Reminder: What is adaptive dynamics?

AD: trait substitution sequence (TSS)

The trait substitution sequence (TSS, Metz et al., 1996) proceeds from the assumption of rare mutations: mutation probability multiplied by γ → 0

- time t rescaled as t/γ
- requires only to know the fixation outcome of two-type populations
- evolution proceeds through a sequence of mutant invasions and fixations: jump process over the trait space, called TSS: trait substitution sequence.

AD: canonical equation of adaptive dynamics

The canonical equation of adaptive dynamics (Dieckmann and Law, 1996) proceeds from an extra assumption of small mutations applied to the TSS: mutation kernel rescaled by ε → 0, and time t is rescaled as t/ε²

- Deterministic ODE:
  \[ \frac{dx}{dt} = \frac{1}{2} \sigma^2 \mu(x) \bar{n}(x) \frac{\partial}{\partial y} f(x, y) \]
  \[ \sigma^2 \text{ variance of the mutation steps} \]
  \[ \mu \text{ probability of mutation at each birth event} \]
  \[ \bar{n} \text{ equilibrium size of a pure x-type population} \]
  \[ f(x, y) \text{ invasion fitness of a mutant type } y \text{ in an equilibrium } x\text{-type population} \]
The canonical equation of adaptive dynamics (Dieckmann and Law, 1996) proceeds from an extra assumption of small mutations applied to the TSS: mutation kernel rescaled by $\varepsilon \to 0$, and time $t$ is rescaled as $t/\varepsilon^2$.

- Deterministic ODE:
  \[
  \frac{dx}{dt} = \frac{1}{2} \sigma(x)^2 \mu(x) \bar{n}(x) \frac{\partial}{\partial y} f(x,y)
  \]
  - $\sigma^2$ variance of the mutation steps
  - $\mu$ probability of mutation at each birth event
  - $\bar{n}$ equilibrium size of a pure $x$-type population
  - $f(x,y)$ invasion fitness of a mutant type $y$ in an equilibrium $x$-type population

### Hidden assumption

- Except in population genetics, isolated populations go extinct a.s.
- Too rare mutations $\implies$ Extinction before first mutation
- $\implies$ Assumption of large populations
- Consequence:
  - Population eventually reaches a stable equilibrium
- Goal: keep population finite and stochastic to include drift in the TSS and the canonical equation.
Hidden assumption

- Except in population genetics, isolated populations go extinct a.s.
- Too rare mutations $\implies$ Extinction before first mutation
- $\implies$ Assumption of large populations
- Consequence:
  - only advantageous mutants can invade and fix
  - direction of evolution is deterministic (no drift).
- Goal: keep population finite and stochastic to include drift in the TSS and the canonical equation.
Model assumptions

- We consider an individual-based model of a discrete, isolated population:
  - continuous-time Markov chain
  - structured: individuals bear types (traits)
  - (possibly) varying size $N_t$ that does not go to $\infty$
  - population never becomes extinct ($N_t \geq 1$)

- Interpretation: separation of timescales of mutations and extinction.
- Mathematical notion of quasistationarity: population size is conditioned to remain $\geq 1$. 
### General self-regulated populations

**Introduction**

- A general structured birth-and-death process with mutation

**Model assumptions**

- Each individual is characterized by a trait \( t \) (individual size, age, gender, tissue type) in a closed subset \( \mathcal{X} \) of \( \mathbb{R} \)

**Dynamics**

- As in the pure multitype branching process:
  - Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

**Mathematical notion of quasi-stationarity**: population size is conditioned to remain \( \mathcal{X} \) at maturity,...) in a closed subset \( \mathcal{X} \) of \( \mathbb{R} \)

**Population size**: continuous-time Markov chain

- Possibly varying size \( \mathcal{N} \), but does not go to \( \infty \)

- Population never becomes extinct \( (\mathcal{N} \geq 1) \)

**Interpretation**

- Separation of timescales of mutations and extinction

**Example: the logistic branching process**

- Etheridge 2004, Lambert 2005

**Logistic branching process**

- Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

- Time interval between two consecutive birth events is exponential of rate \( \beta \)

**Continuous time**

- Births take place at constant rate \( \alpha \)

**Discrete time**

- Births occur at constant rate \( \alpha \), and children are born at the end of each time interval.

- Time intervals between births are exponential of rate \( \beta \)

**Birth process**

- Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

**Definition of quasi-stationarity**: population size is conditioned to remain \( \mathcal{X} \) at maturity,...) in a closed subset \( \mathcal{X} \) of \( \mathbb{R} \)

**Population size**: continuous-time Markov chain

- Possibly varying size \( \mathcal{N} \), but does not go to \( \infty \)

- Population never becomes extinct \( (\mathcal{N} \geq 1) \)

**Interpretation**

- Separation of timescales of mutations and extinction

**Example: the logistic branching process**

- Etheridge 2004, Lambert 2005

**Logistic branching process**

- Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

**Continuous time**

- Births take place at constant rate \( \alpha \)

**Discrete time**

- Births occur at constant rate \( \alpha \), and children are born at the end of each time interval.

- Time intervals between births are exponential of rate \( \beta \)

**Birth process**

- Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

**Definition of quasi-stationarity**: population size is conditioned to remain \( \mathcal{X} \) at maturity,...) in a closed subset \( \mathcal{X} \) of \( \mathbb{R} \)

**Population size**: continuous-time Markov chain

- Possibly varying size \( \mathcal{N} \), but does not go to \( \infty \)

- Population never becomes extinct \( (\mathcal{N} \geq 1) \)

**Interpretation**

- Separation of timescales of mutations and extinction

**Example: the logistic branching process**

- Etheridge 2004, Lambert 2005

**Logistic branching process**

- Each individual of type \( d \) gives birth at rate \( \lambda \) to one single child of the same type.

- Each individual of type \( d \) dies at rate \( \mu \) in sub-

- Time interval between two consecutive birth events is exponential of rate \( \beta \)
Example: the logistic branching process (Etheridge 2004, Lambert 2005)

Dynamics of the multitype logistic branching process:
- as in the pure multitype branching process:
  - each individual with trait $x$ gives birth at rate $b(x)$ to one single individual with trait $x$
  - each individual of type $x$ dies at rate $d(x)$
- in addition, each individual of type $y$ picks any other given individual of type $x$ at rate $c(x, y)$ and then kills her.
- The logistic branching process comes down from infinity. In particular, the population size cannot go to $\infty$.

We define $GL$-populations as those models satisfying
- there is $\bar{b}$ such that for any $\nu$ and $x$, $0 < b(x, \nu) \leq \bar{b}$
- there are $c$ and $\alpha > 0$ such that for any $\nu$ and $x$,
  $$d(x, \nu) \geq c (N - 1)^\alpha$$
- if $\nu = \delta_x$, then $d(x, \nu) = 0$.

In particular, extinction has zero probability.
Basic result

**Theorem**

Consider a GL-population \((v_t; t \geq 0)\) with no mutation. For any initial condition, the fixation time \(T\)

\[
T := \inf\{t \geq 0 : |\text{Supp}(v_t)| = 1\}
\]

is finite a.s.. Let \(x\) be the surviving type. Then conditional on \(T\) and \(x\), the post-\(T\) size process \((N(t); t \geq T)\) converges in distribution to a random integer \(\xi(x)\).

**Notation**

- \(\xi(x)\) : stationary size of a clonal population with trait \(x\)
- \(b(x,n)\) : individual birth rate in a clonal population with trait \(x\) and size \(n\)
- \(d(x,n)\) : individual death rate in a clonal population with trait \(x\) and size \(n\)
- For a two-type GL-population with no mutation starting with \(n\) ind. of type \(x\) (resident) and \(m\) ind. of type \(y\) (mutant), the fixation probability of the mutant is denoted \(u_{n,m}(x,y)\).

Let \(\tau\) be the first mutation time.

**Lemma**

When \(v_0 = n\delta_x\) \(\exp(\gamma(T-N))\) converges in law to \((T, N)\) where \(T\) and \(N\) are independent, \(T \sim \deltaxp(\beta(x))\) where

\[
\beta(x) := \mu_x \mathbb{E}(\xi(x)b(x, \xi(x)))
\]

is the mean production rate of mutants, and

\[
P(N = k) = \frac{kb(x,k)}{\mathbb{E} \xi(x)b(x, \xi(x))}
\]

is the \(b(x,\cdot)\)-size-biased stationary population size.
Convergence of the support

Let \( \rho_k \) be the \( k \)-th time when the population gets monomorphic, and \( V_k \) the then surviving type.

**Theorem**

Assume \( v_0 = n \delta_x \). The process \( (S^\gamma_t; t \geq 0) \) defined as \( S^\gamma_t = V_k \) if \( \rho_k \leq t/\gamma < \rho_{k+1} \)

\[
q(x, dh) = \beta(x)f(x, x + h)M(x, dh),
\]

\[
f(x, y) = \sum_{n \geq 1} P(\xi(x) = n) \frac{nb(x, n)}{E(\xi(x)b(\xi(x)))} u_{n,1}(x, y).
\]

**Interpretation**

- Population is monomorphic at all times
- TSS: resident trait \( x \) jumps from \( x \rightarrow x + h + dh \) at rate

\[
q(x, dh) = \beta(x)f(x, x + h)M(x, dh),
\]
Invasion fitness (Metz et al., 1992)

The invasion fitness $f(x, y)$ is the ability for an initially rare mutant of trait $y$ to invade a monomorphic resident population of trait $x$ at ecological equilibrium.

- Here the invasion fitness is
  $$ f(x, y) = \sum_{n \geq 1} \mathbb{P}(\xi(x) = n) \frac{nb(x, n)}{\mathbb{E}(\xi(x)b(x, \xi(x))))} u_{n, 1}(x, y). $$

- In the large population setting,
  $$ f(x, y) = \left(1 - \frac{D(x, y)}{B(x, y)}\right)^+, $$
  where $B, D$ are the birth/death rates of rare $y$-mutants in the $x$-resident background.

* This invasion fitness is in fact the survival probability for the branching process with birth/death rates $B$ and $D$. 

### Interpretation

- Population is monomorphic at all times
- TSS: resident trait $x$ jumps from $x \rightarrow x + h + dh$ at rate
  $$ q(x, dh) = \beta(x)f(x, x + h)M(x, dh), $$
  where
  $$ \beta(x) = \mu(x)\mathbb{E}(\xi(x)b(x, \xi(x))) $$
  is the mean production rate of mutants (on the mutation timescale $t/\gamma$) in a $b(x, \cdot)$-biased stationary $x$-type population.

### Results

**Introduction**

Invasion fitness (Metz et al., 1992)

The invasion fitness $f(x, y)$ is the ability for an initially rare mutant of trait $y$ to invade a monomorphic resident population of trait $x$ at ecological equilibrium.

- Here the invasion fitness is
  $$ f(x, y) = \sum_{n \geq 1} \mathbb{P}(\xi(x) = n) \frac{nb(x, n)}{\mathbb{E}(\xi(x)b(x, \xi(x))))} u_{n, 1}(x, y). $$

- In the large population setting,
  $$ f(x, y) = \left(1 - \frac{D(x, y)}{B(x, y)}\right)^+, $$
  where $B, D$ are the birth/death rates of rare $y$-mutants in the $x$-resident background.

* This invasion fitness is in fact the survival probability for the branching process with birth/death rates $B$ and $D$. 

### Interpretation

- Population is monomorphic at all times
- TSS: resident trait $x$ jumps from $x \rightarrow x + h + dh$ at rate
  $$ q(x, dh) = \beta(x)f(x, x + h)M(x, dh), $$
  where
  $$ \beta(x) = \mu(x)\mathbb{E}(\xi(x)b(x, \xi(x))) $$
  is the mean production rate of mutants (on the mutation timescale $t/\gamma$) in a $b(x, \cdot)$-biased stationary $x$-type population, and
  $$ f(x, y) = \sum_{n \geq 1} \mathbb{P}(\xi(x) = n) \frac{nb(x, n)}{\mathbb{E}(\xi(x)b(x, \xi(x))))} u_{n, 1}(x, y). $$
  is the fixation probability of a $y$-type mutant in a $b(x, \cdot)$-biased stationary $x$-type population (invasion fitness).
Convergence of the population size

**Theorem**

For any $0 < t_1 < \ldots < t_m$, $(\mathbf{v}^T_{t_1}, \ldots, \mathbf{v}^T_{t_m})$ converges in law to $(\xi_1, \ldots, \xi_m)$ where $\xi_i = N_i \delta z_i$, such that

1. $(Z_i; t \geq 0)$ is the TSS process of the previous theorem
2. Conditional on $(Z_{t_1}, \ldots, Z_{t_k}) = (z_1, \ldots, z_k)$, the $N_i$ are independent and respectively distributed as $\xi_i(z_i)$.

The convergence only holds for f.d.d.

Assumptions

We make the following assumptions.

- $\mathcal{X} = \mathbb{R}^d$ for simplicity
- Smoothness of $b(\cdot, \nu)$ and $d(\cdot, \nu)$ ensuring that the invasion fitness
  
  $$y \mapsto f(x, y) = \sum_{n \geq 1} P(\xi_n = n) \frac{nb(x, n)}{E(\xi_n h(x, \xi_n))} u_{n, 1}(x, y)$$

  is in $\mathcal{E}_0^2$

  - the mutation kernel satisfies

  - $M(x, \cdot)$ has 0 expectation, i.e. $\int \mu \cdot hM(x, dh) = 0$
  - the covariance matrix of $M(x, \cdot)$ has Lipschitz entries and is uniformly elliptic in $x$
  - the third order moments of $M(x, \cdot)$ are uniformly bounded in $x$
Assumptions

We make the following assumptions.

- \( \mathcal{X} = \mathbb{R}^d \) for simplicity
- Smoothness of \( b(\cdot, \nu) \) and \( d(\cdot, \nu) \) ensuring that the invasion fitness
  \[
  y \mapsto f(x,y) = \sum_{n>1} \mathbb{P}(\xi(x) = n) \frac{nb(x,n)}{\mathbb{E}(\xi(x)b(x,\xi(x)))} a_0(x,y)
  \]
  is in \( \mathcal{C} \)
- the mutation kernel satisfies
  - \( M(\cdot, \cdot) \) has 0 expectation, i.e. \( \int_{\mathbb{R}^d} hM(x, dh) = 0 \)
  - the covariance matrix of \( M(\cdot, \cdot) \) has Lipschitz entries and is uniformly elliptic in \( x \)
  - the third order moments of \( M(\cdot, \cdot) \) are uniformly bounded in \( x \)

Scaling of the mutation kernel

We are going to apply a limit of small jumps to the TSS, following the heuristics leading to the canonical equation of adaptive dynamics.

- Replace the mutation law \( M(x, dh) \) with its image by \( h \mapsto \varepsilon h \) \( (\varepsilon > 0) \)
- Rescale time as \( t/\varepsilon^2 \)
Limit of the generator

Making a second-order expansion,

\[(\varphi(x+\varepsilon h) - \varphi(x))f(x,x+\varepsilon h) = \varepsilon (h' \nabla \varphi(x))f(x,x) + \varepsilon^2 (h' \nabla \varphi(x))(h' \nabla g(x,x)) + \frac{\varepsilon^2}{2} (h'H \varphi(x)h)f(x,x) + O(\varepsilon^3 \|h\|^3)\]

Since \(M(x,\cdot)\) has zero mean, \(\int_{\mathbb{R}^d} (h' \nabla \varphi(x)) f(x,x) M(x,\, dh) = 0\).

\(A_0 \varphi\) converges uniformly to the function \(A_0 \varphi\)

\[A_0 \varphi(x) = \int_{\mathbb{R}^d} (h' \nabla \varphi(x)) h' \nabla g(x,x) M(x,\, dh) + \frac{1}{2} \int_{\mathbb{R}^d} (h'H \varphi(x)h) \beta(x) f(x,x) M(x,\, dh).\]

The canonical diffusion of adaptive dynamics

Let \(\sigma(x)\) be the square root of the covariance matrix of \(M(x,\cdot)\).

\[\text{Theorem}\]

As \(\varepsilon \to 0\), \(Z^\varepsilon\) converges in law on \(D([0,\infty); \mathbb{R}^d)\) to the diffusion process solution to the SDE

\[dZ_t = \beta(Z_t) \sigma(Z_t) \cdot \nabla f(Z_t,Z_t) \varepsilon dt + \sqrt{\beta(Z_t)f(Z_t,Z_t)} \sigma(Z_t) \cdot dB_t\]

where \(B\) is a standard \(k\)-dimensional Brownian motion, and \(\nabla_2\) is the gradient w.r.t. the second variable.
Discussion

- We obtain a diffusion model of evolution grounded on a microscopic realistic population dynamics
- Genetic drift proportional to $\beta(x)$, to the neutral fixation probability $f(x, x)$ and to the covariance matrix of $M(x, \cdot)$.
- Directional selection similar to the one of the canonical ODE

$$\frac{dx}{dt} = \frac{1}{2} \sigma^2(x) \mu(x) \hat{n}(x) \frac{\partial}{\partial y} f(x, x)$$

Proportional to
- the covariance matrix of $M(x, \cdot)$
- the total mutant production rate $\beta(x)$
- the gradient of the fixation probability $f(x, y)$ of a $y$-type mutant in a stationary $x$-type resident population.

* $y \rightarrow f(x, y)$ defines a fitness landscape depending on the current state of the population

---

Discussion

- We obtain a diffusion model of evolution grounded on a microscopic realistic population dynamics
- Genetic drift proportional to $\beta(x)$, to the neutral fixation probability $f(x, x)$ and to the covariance matrix of $M(x, \cdot)$.
- Directional selection similar to the one of the canonical ODE

$$\frac{dx}{dt} = \frac{1}{2} \sigma^2(x) \mu(x) \hat{n}(x) \frac{\partial}{\partial y} f(x, x)$$

Proportional to
- the covariance matrix of $M(x, \cdot)$
- the total mutant production rate $\beta(x)$
- the gradient of the fixation probability $f(x, y)$ of a $y$-type mutant in a stationary $x$-type resident population.

* $y \rightarrow f(x, y)$ defines a fitness landscape depending on the current state of the population
**Introduction**

Model  
TSS  
Canonical diffusion of AD  
Logistic branching

**Results**

When $M(x, \cdot)$ has non-zero expectation

When $\int_{R^k} hM(x, dh) \neq 0$, the first-order term in the generator $A_\epsilon$ does not vanish.

Therefore, the correct timescaling is $t/\epsilon$, and $Z_\epsilon$ converges to the deterministic ODE

$$\frac{dz}{dt} = \beta(z)f(z, z) \int_{R^k} hM(z, dh).$$

In this case, the main force driving evolution is the mutation bias. The mutation rate $\beta(x)$ and the fixation probability $f(x, x)$ only affect the speed of evolution.

**The two-type logistic branching process**

Parameters of the two-type logistic branching process

The two-type logistic branching process is characterized by:

- Birth vector $B$, competition matrix $C$, and death vector $D$

$$B = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}, \quad C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \quad D = \begin{pmatrix} d_1 \\ d_2 \end{pmatrix}$$

- Where 1 refers to the resident type, and 2 refers to the mutant type

- $n$ is the initial number of residents

- $m$ is the initial number of mutants

- $p = m/(n + m)$ denotes the initial frequency of mutants.
The two-type logistic branching process is characterized by: birth vector $B$, competition matrix $C$ and death vector $D$

$$B = \begin{pmatrix} b_1 \\ b_2 \end{pmatrix}, \quad C = \begin{pmatrix} c_{11} & c_{12} \\ c_{21} & c_{22} \end{pmatrix}, \quad D = \begin{pmatrix} d_1 \\ d_2 \end{pmatrix}$$

where 1 refers to the resident type, and 2 refers to the mutant type

- $n$ is the initial number of residents
- $m$ is the initial number of mutants

$p = m / (n + m)$ denotes the initial frequency of mutants.

- under neutrality, the fixation probability $u$ equals the initial frequency $p$ of the mutant

$$u_{n,m} = \frac{m}{n + m} = p$$

Five fundamental selection coefficients (1)

We will express deviations from neutrality as

$$B = \begin{pmatrix} b \\ b \end{pmatrix} + \begin{pmatrix} 0 \\ \lambda \end{pmatrix}, \quad D = \begin{pmatrix} d \\ d \end{pmatrix} - \begin{pmatrix} 0 \\ \sigma \end{pmatrix}, \quad C = \begin{pmatrix} c \\ c \end{pmatrix} - \begin{pmatrix} 0 & 0 \\ \delta & \delta \end{pmatrix} + \begin{pmatrix} 0 \\ \alpha \end{pmatrix} - \begin{pmatrix} 0 \\ \epsilon \end{pmatrix}.$$ 

The coefficients $\lambda$, $\delta$, $\alpha$, $\epsilon$, $\sigma$ are chosen to be positive when they confer an advantage to the mutant, and are called the five fundamental (additive) selection coefficients.

- fertility $\lambda$: positive $\lambda$ means increased mutant birth rate
- defence capacity $\delta$: positive $\delta$ means reduced competition sensitivity of mutant individuals from the rest of the population
- aggressiveness $\alpha$: positive $\alpha$ means raised competition pressure exerted from any mutant individual onto the rest of the population
- isolation $\epsilon$: positive $\epsilon$ means lighter cross-competition between different morphs
- survival $\sigma$: positive $\sigma$ means reduced mutant death rate.
Five fundamental selection coefficients (2)

1. **fertility** $\lambda$: positive $\lambda$ means increased mutant birth rate
2. **defence capacity** $\delta$: positive $\delta$ means reduced competition sensitivity of mutant individuals from the rest of the population
3. **aggressiveness** $\alpha$: positive $\alpha$ means raised competition pressure exerted from any mutant individual onto the rest of the population
4. **isolation** $\varepsilon$: positive $\varepsilon$ means lighter cross-competition between different morphs
5. **survival** $\sigma$: positive $\sigma$ means reduced mutant death rate.

The fundamental result

Introduction

Factorization of second-order terms

**Theorem**

As a function of the multidimensional selection coefficient $s = (\lambda, \delta, \alpha, \varepsilon, \sigma)^t$, the probability $u$ is differentiable, and in a neighborhood of $s = 0$ (selective neutrality),

$$u = p + v.s + o(s),$$

where the selection gradient $v = (v^\lambda, v^\delta, v^\alpha, v^\varepsilon, v^\sigma)^t$ can be expressed as

$$v_{n,m}^t = p(1-p) g_{n+m}^t \quad t \neq \varepsilon,$$

$$v_{n,m}^\varepsilon = p(1-p)(1-2p) g_{n+m}^\varepsilon.$$

And the $g$'s depend solely on the resident's characteristics $b, c, d, \text{and on the total initial population size } n + m$. They are called **invasibility coefficients**.

Invasibility coefficients

Consider a monomorphic logistic branching population $(b, c, 0)$.

- Invasibility by mutants with increased fertility:
  $$g_{n+m}^\lambda = \frac{n}{2c(n+1)} \xrightarrow{n \to \infty} \frac{1}{2c}$$

- Invasibility by mutants with increased aggressiveness or survival:
  $$\lim g_{n+m}^\alpha = \lim g_{n+m}^\varepsilon = \frac{1}{2c} + \frac{1}{2d} \left(1 - \frac{c}{b}\right),$$

  where $b = b(1 - 2q_1/3)/q_0$ and $q_0 = P_1$ (last two survivors have distinct ancestors).

- Invasibility by mutants with increased isolation or defence capacity:
  $$g_{n+m}^\alpha \sim (\varepsilon)g_{n+m}^\alpha \sim e^{-1} \ln(n) \quad \text{as } n \to \infty.$$
Invasibility coefficients

Consider a monomorphic logistic branching population \((b, c, 0)\).

- Invasibility by mutants with increased fertility:
  \[
  g_n^a = \frac{n}{2c(n+1)} - \frac{1}{2c}
  \]

- Invasibility by mutants with increased aggressiveness or survival:
  \[
  \lim_{n \to \infty} g_n^a = \lim_{n \to \infty} g_n^c = \frac{1}{2c} + \frac{1}{2b} \left(1 - \frac{c}{k}\right),
  \]
  where \(k = b(1 - 2q_3/3)/q_w\) and
  \[
  q_k = \mathbb{P}_k(\text{last two survivors have distinct ancestors})
  \]

- Invasibility by mutants with increased isolation or defence capacity:
  \[
  g_n^e \sim \langle < \rangle g_n^e \sim e^{-1} \ln(n) \quad \text{as } n \to \infty.
  \]

Example

Assume the model is logistic branching, and that

- \(X = \mathbb{R}\)
- \(c(x, y) = C(|x - y|)\) and \(C(0) = 1\)
- \(\sigma(x)\) is the standard deviation of \(M(x, \cdot)\)

The canonical diffusion of adaptive dynamics is given by

\[
\frac{dZ_t}{dt} + \sigma(Z_t) \mu(Z_t) \frac{d}{dt} \left( \frac{b(Z_t)}{1 - e^{-b(Z_t)}} - 1 \right)^{1/2} dB_t
\]

where

\[
r(x) = \frac{\mu(x) \sigma(x)^2}{2} \left( 1 + \frac{4}{b(x)} + \frac{b(x) - 4}{1 - e^{-b(x)}} \right) b'(x).
\]
Other example: Moran model

- Two-type Moran model, constant size \( N + 1 \)
  - If \( x \) is the resident trait, each pair of individuals with traits \( (x, y) \) is replaced with:
    - A pair of type \((y, y)\) at rate \( c_1(x, y) \)
    - A pair of type \((x, x)\) at rate \( c_2(y, x) \)
  - The canonical diffusion of adaptive dynamics becomes:
    \[
    dX_t = \frac{1}{2} \mu(X_t) N^3 \sigma(X_t)^2 \frac{\partial}{\partial y} f(X_t, X_t) dt + \sigma(X_t) \sqrt{N \mu(X_t)} c(X_t, X_t) dB_t,
    \]
    where \( c(x, x) := c_1(x, x) = c_2(y, x) \) and the invasion fitness \( f(x, y) \) is \( c_1(x, y) - c_2(y, x) \).

- Other example: Moran model

- Two-type Moran model, constant size \( N + 1 \)
  - If \( x \) is the resident trait, each pair of individuals with traits \( (x, y) \) is replaced with:
    - A pair of type \((y, y)\) at rate \( c_1(x, y) \)
    - A pair of type \((x, x)\) at rate \( c_2(y, x) \)
  - The canonical diffusion of adaptive dynamics becomes:
    \[
    dX_t = \frac{1}{2} \mu(X_t) N^3 \sigma(X_t)^2 \frac{\partial}{\partial y} f(X_t, X_t) dt + \sigma(X_t) \sqrt{N \mu(X_t)} c(X_t, X_t) dB_t,
    \]
    where \( c(x, x) := c_1(x, x) = c_2(y, x) \) and the invasion fitness \( f(x, y) \) is \( c_1(x, y) - c_2(y, x) \).
Other example: Moran model

- Two-type Moran model, constant size $N + 1$
- If $x$ is the resident trait, each pair of individuals with traits $(x, y)$ is replaced with:
  - a pair of type $(y, y)$ at rate $c_1(x, y)$
  - a pair of type $(x, x)$ at rate $c_2(y, x)$
- The canonical diffusion of adaptive dynamics becomes:

$$dX_t = \frac{1}{2} \mu(X_t) N^2 \sigma(X_t)^2 \frac{\partial}{\partial y} f(X_t, X_t) dt + \sigma(X_t) \sqrt{N} \mu(X_t) c(X_t, X_t) dB_t,$$

where $c(x, x) := c_1(x, x) = c_2(x, x)$,
and the invasion fitness $f(x, y)$ is $c_1(x, y) - c_2(y, x)$.

...That’s all, thanks for listening.