{n} Q_t\right] \le \left(\prod_{t=1}^{n} \mathrm{E}\left[Q_t^n\right]\right)^{\frac{1}{n}} = \mathrm{E}\left[Q^n\right]$ $\qquad Q_{seq} \le Q_{sim}$

Haccou & Vatutin (TPB, 2003): $Q_{ind} \le Q_{seq}$ if m_t are independent

Numerical results



m_t i.i.d. uniform, $\mathrm{E}[m_t] = 1.3$, $\mathrm{Var}[m_t] = 0.5$, Poisson distr. offspring