Evolutionary consequences of the physiological costs of reproduction: An application of Multitrait Population Projection Matrix models

Christophe Coste

Musée de l'Homme - MNHN - Chaire MMB - ED FdV

15th December 2017

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

⇒ For an **individual**, the sequence of these life history features compose its life history **trajectory**.

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

⇒ For an **individual**, the sequence of these life history features compose its life history **trajectory**.

⇒ For a **population**, the combination of these **evolved** life history features compose its life history **strategy**.

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

⇒ For an **individual**, the sequence of these life history features compose its life history **trajectory**.

⇒ For a **population**, the combination of these **evolved** life history features compose its life history **strategy**.

Trade-offs

Life history features are constrained by trade-offs

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

⇒ For an **individual**, the sequence of these life history features compose its life history **trajectory**.

⇒ For a **population**, the combination of these **evolved** life history features compose its life history **strategy**.

Trade-offs

Life history features are constrained by trade-offs

- For an individual: **principle of allocation**[1] of finite resources ⇒ **physiological trade-offs**

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Life History Theory

Life History Theory focuses on the **life cycle** of organisms.

LHT focuses on **Life history features**

- **key evolutionary** characteristics of life cycles
- with **diversity**
  - e.g. age at maturity, size at maturity etc.

⇒ For an **individual**, the sequence of these life history features compose its life history **trajectory**.

⇒ For a **population**, the combination of these **evolved** life history features compose its life history **strategy**.

Trade-offs

Life history features are constrained by trade-offs

- For an individual: **principle of allocation**[1] of finite resources ⇒ **physiological trade-offs**
- For a population: **antagonistic pleiotropy** of genes ⇒ **genetic trade-offs**

---

[1] Cody, M. L. (1966). A general theory of clutch size. Evolution.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.
- **Projection** yields key **evolutionary demography metrics**
  - e.g. ergodic growth rate, stable state structure

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.
- **Projection** yields key **evolutionary demography metrics**
  - e.g. ergodic growth rate, stable state structure

- Evolutionary demography studies populations $\Rightarrow$ no physiological trade-off

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.
- **Projection** yields key **evolutionary demography metrics**
  - e.g. ergodic growth rate, stable state structure

- Evolutionary demography studies populations ⇒ no physiological trade-off

⇒ To understand their evolutionary consequences, we need to integrate physiological trade-offs into Evolutionary Demography

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.
- **Projection** yields key **evolutionary demography metrics**
  - e.g. ergodic growth rate, stable state structure

- Evolutionary demography studies populations ⇒ no physiological trade-off

⇒ To understand their evolutionary consequences, we need to integrate physiological trade-offs into Evolutionary Demography

The costs of reproduction

- Current reproduction trades off with future fitness (fertility, survival)
- The most prominent of all trade-offs[1].

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Introduction : Life History Theory and Evolutionary Demography

Evolutionary Demography

Evolutionary Demography focuses on population dynamics of **structured populations**.

- **Traits** structure the population into classes
  - e.g. age, size, sex, location, etc.
- **Vital rates** allow to project the population dynamics over time
  - fertility rates, survival rates, growth rates, migration rates.
- **Projection** yields key **evolutionary demography metrics**
  - e.g. ergodic growth rate, stable state structure

- Evolutionary demography studies populations ⇒ no physiological trade-off

⇒ To understand their evolutionary consequences, we need to integrate physiological trade-offs into Evolutionary Demography

The costs of reproduction

- Current reproduction trades off with future fitness (fertility, survival)
- The most prominent of all trade-offs[1].
- Physiological and genetic costs are related to the main evolutionary theories of aging.
  - Antagonistic Pleiotropy Theory[2] ⇔ Genetic costs
  - Disposable Soma Theory[3] ⇔ Physiological costs

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

[2] Williams, G. C. (1957). Pleiotropy, natural selection and the evolution of senescence. Evolution.

[3] Kirkwood, T. B. L. (1977). Evolution of ageing. Nature.

Overview

The two sides of Williams' physiological costs of reproduction

In 1930, Fisher[1] asks : " ... what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction"

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

In 1930, Fisher[1] asks : " ... what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction"

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} \qquad = \qquad\qquad\qquad + $$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

In 1930, Fisher[1] asks : " ... what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction"

Williams' 1966 article[2]

An individual of a certain age *i* has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} = \underbrace{f_i}_{\textit{reproductive value immediately at stake}} +$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

In 1930, Fisher[1] asks : " ... what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction"

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} = \underbrace{f_i}_{\textit{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \left(\prod_{k=i}^{j-1} s_k\right)}_{\text{residual } \textit{reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

In 1930, Fisher[1] asks : " ... what circumstances in the life-history and environment would render profitable the diversion of a greater or lesser share of the available resources towards reproduction"

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} = \underbrace{f_i}_{\textit{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \left(\prod_{k=i}^{j-1} s_k\right)}_{\text{residual } \textit{reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

⇒ An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} = \underbrace{f_i}_{\textit{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \Big(\prod_{k=i}^{j-1} s_k\Big)}_{\text{residual } \textit{reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

⇒ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

- An **individual/physiological** side[3]; whereby an **individual allocates** more or less **resources** towards current reproduction.

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\text{reproductive value at age } i} = \underbrace{f_i}_{\text{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} (\prod_{k=i}^{j-1} s_k)}_{\text{residual reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

$\Rightarrow$ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

- An **individual/physiological** side[3]; whereby an **individual allocates** more or less **resources** towards current reproduction.
- A **population/evolutionary** side, whereby **populations evolve** different allocation strategies

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\textit{reproductive value at age } i} = \underbrace{f_i}_{\textit{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \Big(\prod_{k=i}^{j-1} s_k\Big)}_{\text{residual } \textit{reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

$\Rightarrow$ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

- An **individual/physiological** side[3]; whereby an **individual allocates** more or less **resources** towards current reproduction.
- A **population/evolutionary** side, whereby **populations evolve** different allocation strategies

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\text{reproductive value at age } i} = \underbrace{f_i}_{\text{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \left(\prod_{k=i}^{j-1} s_k\right)}_{\text{residual reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

$\Rightarrow$ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

- An **individual/physiological** side[3]; whereby an **individual allocates** more or less **resources** towards current reproduction.
- A **population/evolutionary** side, whereby **populations evolve** different allocation strategies

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\text{reproductive value at age } i} = \underbrace{f_i}_{\text{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \left(\prod_{k=i}^{j-1} s_k\right)}_{\text{residual reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

⇒ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

Two sides – two resource capitals

- Physiological side → a **Fluctuating Capital** which is **supplied** by resources acquired from the **environment**

  ⇒ FC is related to acquirable resources e.g. food, energy

---

[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

The two sides of Williams' physiological costs of reproduction

Williams' definition mixes two sides:

- An **individual/physiological** side[3]; whereby an **individual allocates** more or less **resources** towards current reproduction.
- A **population/evolutionary** side, whereby **populations evolve** different allocation strategies

Williams' 1966 article[2]

An individual of a certain age i has a *reproductive value*[1] v_i, made of two components:

$$\underbrace{v_i}_{\text{reproductive value at age } i} = \underbrace{f_i}_{\text{reproductive value immediately at stake}} + \underbrace{\sum_{j=i+1}^{\omega} f_j \lambda^{i-j} \left(\prod_{k=i}^{j-1} s_k\right)}_{\text{residual reproductive value}}$$

with f_i, s_i, the fertility and survival rates at age i and λ the asymptotic growth rate.

⇒ **An individual allocates towards its *reproductive value immediately at stake* at the *cost* of its *residual reproductive value*.**

Two sides – two resource capitals

- Physiological side → a **Fluctuating Capital** which is **supplied** by resources acquired from the **environment**

  ⇒ FC is related to acquirable resources e.g. food, energy
- Evolutionary side → a **Ratchet Capital** which is **invested** according to an **evolved** reproductive strategy.

  ⇒ RC is related to non-acquirable resources e.g. time, DNA maintenance capital

---

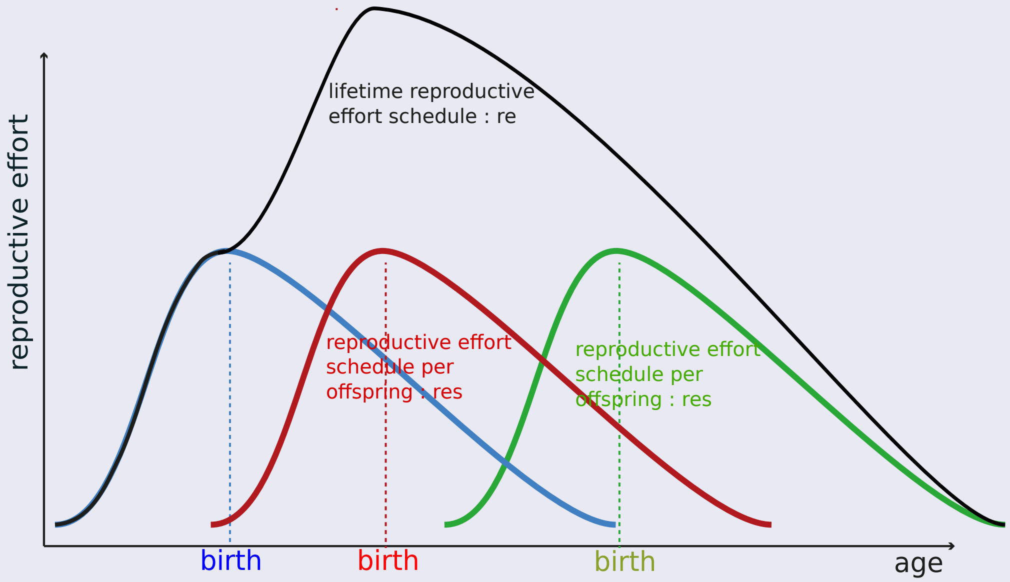
[1] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford University Press

[2] Williams, G. C. (1966). Natural Selection, the Costs of Reproduction, and a Refinement of Lack's Principle. The American Naturalist.

[3] Calow, P. (1979). The cost of reproduction - a physiological approach. Biological Review.

Fluctuating and Ratchet Capitals

Lifetime reproductive effort schedule re

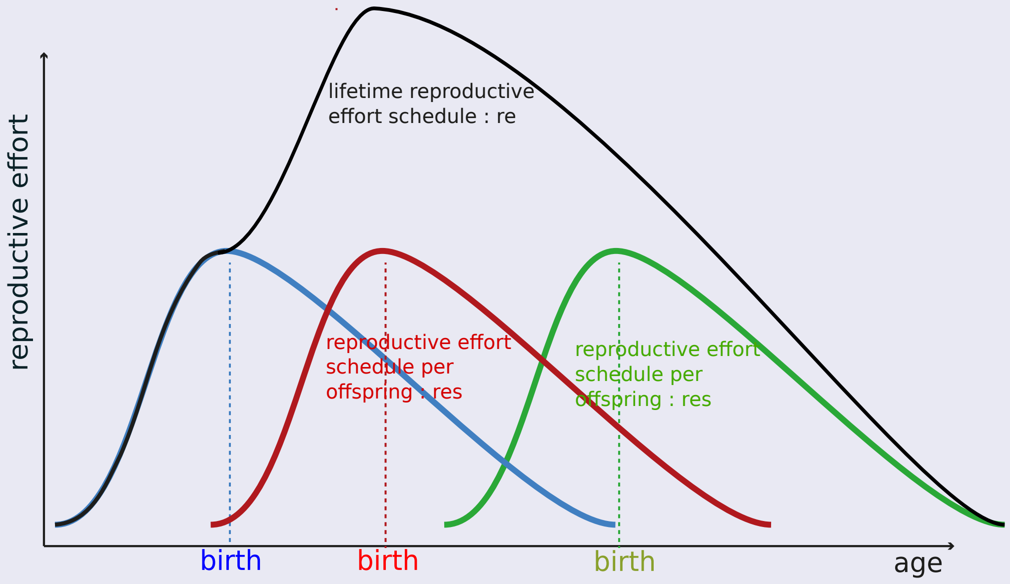


re is the convolution of

- the reproductive effort schedule per offspring res

Fluctuating and Ratchet Capitals

Lifetime reproductive effort schedule re



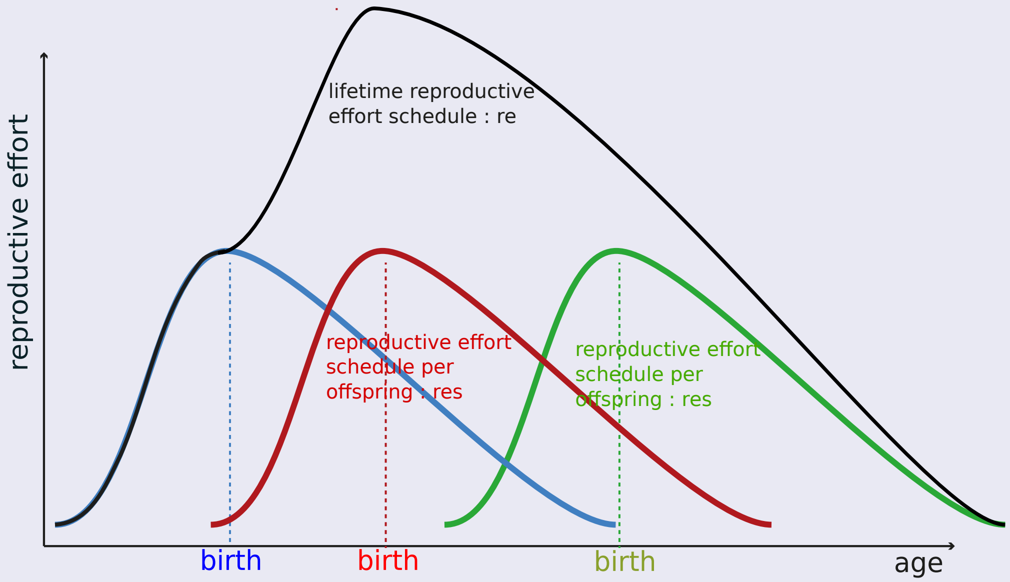
re is the convolution of

- the reproductive effort schedule per offspring res
- with fertility schedule f :

$$re(a) = (f * res)(a) = \int_{t=0}^{e(0)} f(t).res(t-a).dt$$

Fluctuating and Ratchet Capitals

Lifetime reproductive effort schedule re



re is the convolution of

- the reproductive effort schedule per offspring res
- with fertility schedule f :

$$re(a) = (f * res)(a) = \int_{t=0}^{e(0)} f(t).res(t-a).dt$$

Among the different moments of *re*:

$$sfc = \frac{\sum i.re(i)}{\sum re(i)}$$

⇒ *sfc* positions organism on **Slow-Fast continuum**.

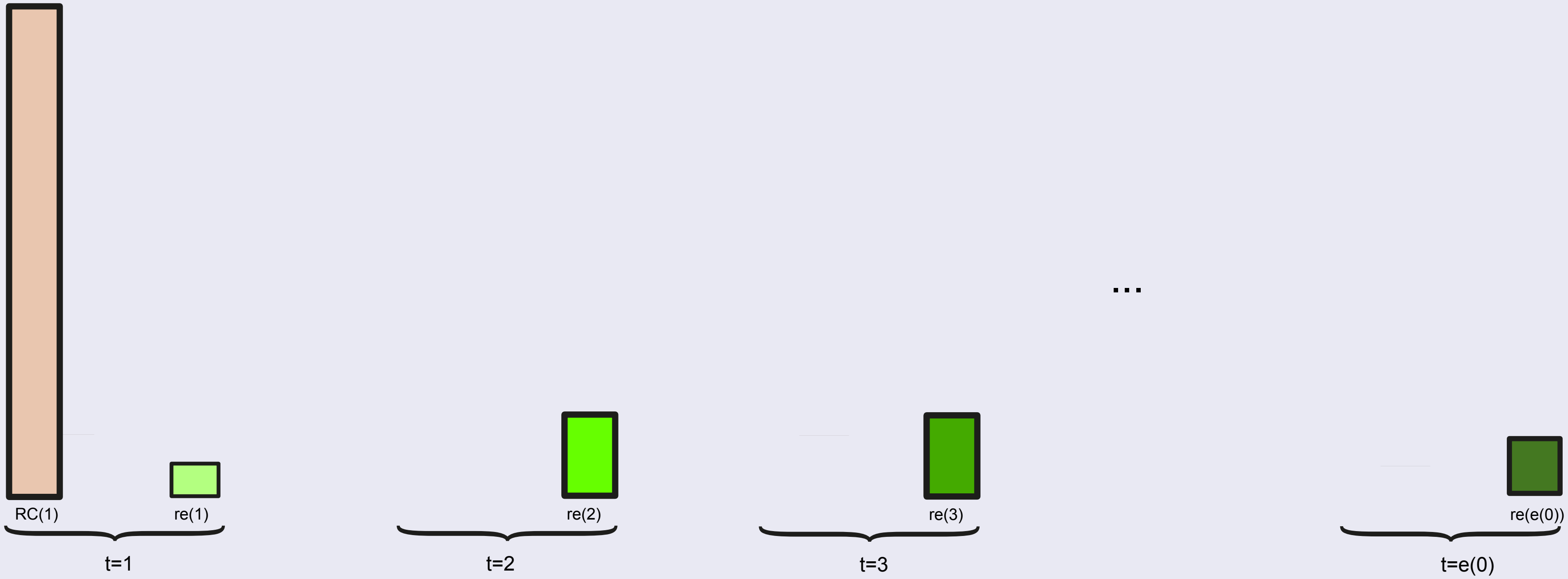
Fluctuating and Ratchet Capitals

Ratchet Capital RC

- Its initial value RC_1 is generated *backwards* from the species *evolved* lifetime reproductive effort schedule re

$$\begin{cases} RC_1 = \Sigma_{a=1}^{e(0)} \mathrm{re}(a) \\ \end{cases}$$

Capital Dynamics



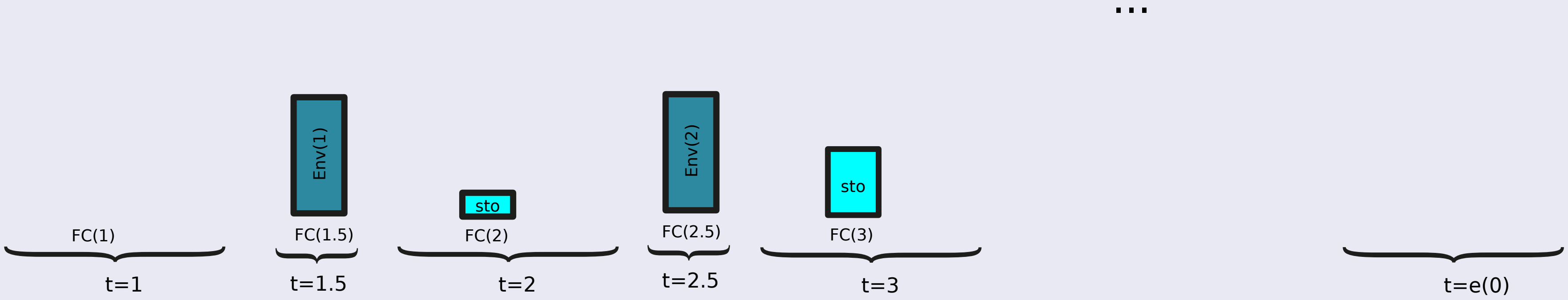
Fluctuating and Ratchet Capitals

Fluctuating Capital FC

- FC starts at zero

$$\begin{cases} FC_1 = 0 \\ \end{cases}$$

Capital Dynamics



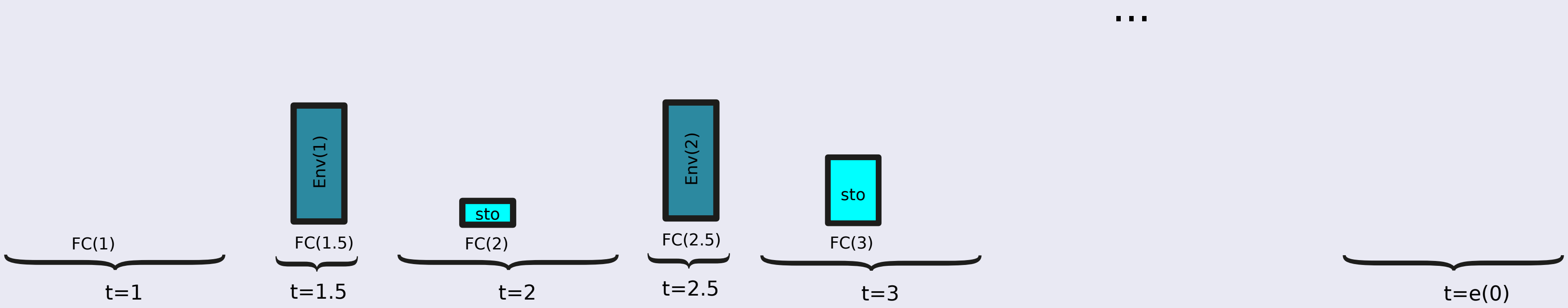
Fluctuating and Ratchet Capitals

Fluctuating Capital FC

- FC starts at zero
- Each season, FC resources are acquired from the environment, some can be stored
- *stor* positions organism on Income-Capital Breeding spectrum

$$\begin{cases} \\ FC_{t+1} = stor.(FC_t + Env_t - RE_t) \end{cases}$$

Capital Dynamics



Fluctuating and Ratchet Capitals

Ratchet Capital RC

- Its initial value RC_1 is generated *backwards* from the species *evolved* lifetime reproductive effort schedule re

$$\begin{cases} RC_{t+1} = RC_t - RE_t \end{cases}$$

Fluctuating Capital FC

- FC starts at zero
- Each season, FC resources are acquired from the environment, some can be stored
- *stor* positions organism on Income-Capital Breeding spectrum

$$\begin{cases} FC_{t+1} = stor.(FC_t + Env_t - RE_t) \end{cases}$$

Capital Dynamics

Fluctuating and Ratchet Capitals

Ratchet Capital RC

- Its initial value RC_1 is generated *backwards* from the species *evolved* lifetime reproductive effort schedule re
- Each period, RC is reduced by RE

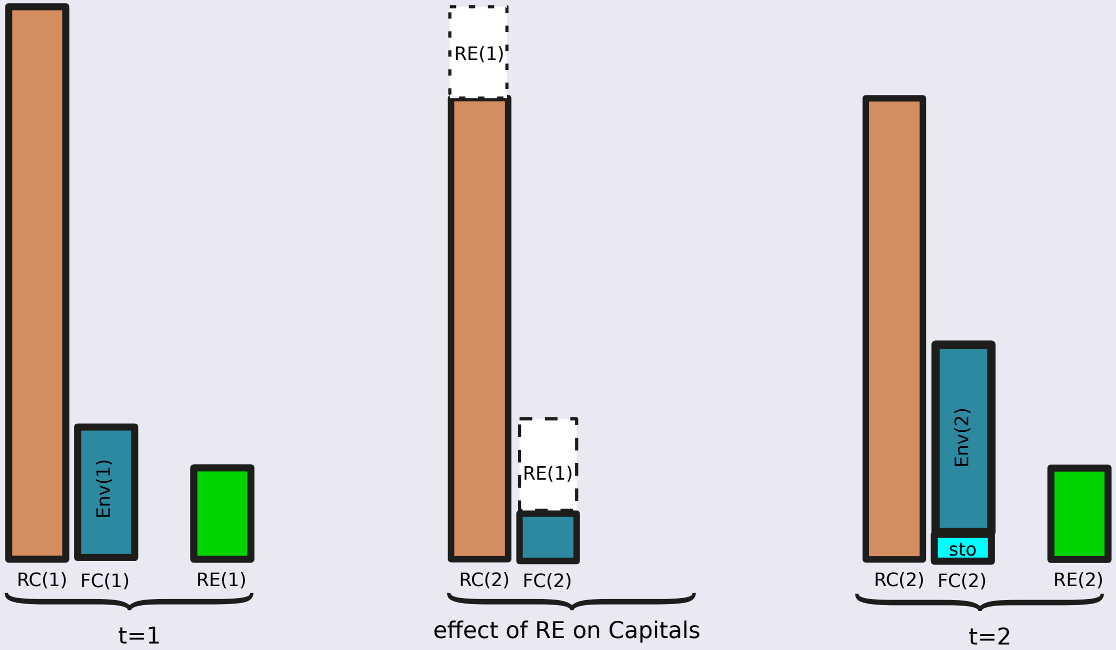
$$\begin{cases} RC_{t+1} = RC_t - RE_t \end{cases}$$

Fluctuating Capital FC

- FC starts at zero
- Each season, FC resources are acquired from the environment, some can be stored
- *stor* positions organism on Income-Capital Breeding spectrum

$$\begin{cases} FC_{t+1} = stor.(FC_t + Env_t - RE_t) \end{cases}$$

Capital Dynamics



Fluctuating and Ratchet Capitals

Ratchet Capital RC

- Its initial value RC_1 is generated *backwards* from the species *evolved* lifetime reproductive effort schedule re
- Each period, RC is reduced by RE

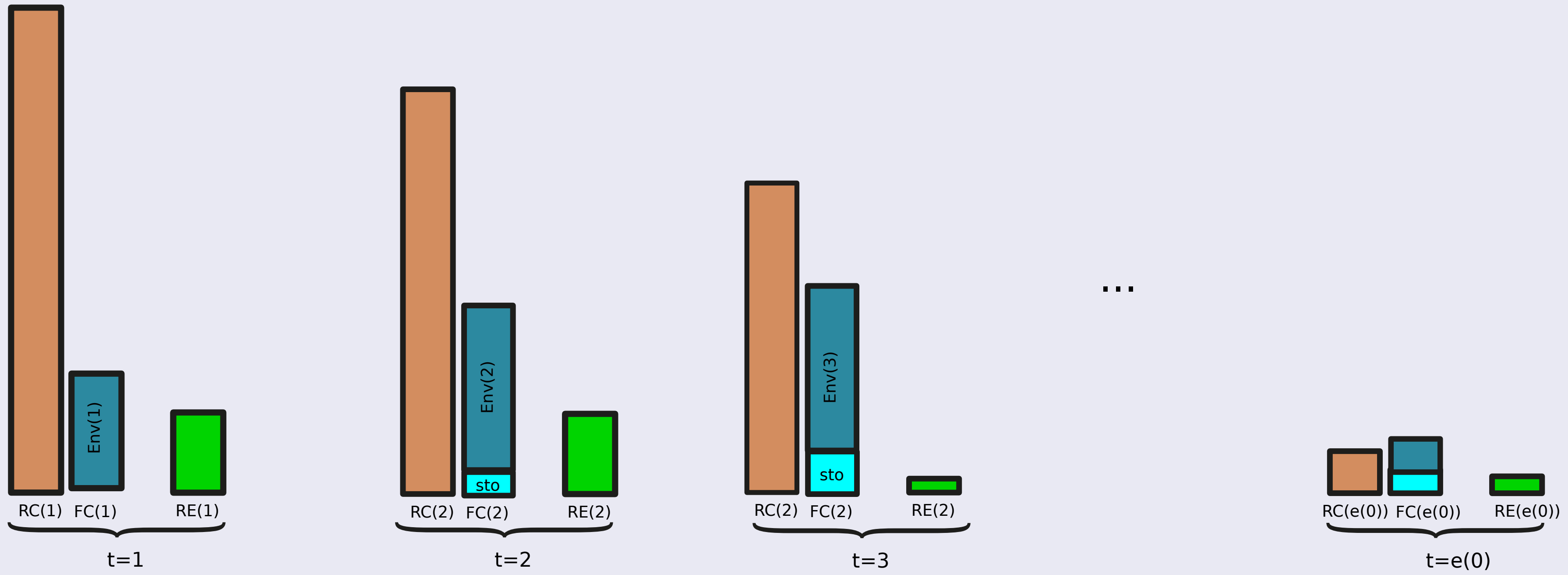
$$\begin{cases} RC_1 = \sum_{a=1}^{e(0)} \mathrm{re}(a) \\ RC_{t+1} = RC_t - RE_t \end{cases}$$

Fluctuating Capital FC

- FC starts at zero
- Each season, FC resources are acquired from the environment, some can be stored
- *stor* positions organism on Income-Capital Breeding spectrum

$$\begin{cases} FC_1 = 0 \\ FC_{t+1} = stor.(FC_t + Env_t - RE_t) \end{cases}$$

Capital Dynamics



Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t))) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n, p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t)) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n, p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

- Allocation requires both capitals (reproductive efforts require both types of resources)

Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t))) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n,p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

- Allocation requires both capitals (reproductive efforts require both types of resources)
- The dependency on FC is modulated by evolved storage capacity *stor*.

Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t))) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n, p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

- Allocation requires both capitals (reproductive efforts require both types of resources)
- The dependency on FC is modulated by evolved storage capacity *stor*.
- The dependency on RC is modulated by the position on the slow-fast continuum *sfc*

Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t)) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n, p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

- Allocation requires both capitals (reproductive efforts require both types of resources)
- The dependency on FC is modulated by evolved storage capacity *stor*.
- The dependency on RC is modulated by the position on the slow-fast continuum *sfc*
- The realization, $RE(t)$, from the allowed (maximum) Reproductive Effort at time t $aRE(t)$, is stochastic and depends on granularity $gr = \frac{bre}{\bar{re}}$

$\Rightarrow$ *gr* positions an organism on the quantity-quality life history continuum.

Allocation Process

Allocation depends on both capitals and life history strategies

$$\begin{cases} aRE(t) \approx \min(FC(t) - stor.\overline{RE}, RC(t) - \bar{re}.K(2.sfc - t))) \\ RE(t) \sim \mathcal{B}(\lfloor \frac{aRE(t)}{\bar{re}}.\frac{1}{gr} \rfloor, p).bre \end{cases}$$

with $0 < K < 1$ an RC flexibility parameter, bre the basic RE and $\mathcal{B}(n, p)$ a n-nomial Bernoulli of parameter p.

Allocation in detail

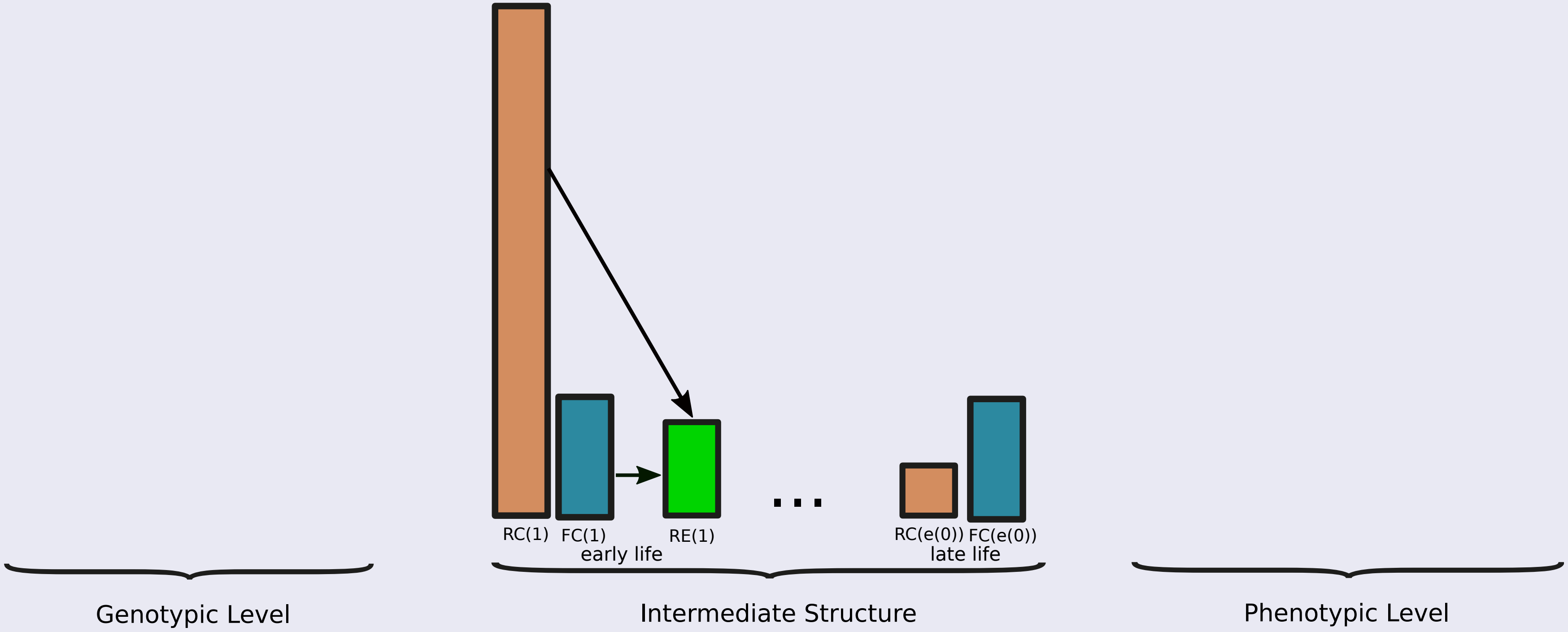
- Allocation requires both capitals (reproductive efforts require both types of resources)
- The dependency on FC is modulated by evolved storage capacity *stor*.
- The dependency on RC is modulated by the position on the slow-fast continuum *sfc*
- The realization, $RE(t)$, from the allowed (maximum) Reproductive Effort at time t $aRE(t)$, is stochastic and depends on granularity $gr = \frac{bre}{\bar{re}}$

$\Rightarrow$ gr positions an organism on the quantity-quality life history continuum.

- Allocation process is a function of the position of the organism on:
  - The Slow-Fast continuum
  - The Income-Capital Breeding continuum
  - The Quantity-Quality continuum

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Stearns[1] trade-off architecture

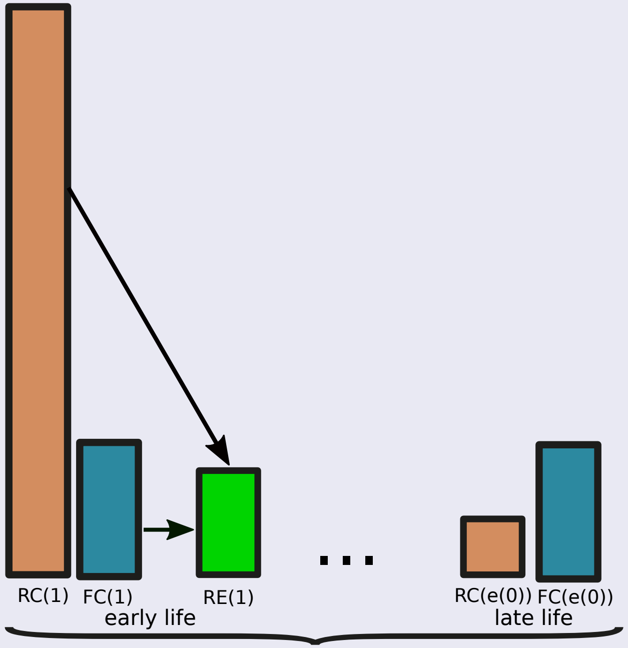
- genotypic level : genetic basis of the trade-off.
- phenotypic level :
  - ⇒ where negative correlations may emerge
  - ⇒ where natural selection acts
- intermediate structure : physiological mechanism in-between.

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Survival rates by age s(t)
Fertility rates by age f(t)

Correlations:

Individual level
Corr(f(t), f(t+T))

Genotypic Level

Intermediate Structure

Phenotypic Level

Stearns[1] trade-off architecture for **costs of reproduction**

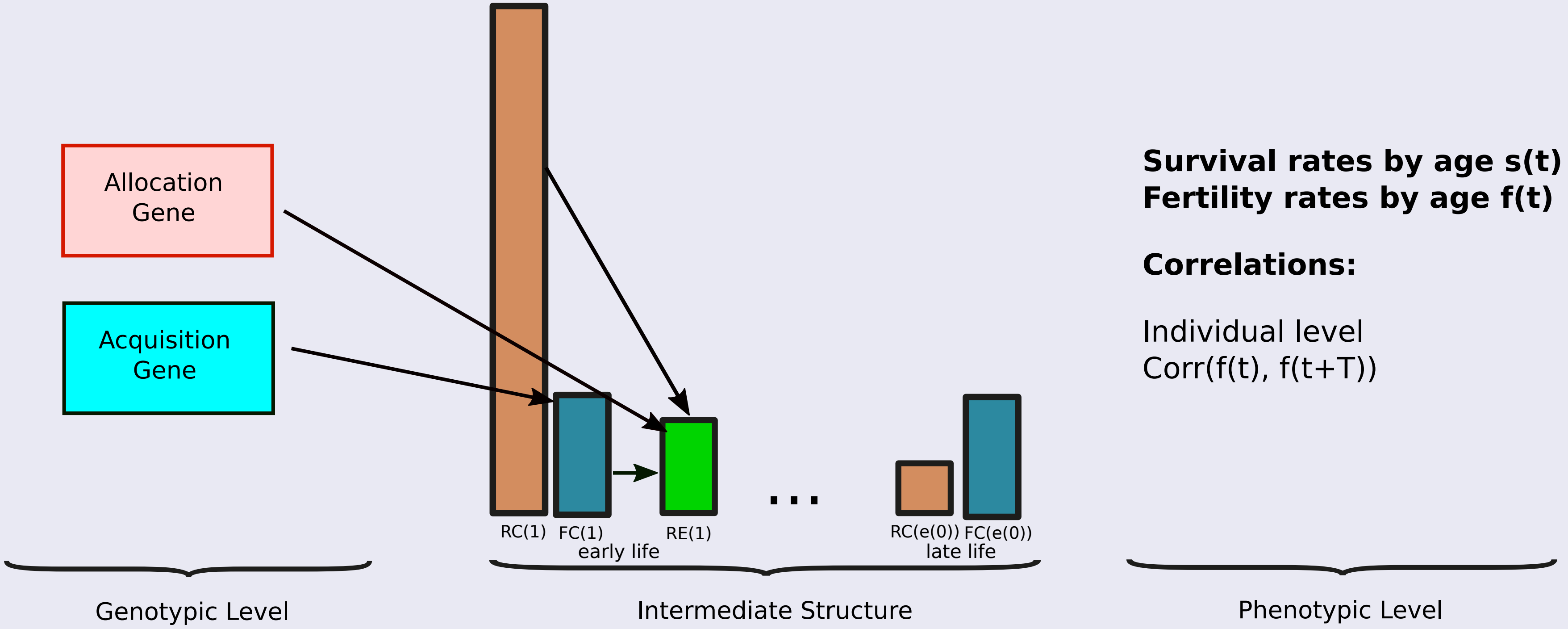
- intermediate structure : location of the allocation process.
- phenotypic level:
  - ⇒ fitness components : fertility and survival rates impacted directly by allocation process
  - ⇒ negative correlations ⇐ costs buffer the realization of fertility events

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Allocation Gene

Acquisition Gene

Survival rates by age s(t)
Fertility rates by age f(t)

Correlations:

Individual level
Corr(f(t), f(t+T))

Genotypic Level

Intermediate Structure

Phenotypic Level

Stearns[1] trade-off architecture for **costs of reproduction**

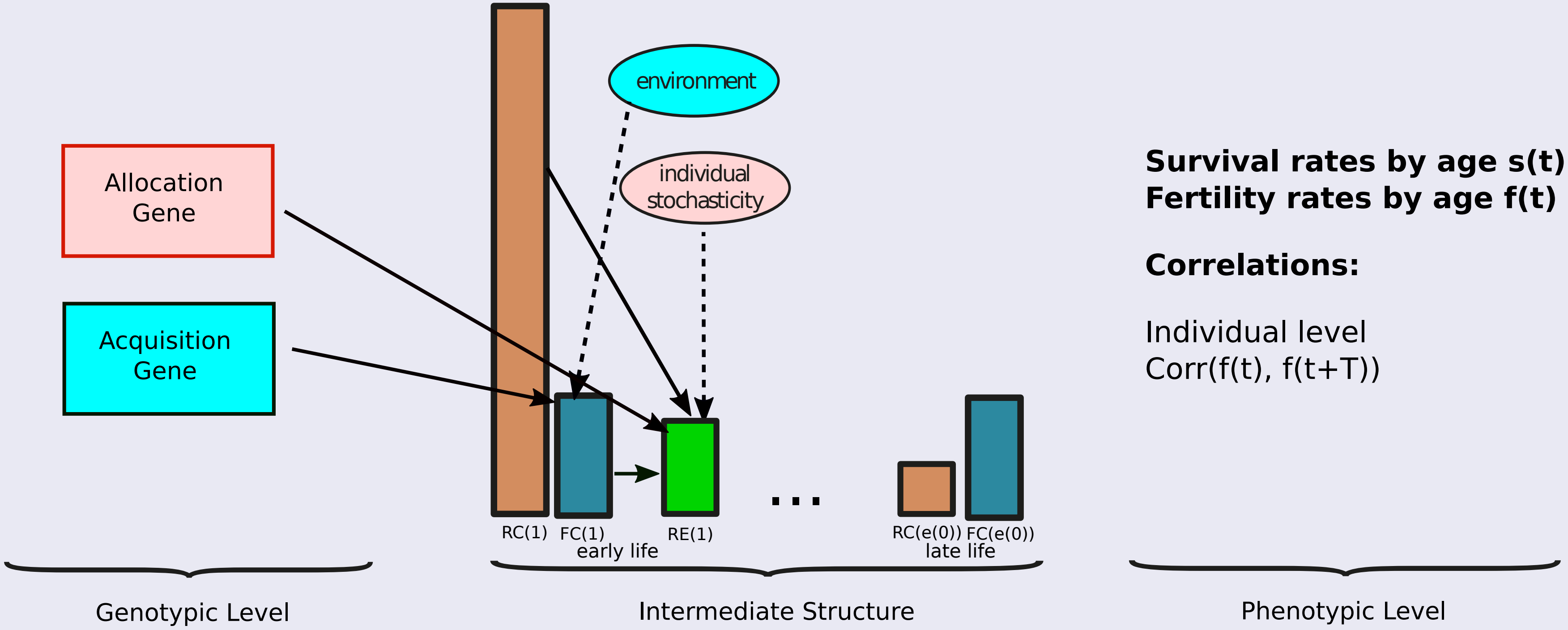
- intermediate structure : location of the allocation process.
- phenotypic level:
  - ⇒ fitness components : fertility and survival rates impacted directly by allocation process
  - ⇒ negative correlations ⇐ costs buffer the realization of fertility events
- genetic level : position of organism on life history strategies

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Survival rates by age s(t)
Fertility rates by age f(t)

Correlations:

Individual level
Corr(f(t), f(t+T))

Stearns[1] trade-off architecture for **costs of reproduction**

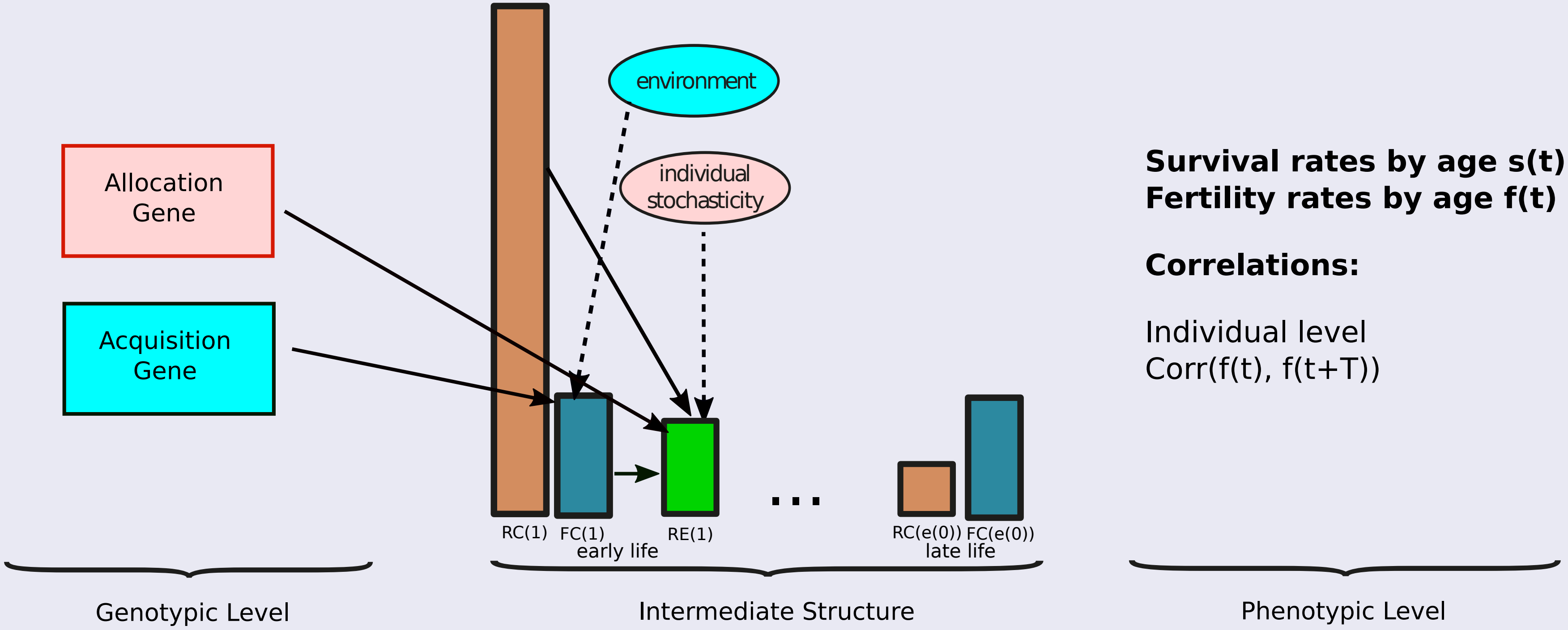
- intermediate structure : location of the allocation process.
- phenotypic level:
  - ⇒ fitness components : fertility and survival rates impacted directly by allocation process
  - ⇒ negative correlations ⇐ costs buffer the realization of fertility events
- genetic level : position of organism on life history strategies
- phenotypic trade-off = constraint + variance
  - ⇒ environmental and individual stochasticities also located at the intermediate level

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Survival rates by age s(t)
Fertility rates by age f(t)

Correlations:

Individual level
Corr(f(t), f(t+T))

Predictions of Detectability of Physiological Costs of Reproduction

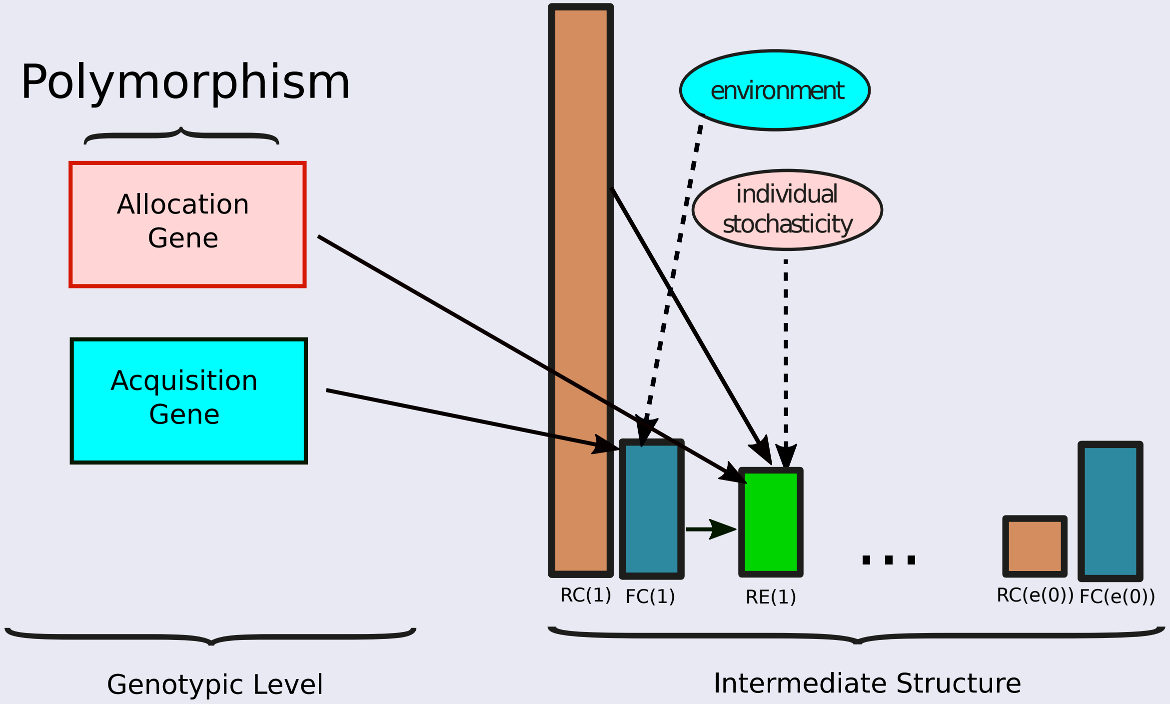
- Early-Mid life costs are function of position on Income-Capital Breeding spectrum.
- Long-term and Late-life costs are function of position on Slow-Fast Continuum.
- Low Environment increases detectability
- Individual Stochasticity fuels detectability
- Environmental Variance hinders detectability

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genotypic and Phenotypic Levels

Stearns[1] Trade-off Triptych



Survival rates by age s(t)
Fertility rates by age f(t)

Correlations:

Individual level
Corr(f(t), f(t+T))

Population level
Corr(f(t), f(t+T))
Corr(f(t), s(t+T))

Phenotypic Level

Variance at the genotypic level

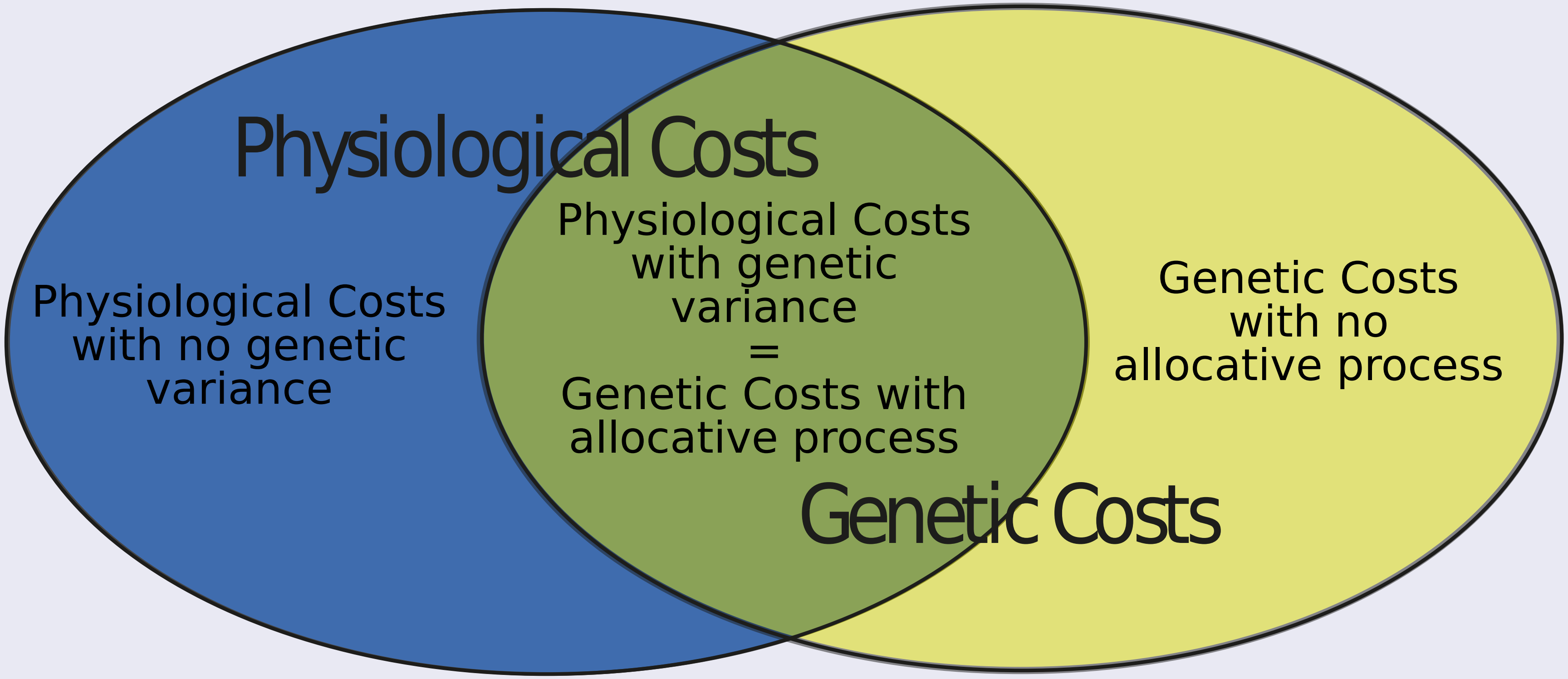
- Allocation gene has antagonistic pleiotropic effects on early fertility rates and later vital rates
  - variance in allocation gene $\Rightarrow$ genetic costs of reproduction
  - positions an organism on the slow-fast continuum
- However genetic costs $\not\Rightarrow$ physiological costs

---

[1] Stearns, S. C. (1989). Trade-offs in life-history evolution. Functional Ecology.

Genetic and Physiological Costs of reproduction

Genetic and Physiological Costs



Physiological Costs

Physiological Costs with no genetic variance

Physiological Costs with genetic variance = Genetic Costs with allocative process

Genetic Costs with no allocative process

Genetic Costs

Genetic Costs as variance in 2 orthogonal genes

allocation and acquisition

We extend Genetic Costs
⇒ include **genetic variance** in both **allocation** and **acquisition** genes

We consider **two ”orthogonal” genes**:

---

[1] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Genetic Costs as variance in 2 orthogonal genes

allocation and acquisition

We extend Genetic Costs
$\Rightarrow$ include **genetic variance** in both **allocation** and **acquisition** genes

We consider **two ”orthogonal” genes**:

- **variance in the *allocation gene*** is **iso-fitness**
- **variance in the *acquisition gene*** is **iso-strategy**

---

[1] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Genetic Costs as variance in 2 orthogonal genes

allocation and acquisition

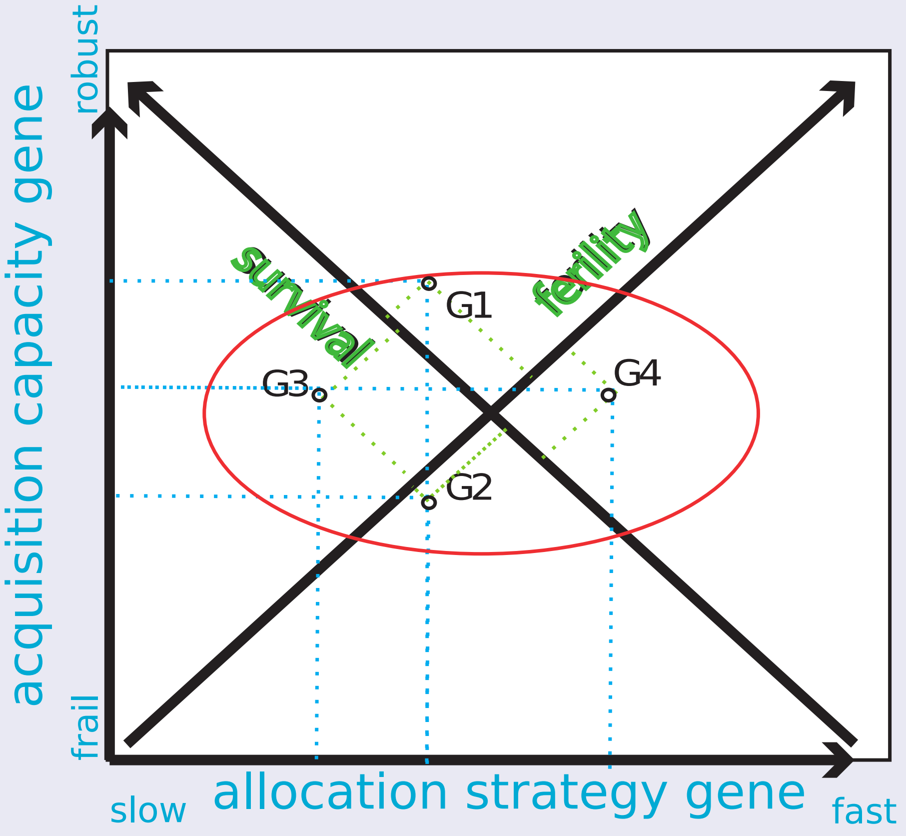
We extend Genetic Costs
⇒ include **genetic variance** in both **allocation** and **acquisition** genes

We consider **two "orthogonal" genes**:

- **variance in the *allocation gene*** is **iso-fitness**
- **variance in the *acquisition gene*** is **iso-strategy**

- G3 and G4 are iso-fitness ⇒ can cohabit
  ⇒ buffers populations against environmental changes
- G1 and G2 cohabit because of environmental variance
  ⇒ In other/recent environments G2 is fitter than G1

Genotypic map



---

[1] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Genetic Costs as variance in 2 orthogonal genes

allocation and acquisition

We extend Genetic Costs
⇒ include **genetic variance** in both **allocation** and **acquisition** genes

We consider **two "orthogonal" genes**:

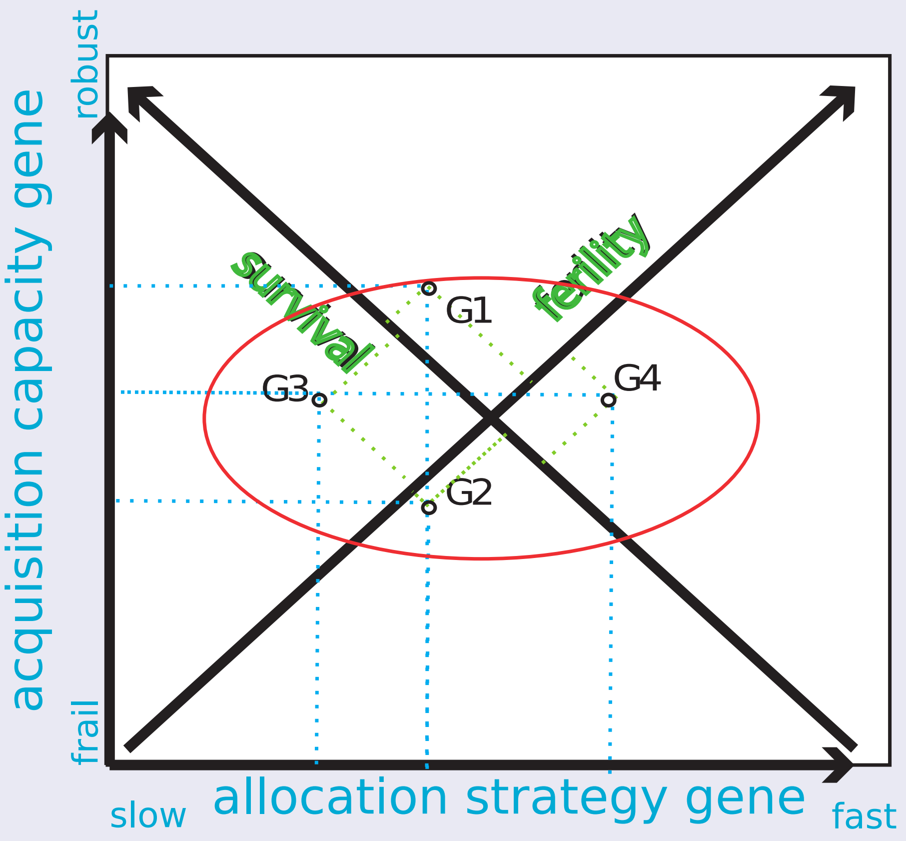
- **variance in the *allocation gene*** is **iso-fitness**
- **variance in the *acquisition gene*** is **iso-strategy**

- G3 and G4 are iso-fitness ⇒ can cohabit
  - ⇒ buffers populations against environmental changes
- G1 and G2 cohabit because of environmental variance
  - ⇒ In other/recent environments G2 is fitter than G1

Detectability of Genetic Costs depends on ratio[1]

- allocation gene variance vs
- acquisition gene variance

Genotypic map



---

[1] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Questions

Summary and Questions

- **Physiological costs** are **evolutionary mechanisms**, but this does not make them genetic costs.
- **Physiological and genetic costs** both **buffer the environment** and **generate negative correlations** between early fertility and late fitness
- But they are **different** and **operate on different scales**

⇒ Physiological costs work at the individual level, within life history trajectories

⇒ Genetic costs work at the population level, and on an evolutionary timescale

Questions

Summary and Questions

- **Physiological costs** are **evolutionary mechanisms**, but this does not make them genetic costs.
- **Physiological and genetic costs** both **buffer the environment** and **generate negative correlations** between early fertility and late fitness
- But they are **different** and **operate on different scales**

⇒ Physiological costs work at the individual level, within life history trajectories

⇒ Genetic costs work at the population level, and on an evolutionary timescale

- **Genetic and Physiological Costs can cohabit** at the population level :

⇒ **What are their** (relative, cross and joint) **evolutionary and demographic effects** ?

Questions

Summary and Questions

- **Physiological costs** are **evolutionary mechanisms**, but this does not make them genetic costs.
- **Physiological and genetic costs** both **buffer the environment** and **generate negative correlations** between early fertility and late fitness
- But they are **different** and **operate on different scales**

⇒ Physiological costs work at the individual level, within life history trajectories

⇒ Genetic costs work at the population level, and on an evolutionary timescale

- **Genetic and Physiological Costs can cohabit** at the population level :

⇒ **What are their** (relative, cross and joint) **evolutionary and demographic effects** ?

Model Issue

- To answer such questions requires to be able to **implement physiological trade-offs in an evolutionary demography model**.

⇒ Individual dynamics such as physiological costs are classically modeled by Agent-Based Models.

⇒ Population dynamics can be modeled by projection matrices

Questions

Summary and Questions

- **Physiological costs** are **evolutionary mechanisms**, but this does not make them genetic costs.
- **Physiological and genetic costs** both **buffer the environment** and **generate negative correlations** between early fertility and late fitness
- But they are **different** and **operate on different scales**

$\Rightarrow$ Physiological costs work at the individual level, within life history trajectories

$\Rightarrow$ Genetic costs work at the population level, and on an evolutionary timescale

- **Genetic and Physiological Costs can cohabit** at the population level :

$\Rightarrow$ **What are their** (relative, cross and joint) **evolutionary and demographic effects** ?

Model Issue

- To answer such questions requires to be able to **implement physiological trade-offs in an evolutionary demography model**.

$\Rightarrow$ Individual dynamics such as physiological costs are classically modeled by Agent-Based Models.

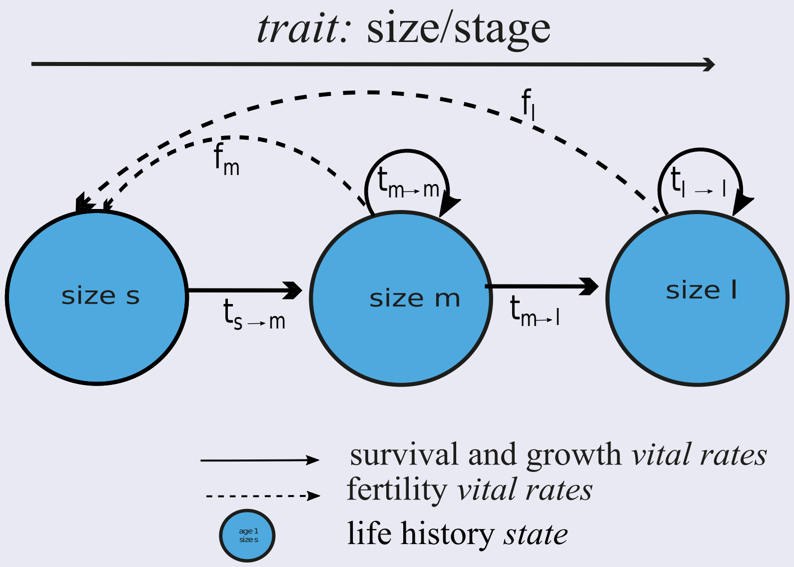
$\Rightarrow$ Population dynamics can be modeled by projection matrices

- **How to implement a multivariate constraint such as the physiological costs of reproduction into a matrix model ?**

Overview

One-trait structured life-cycle in matrix form

From a life history structured by size/stage ...



... to the related Lefkovitch/Usher matrix

Matrix form of life cycle, projection, eigen-analysis and sensibility

- q *states* $\longrightarrow$ $q \times q$ projection matrix $\mathbf{M}$.

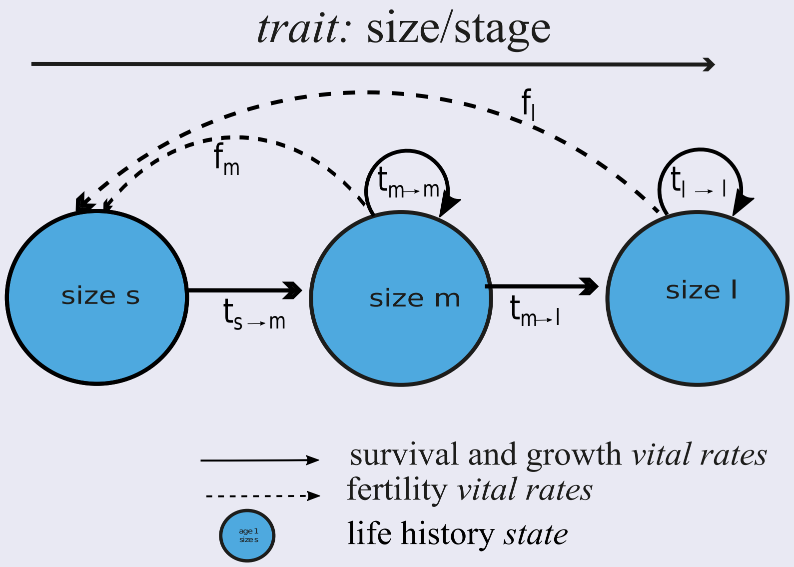
---

[1] Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. 14, 215–229.

[2] Lande, R. (1982). A quantitative genetic theory of life history evolution. Ecology, 63(3), 607âĂŞ615.

One-trait structured life-cycle in matrix form

From a life history structured by size/stage ...



... to the related Lefkovitch/Usher matrix

$$\mathbf{M} = \begin{bmatrix} f_s & f_m & f_l \\ t_{s\to m} & t_{m\to m} & 0 \\ 0 & t_{m\to l} & t_{l\to l} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- q *states* $\longrightarrow q \times q$ projection matrix $\mathbf{M}$.
- $\mathbf{M}$ projects population $\boldsymbol{n}_t$ over time : $\boldsymbol{n}_{t+1} = \mathbf{M}.\boldsymbol{n}_t$

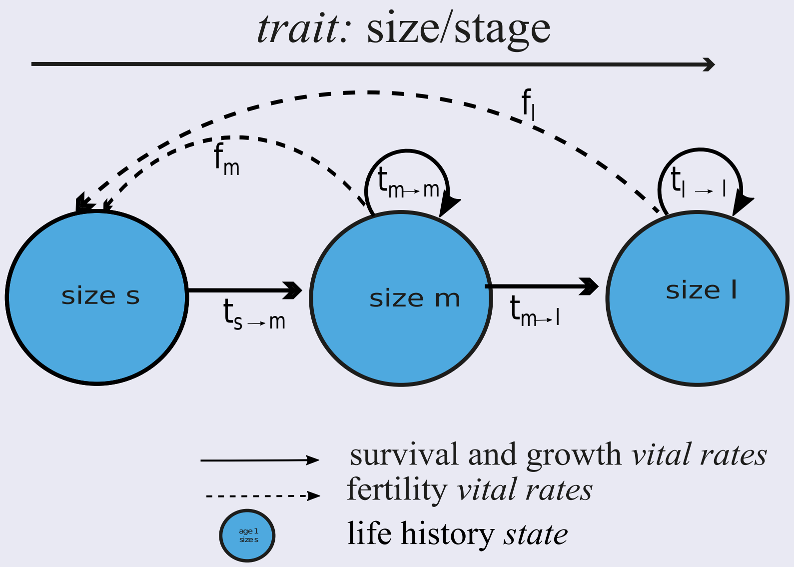
---

[1] Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. 14, 215–229.

[2] Lande, R. (1982). A quantitative genetic theory of life history evolution. Ecology, 63(3), 607âĂŞ615.

One-trait structured life-cycle in matrix form

From a life history structured by size/stage ...



... to the related Lefkovitch/Usher matrix

$$\mathbf{M} = \begin{bmatrix} f_s & f_m & f_l \\ t_{s\to m} & t_{m\to m} & 0 \\ 0 & t_{m\to l} & t_{l\to l} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- q *states* $\longrightarrow q \times q$ projection matrix $\mathbf{M}$.
- $\mathbf{M}$ projects population $\boldsymbol{n}_t$ over time : $\boldsymbol{n}_{t+1} = \mathbf{M}.\boldsymbol{n}_t$
- From $\mathbf{M}$ $\Rightarrow$ asymptotic growth rate (fitness) λ, solution of characteristic equation : $det(\mathbf{M} - x.\mathbf{I}) = 0$
- λ's associated left-eigenvector is the reproductive value $\boldsymbol{v}$: $\boldsymbol{v}.\mathbf{M} = \lambda.\boldsymbol{v}$
- λ's associated right-eigenvector is the stable state abundance distribution $\boldsymbol{w}$: $\mathbf{M}.\boldsymbol{w} = \lambda.\boldsymbol{w}$

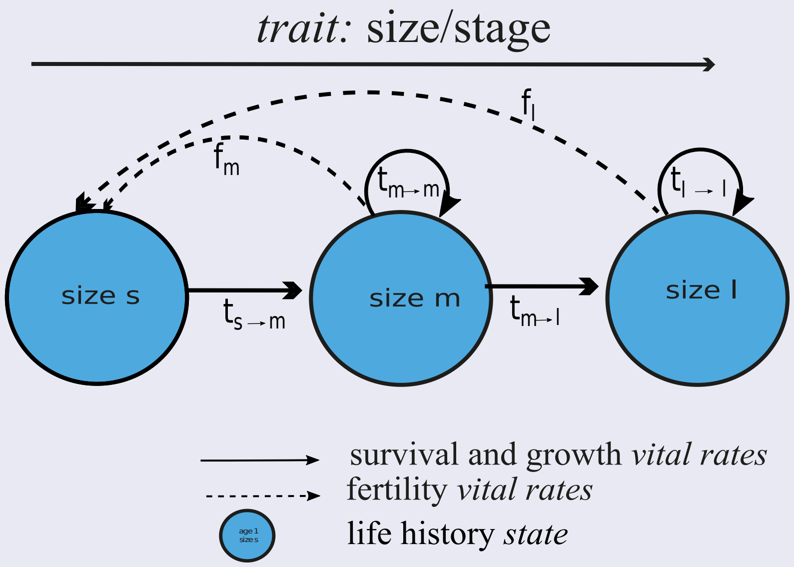
---

[1] Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. 14, 215–229.

[2] Lande, R. (1982). A quantitative genetic theory of life history evolution. Ecology, 63(3), 607âĂŞ615.

One-trait structured life-cycle in matrix form

From a life history structured by size/stage ...



... to the related Lefkovitch/Usher matrix

$$\mathbf{M} = \begin{bmatrix} f_s & f_m & f_l \\ t_{s\to m} & t_{m\to m} & 0 \\ 0 & t_{m\to l} & t_{l\to l} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- q *states* $\longrightarrow q \times q$ projection matrix $\mathbf{M}$.
- $\mathbf{M}$ projects population $\boldsymbol{n}_t$ over time : $\boldsymbol{n}_{t+1} = \mathbf{M}.\boldsymbol{n}_t$
- From $\mathbf{M}$ $\Rightarrow$ asymptotic growth rate (fitness) λ, solution of characteristic equation : $det(\mathbf{M} - x.\mathbf{I}) = 0$
- λ's associated left-eigenvector is the reproductive value $\boldsymbol{v}$: $\boldsymbol{v}.\mathbf{M} = \lambda.\boldsymbol{v}$
- λ's associated right-eigenvector is the stable state abundance distribution $\boldsymbol{w}$: $\mathbf{M}.\boldsymbol{w} = \lambda.\boldsymbol{w}$
- From these we can infer the sensitivity of fitness λ to any transition[1]: $\mathbf{S} = \frac{\partial\lambda}{\partial\mathbf{M}} = [\boldsymbol{w}.\boldsymbol{v}']$

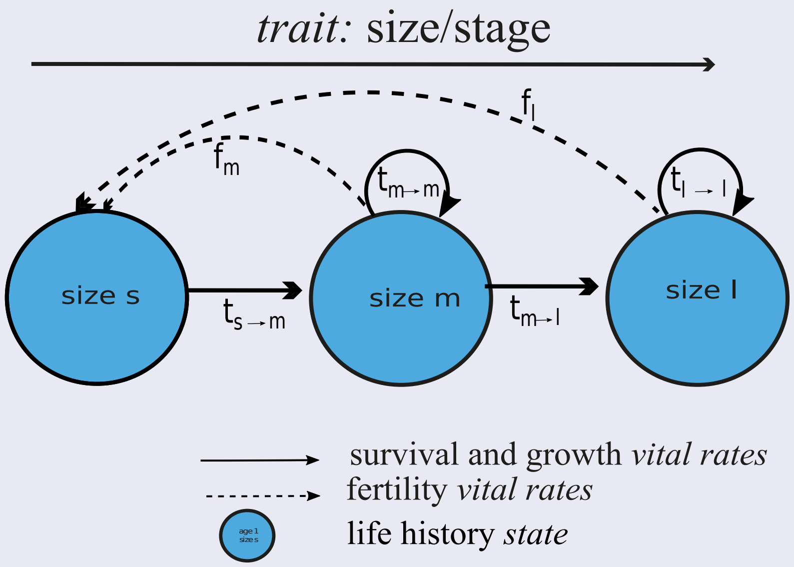
---

[1] Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. 14, 215–229.

[2] Lande, R. (1982). A quantitative genetic theory of life history evolution. Ecology, 63(3), 607âĂŞ615.

One-trait structured life-cycle in matrix form

From a life history structured by size/stage ...



... to the related Lefkovitch/Usher matrix

$$\mathbf{M} = \begin{bmatrix} f_s & f_m & f_l \\ t_{s\rightarrow m} & t_{m\rightarrow m} & 0 \\ 0 & t_{m\rightarrow l} & t_{l\rightarrow l} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- q *states* $\longrightarrow q \times q$ projection matrix $\mathbf{M}$.
- $\mathbf{M}$ projects population $\boldsymbol{n}_t$ over time : $\boldsymbol{n}_{t+1} = \mathbf{M}.\boldsymbol{n}_t$
- From $\mathbf{M}$ $\Rightarrow$ asymptotic growth rate (fitness) λ, solution of characteristic equation : $det(\mathbf{M} - x.\mathbf{I}) = 0$
- λ's associated left-eigenvector is the reproductive value $\boldsymbol{v}$: $\boldsymbol{v}.\mathbf{M} = \lambda.\boldsymbol{v}$
- λ's associated right-eigenvector is the stable state abundance distribution $\boldsymbol{w}$: $\mathbf{M}.\boldsymbol{w} = \lambda.\boldsymbol{w}$
- From these we can infer the sensitivity of fitness λ to any transition[1]: $\mathbf{S} = \frac{\partial\lambda}{\partial\mathbf{M}} = [\boldsymbol{w}.\boldsymbol{v}']$
- But for any vector of features, e.g. $\boldsymbol{y} = \begin{bmatrix} f_1 \\ f_3 \end{bmatrix}$, we have[2] $\frac{d\boldsymbol{y}}{dt} = \mathbf{G}.\nabla\lambda$ where $\nabla\lambda = \begin{bmatrix} \partial\lambda/\partial f_1 \\ \partial\lambda/\partial f_3 \end{bmatrix}$.

$\Rightarrow$ If strategy is optimal (ESS) i.e. $\frac{d\boldsymbol{y}}{dt} = 0 \Rightarrow$ we have genetic constraints $\mathbf{G}$ from sensitivities $\nabla\lambda = \frac{\partial\lambda}{\partial\mathbf{M}}$.

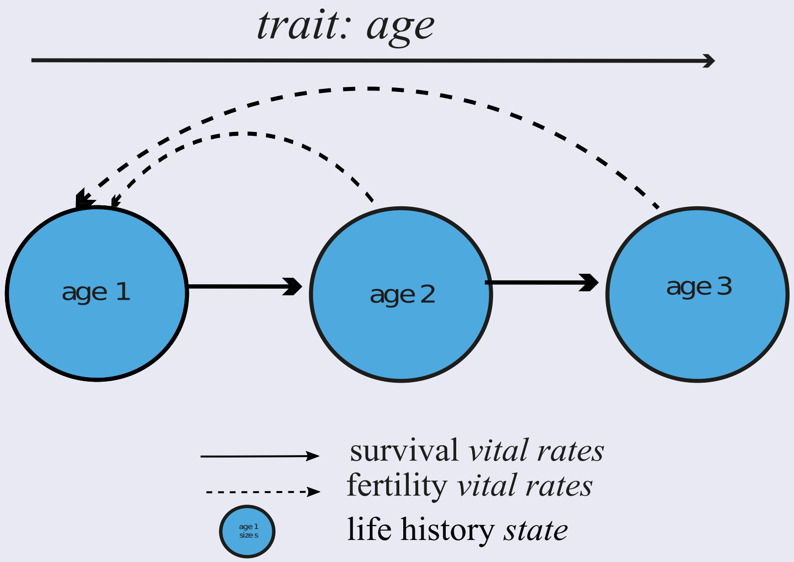
---

[1] Caswell, H., 1978. A general formula for the sensitivity of population growth rate to changes in life history parameters. Theor. Popul. Biol. 14, 215–229.

[2] Lande, R. (1982). A quantitative genetic theory of life history evolution. Ecology, 63(3), 607âĂŞ615.

Special case of age-structured life-cycle in matrix form

From a life history structured by age ...



... to the related Leslie matrix

$$\mathbf{M} = \begin{bmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility: familiar results from Leslie matrices

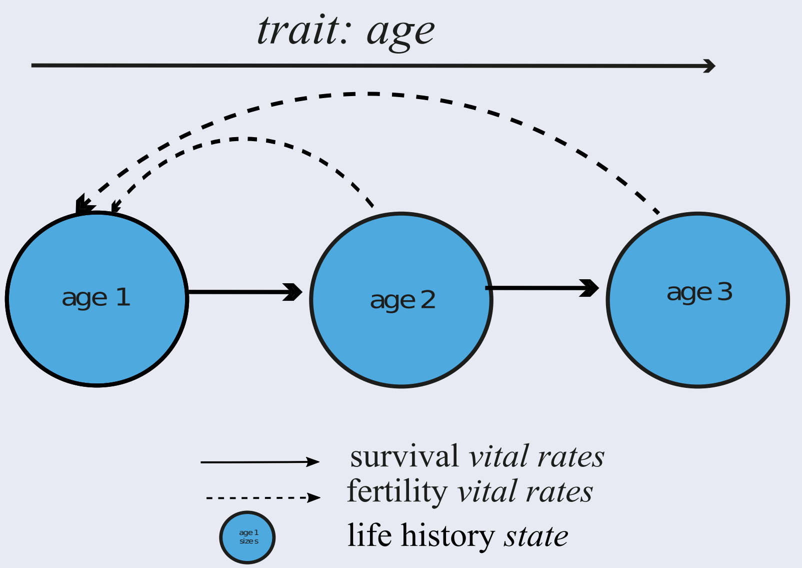
The matrix form yields the same result than the classical age-structure (discrete and continuous times) analyses[1]:

---

[1] Keyfitz, N. (1967). Reconciliation of population models: matrix, integral equation and partial fraction. JRSS. [2] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford U.P. [3] Demetrius, L. (1969). The sensitivity of population growth rate to pertubations in the life cycle components. MB. [4] Hamilton, W. D. (1966). The moulding of senescence by natural selection. JoTB

Special case of age-structured life-cycle in matrix form

From a life history structured by age ...



... to the related Leslie matrix

$$\mathbf{M} = \begin{bmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility: familiar results from Leslie matrices

The matrix form yields the same result than the classical age-structure (discrete and continuous times) analyses[1]:

- The age-structured characteristic equation is the Euler-Lotka equation :
  $det(\mathbf{M} - x.\mathbf{I}) = 0 \quad \Leftrightarrow \quad f_1.\lambda^{-1} + f_2.s_1.\lambda^{-2} + f_3.s_1.s_2.\lambda^{-3} = 0$

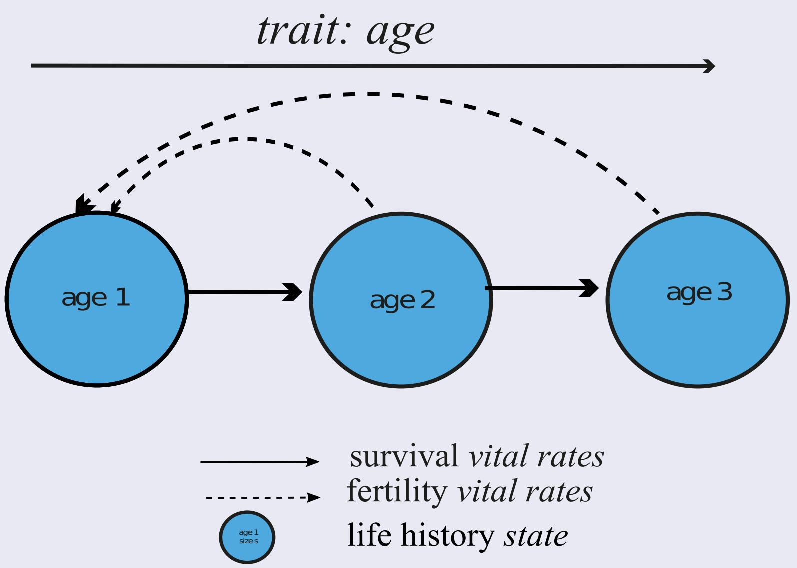
---

[1] Keyfitz, N. (1967). Reconciliation of population models: matrix, integral equation and partial fraction. JRSS. [2] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford U.P.

[3] Demetrius, L. (1969). The sensitivity of population growth rate to pertubations in the life cycle components. MB. [4] Hamilton, W. D. (1966). The moulding of senescence by natural selection. JoTB

Special case of age-structured life-cycle in matrix form

From a life history structured by age ...



... to the related Leslie matrix

$$\mathbf{M} = \begin{bmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility: familiar results from Leslie matrices

The matrix form yields the same result than the classical age-structure (discrete and continuous times) analyses[1]:

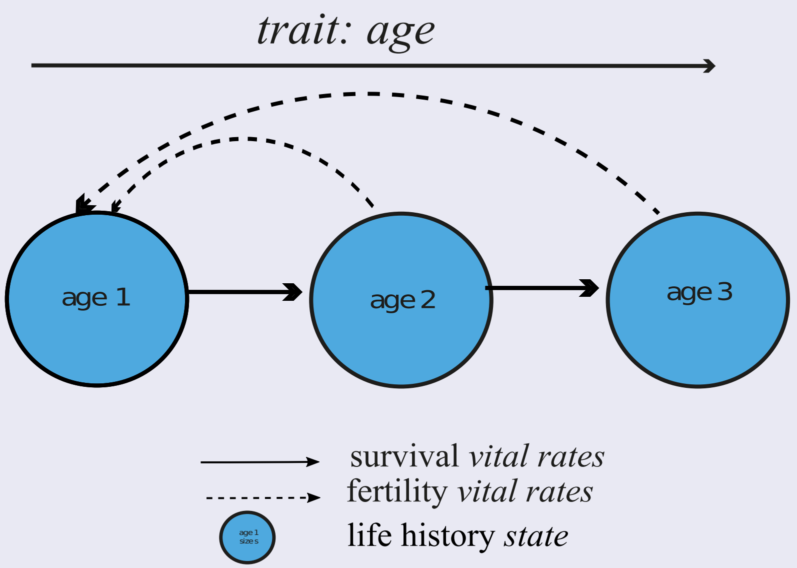
- The age-structured characteristic equation is the Euler-Lotka equation :
  $det(\mathbf{M} - x.\mathbf{I}) = 0 \quad \Leftrightarrow \quad f_1.\lambda^{-1} + f_2.s_1.\lambda^{-2} + f_3.s_1.s_2.\lambda^{-3} = 0$
- The associated left-eigenvector (scaled so its first element is 1) is Fisher's reproductive value[2]:
  $\boldsymbol{v} = \begin{bmatrix} 1 & \frac{f_2}{\lambda} + \frac{f_3.s_2}{\lambda^2} & \frac{f_3}{\lambda} \end{bmatrix}$

---

[1] Keyfitz, N. (1967). Reconciliation of population models: matrix, integral equation and partial fraction. JRSS. [2] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford U.P.
[3] Demetrius, L. (1969). The sensitivity of population growth rate to pertubations in the life cycle components. MB. [4] Hamilton, W. D. (1966). The moulding of senescence by natural selection. JoTB

Special case of age-structured life-cycle in matrix form

From a life history structured by age ...



... to the related Leslie matrix

$$\mathbf{M} = \begin{bmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility: familiar results from Leslie matrices

The matrix form yields the same result than the classical age-structure (discrete and continuous times) analyses[1]:

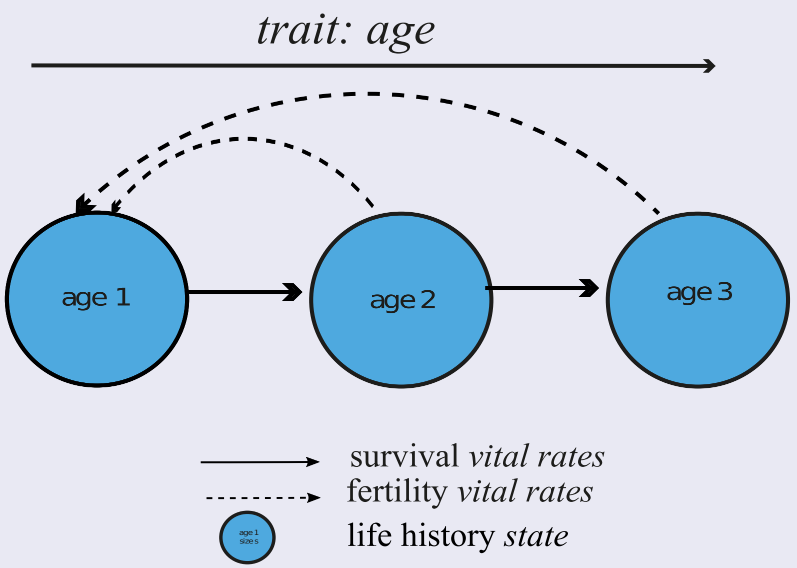
- The age-structured characteristic equation is the Euler-Lotka equation :
  $det(\mathbf{M} - x.\mathbf{I}) = 0 \quad \Leftrightarrow \quad f_1.\lambda^{-1} + f_2.s_1.\lambda^{-2} + f_3.s_1.s_2.\lambda^{-3} = 0$
- The associated left-eigenvector (scaled so its first element is 1) is Fisher's reproductive value[2]:
  $\boldsymbol{v} = \begin{bmatrix} 1 & \frac{f_2}{\lambda} + \frac{f_3.s_2}{\lambda^2} & \frac{f_3}{\lambda} \end{bmatrix}$
- The associated right-eigenvector (scaled to sum to 1) is Demetrius's relative abundance distribution[3]:
  $\boldsymbol{w} = \frac{1}{1+s_1.\lambda^{-1}+s_1.s_2.\lambda^{-2}} \begin{bmatrix} 1 & \frac{s_1}{\lambda} & \frac{s_1.s_2}{\lambda^2} \end{bmatrix}$

---

[1] Keyfitz, N. (1967). Reconciliation of population models: matrix, integral equation and partial fraction. JRSS. [2] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford U.P. [3] Demetrius, L. (1969). The sensitivity of population growth rate to pertubations in the life cycle components. MB. [4] Hamilton, W. D. (1966). The moulding of senescence by natural selection. JoTB

Special case of age-structured life-cycle in matrix form

From a life history structured by age ...



... to the related Leslie matrix

$$\mathbf{M} = \begin{bmatrix} f_1 & f_2 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & 0 \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility: familiar results from Leslie matrices

The matrix form yields the same result than the classical age-structure (discrete and continuous times) analyses[1]:

- The age-structured characteristic equation is the Euler-Lotka equation :
  $det(\mathbf{M} - x.\mathbf{I}) = 0 \quad \Leftrightarrow \quad f_1.\lambda^{-1} + f_2.s_1.\lambda^{-2} + f_3.s_1.s_2.\lambda^{-3} = 0$
- The associated left-eigenvector (scaled so its first element is 1) is Fisher's reproductive value[2]:
  $\boldsymbol{v} = \begin{bmatrix} 1 & \frac{f_2}{\lambda} + \frac{f_3.s_2}{\lambda^2} & \frac{f_3}{\lambda} \end{bmatrix}$
- The associated right-eigenvector (scaled to sum to 1) is Demetrius's relative abundance distribution[3]:
  $\boldsymbol{w} = \frac{1}{1+s_1.\lambda^{-1}+s_1.s_2.\lambda^{-2}} \begin{bmatrix} 1 & \frac{s_1}{\lambda} & \frac{s_1.s_2}{\lambda^2} \end{bmatrix}$
- Denoting $d_i = f_i.\lambda^{-i}.\Pi_{j=1}^{i-1} s_j$ the distribution of parental age, and $c_i = v_i.w_i$ the age-*class* reproductive value, selection gradients correspond to Hamilton's elasticity formulae[4] : $\frac{\partial \log \lambda}{\partial \log f_i} = v_1.w_1.d_i$ and $\frac{\partial \log \lambda}{\partial \log s_i} = c_{i+1}$

---

[1] Keyfitz, N. (1967). Reconciliation of population models: matrix, integral equation and partial fraction. JRSS. [2] Fisher, R. A. (1930). The Genetical Theory of Natural Selection. Genetics. Oxford U.P. [3] Demetrius, L. (1969). The sensitivity of population growth rate to pertubations in the life cycle components. MB. [4] Hamilton, W. D. (1966). The moulding of senescence by natural selection. JoTB

Implementation of physiological costs with genetic basis in a multitrait framework

Incorporation physiological or genetic trade-offs require addition of traits from different families:

Implementation of physiological costs with genetic basis in a multitrait framework

Incorporation physiological or genetic trade-offs require addition of traits from different families:

Basic traits

Basic traits correspond to the **best determinants of life-history**

- age (inherent to any projection model)
- other basic traits can be added: e.g. stage, size, sex, location ..

Implementation of physiological costs with genetic basis in a multitrait framework

Incorporation physiological or genetic trade-offs require addition of traits from different families:

Basic traits

Basic traits correspond to the **best determinants of life-history**

- age (inherent to any projection model)
- other basic traits can be added: e.g. stage, size, sex, location ..

Fixed Heterogeneity for genetic costs

- **Fixed-heterogeneity traits** correspond to fixed-at-birth heterogeneity/genotypes.

$\Rightarrow$ Fixed-heterogeneity traits can implement **genetic trade-offs**

- Structured Population Genetics Model:

$\Rightarrow$ asymptotic stable-state of evolutionary population dynamics $\Leftrightarrow$ mutation/selection equilibrium of population genetics

Implementation of physiological costs with genetic basis in a multitrait framework

Incorporation physiological or genetic trade-offs require addition of traits from different families:

Basic traits

Basic traits correspond to the **best determinants of life-history**

- age (inherent to any projection model)
- other basic traits can be added: e.g. stage, size, sex, location ..

Fixed Heterogeneity for genetic costs

- **Fixed-heterogeneity traits** correspond to fixed-at-birth heterogeneity/genotypes.

⇒ Fixed-heterogeneity traits can implement **genetic trade-offs**

- Structured Population Genetics Model:

⇒ asymptotic stable-state of evolutionary population dynamics ⇔ mutation/selection equilibrium of population genetics

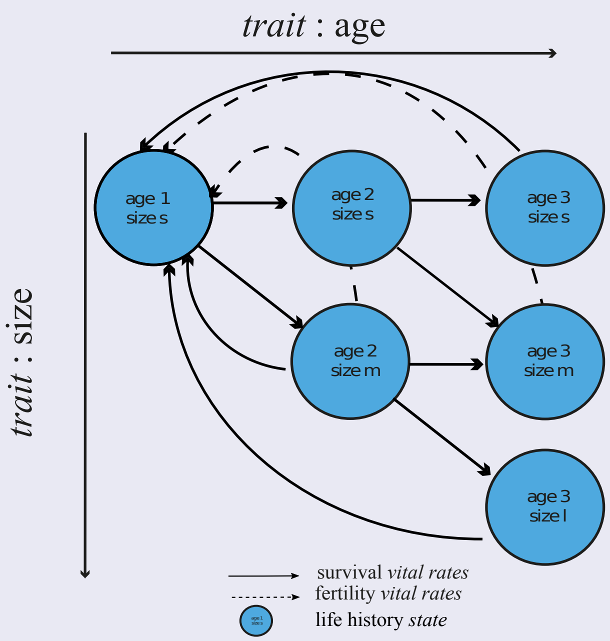
Dynamic Heterogeneity for physiological costs

- **Dynamic-heterogeneity traits** track variations in life trajectories between individuals with the same genotype.

⇒ Dynamic-heterogeneity traits can implement **physiological trade-offs**

Multitrait structured life-cycle in matrix form

A multitrait life history in matrix form, how ?



multidimensional population vectors have to be vectorized

$$\mathbb{N} = \begin{bmatrix} n_{1,1} & n_{2,1} & n_{3,1} \\ n_{1,2} & n_{2,2} & n_{3,2} \\ n_{1,3} & n_{2,3} & n_{3,3} \end{bmatrix} \rightarrowtail \boldsymbol{n} = vec(\mathbb{N}) = \begin{bmatrix} n_{1,1} \\ n_{2,1} \\ n_{3,1} \\ n_{1,2} \\ n_{2,2} \\ n_{3,2} \\ n_{1,3} \\ n_{2,3} \\ n_{3,3} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

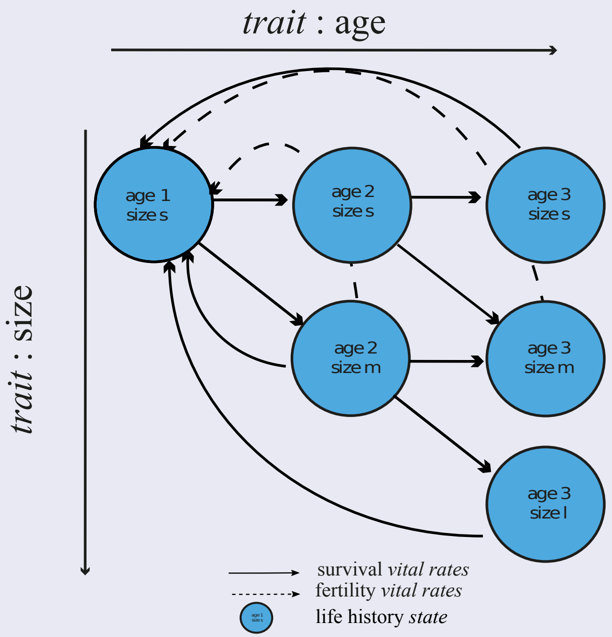
---

[1] Roth G., & Caswell H. (2016). Hyperstate matrix models: extending demographic state spaces to higher dimensions. Methods in Ecology and Evolution.

[2] Coste C.F.D., Austerlitz F. & Pavard S. (2017). Trait level analysis of multitrait population projection matrices. Theoretical Population Biology

Multitrait structured life-cycle in matrix form

A multitrait life history in matrix form, how ?



multidimensional population vectors have to be vectorized

$$\mathbb{N} = \begin{bmatrix} n_{1,1} & n_{2,1} & n_{3,1} \\ n_{1,2} & n_{2,2} & n_{3,2} \\ n_{1,3} & n_{2,3} & n_{3,3} \end{bmatrix} \rightarrowtail \boldsymbol{n} = vec(\mathbb{N}) = \begin{bmatrix} n_{1,1} \\ n_{2,1} \\ n_{3,1} \\ n_{1,2} \\ n_{2,2} \\ n_{3,2} \\ n_{1,3} \\ n_{2,3} \\ n_{3,3} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- Multitrait life cycle is multidimensional $\Rightarrow$ space of states has to be vectorized.
- trait structure $\boldsymbol{s}$ stores position and dimension of traits, here $\boldsymbol{s} = (3, 3)$. There are $q = \Pi_{k=1}^{n} s_k$ states.

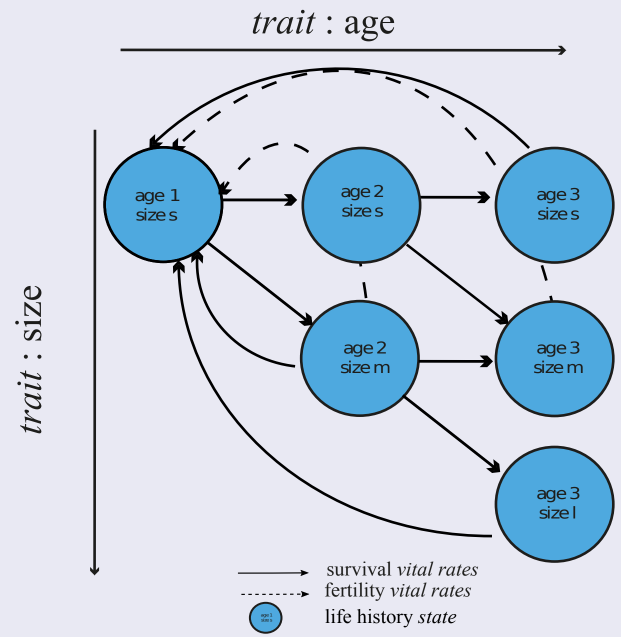
---

[1] Roth G., & Caswell H. (2016). Hyperstate matrix models: extending demographic state spaces to higher dimensions. Methods in Ecology and Evolution.

[2] Coste C.F.D., Austerlitz F. & Pavard S. (2017). Trait level analysis of multitrait population projection matrices. Theoretical Population Biology

Multitrait structured life-cycle in matrix form

A multitrait life history in matrix form, how ?



multidimensional population vectors have to be vectorized

$$\mathbb{N} = \begin{bmatrix} n_{1,1} & n_{2,1} & n_{3,1} \\ n_{1,2} & n_{2,2} & n_{3,2} \\ n_{1,3} & n_{2,3} & n_{3,3} \end{bmatrix} \rightarrowtail \boldsymbol{n} = vec(\mathbb{N}) = \begin{bmatrix} n_{1,1} \\ n_{2,1} \\ n_{3,1} \\ n_{1,2} \\ n_{2,2} \\ n_{3,2} \\ n_{1,3} \\ n_{2,3} \\ n_{3,3} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- Multitrait life cycle is multidimensional ⇒ space of states has to be vectorized.
- trait structure $\boldsymbol{s}$ stores position and dimension of traits, here $\boldsymbol{s} = (3, 3)$. There are $q = \Pi_{k=1}^{n} s_k$ states.
- Construction of Multitrait Population Projection Matrix **M** of size $q \times q$:

⇒ the vec-permutation approach[1]

⇒ the vector-based method[2]

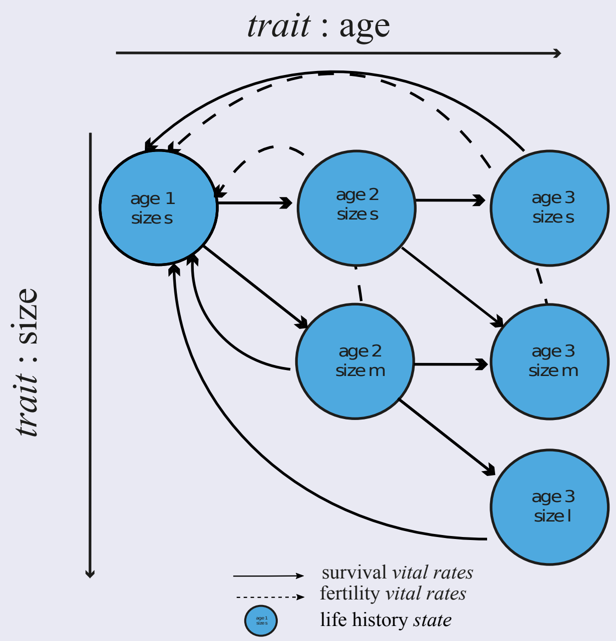
---

[1] Roth G., & Caswell H. (2016). Hyperstate matrix models: extending demographic state spaces to higher dimensions. Methods in Ecology and Evolution.

[2] Coste C.F.D., Austerlitz F. & Pavard S. (2017). Trait level analysis of multitrait population projection matrices. Theoretical Population Biology

Multitrait structured life-cycle in matrix form

A multitrait life history in matrix form, how ?



multidimensional population vectors have to be vectorized

$$\mathbb{N} = \begin{bmatrix} n_{1,1} & n_{2,1} & n_{3,1} \\ n_{1,2} & n_{2,2} & n_{3,2} \\ n_{1,3} & n_{2,3} & n_{3,3} \end{bmatrix} \rightarrowtail \boldsymbol{n} = vec(\mathbb{N}) = \begin{bmatrix} n_{1,1} \\ n_{2,1} \\ n_{3,1} \\ n_{1,2} \\ n_{2,2} \\ n_{3,2} \\ n_{1,3} \\ n_{2,3} \\ n_{3,3} \end{bmatrix}$$

Matrix form of life cycle, projection, eigen-analysis and sensibility

- Multitrait life cycle is multidimensional ⇒ space of states has to be vectorized.
- trait structure $\boldsymbol{s}$ stores position and dimension of traits, here $\boldsymbol{s} = (3, 3)$. There are $q = \Pi_{k=1}^{n} s_k$ states.
- Construction of Multitrait Population Projection Matrix $\mathbf{M}$ of size $q \times q$:
  - ⇒ the vec-permutation approach[1]
  - ⇒ the vector-based method[2]
- From the eigen-analysis of $\mathbf{M}$, we can extract $\mathbb{W} = vec_{\boldsymbol{s}}^{-1}(w)$ and $\mathbb{V} = vec_{\boldsymbol{s}}^{-1}(v)$
- From $\mathbb{S}$ the parameter sensitivity matrix, we can calculate sensitivities: $\mathbb{S} \circ \mathbf{S}$

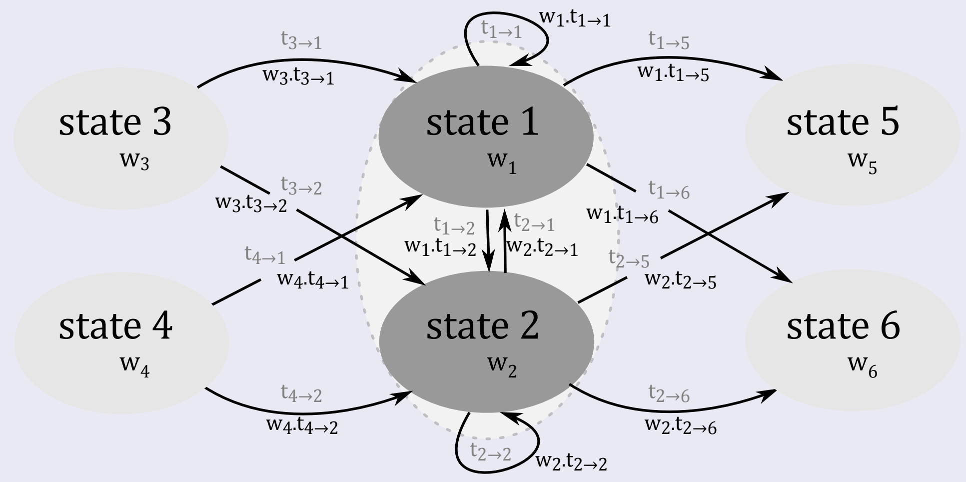
---

[1] Roth G., & Caswell H. (2016). Hyperstate matrix models: extending demographic state spaces to higher dimensions. Methods in Ecology and Evolution.

[2] Coste C.F.D., Austerlitz F. & Pavard S. (2017). Trait level analysis of multitrait population projection matrices. Theoretical Population Biology

Ergodic Flow Preserving - Merging

Ergodic-Flow Preserving Merging (before)



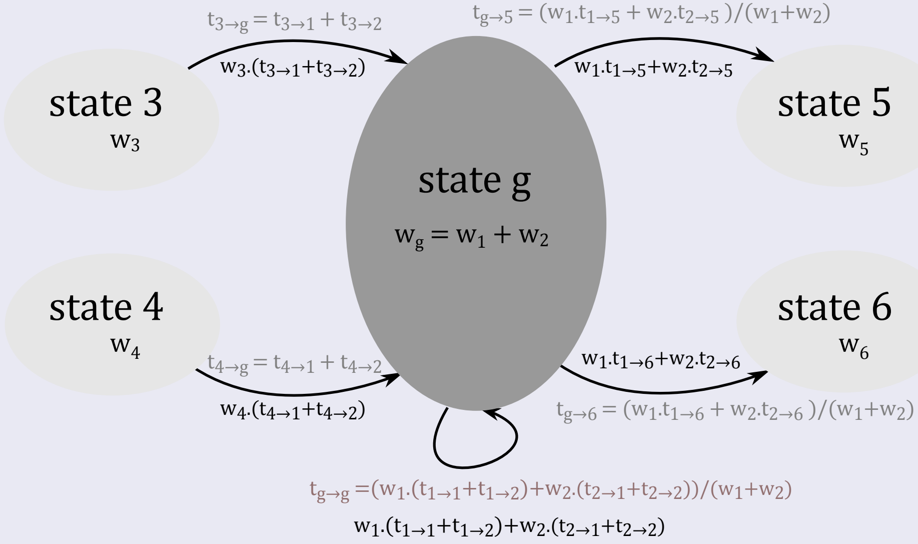
Two states are grouped, via *EFP*-merging, by ...

– summing, for each state, transition rates towards the group
– summing, for each state, the ergodic-abundances-weighted transition rates from the group

From EFP-Merging to *folding*

- EFP-Merging preserves ergodic flows, λ and $\boldsymbol{w}$.
- at the cost of other properties $\Rightarrow$ $\boldsymbol{v}$ and therefore $\mathbf{S} = [\boldsymbol{w}.\boldsymbol{v}']$ are not preserved.

Ergodic-Flow Preserving Merging (after)



w_i : relative ergodic abundance of state i
$t_{i\to j}$: edge/ transition value
$w_i.t_{i\to j}$: relative ergodic flow

Folding and Trait Level Analysis

EFP-merging can be extended from states to traits:

- **M** MPPM with trait vector $\boldsymbol{s} = (t_1, t_2)$ can be *folded* over trait t_2 -yielding $\mathbf{M^{fold}_{t_1}}$ - by EFP-merging all states sharing the same values for trait t_1.

Folding and Trait Level Analysis

EFP-merging can be extended from states to traits:

- **M** MPPM with trait vector $\boldsymbol{s} = (t_1, t_2)$ can be *folded* over trait t_2 -yielding $\mathbf{M}^{\mathbf{fold}}_{\mathbf{t_1}}$ - by EFP-merging all states sharing the same values for trait t_1.

2 traits, each of size 2

$$\mathbf{M}_{\mathbf{t_1},\mathbf{t_2}} = \left[\begin{array}{cc:cc} M_{(1,1)\to(1,1)} & M_{(2,1)\to(1,1)} & M_{(1,2)\to(1,1)} & M_{(2,2)\to(1,1)} \\ M_{(1,1)\to(2,1)} & M_{(2,1)\to(2,1)} & M_{(1,2)\to(2,1)} & M_{(2,2)\to(2,1)} \\ \hdashline M_{(1,1)\to(1,2)} & M_{(2,1)\to(1,2)} & M_{(1,2)\to(1,2)} & M_{(2,2)\to(1,2)} \\ M_{(1,1)\to(2,2)} & M_{(2,1)\to(2,2)} & M_{(1,2)\to(2,2)} & M_{(2,2)\to(2,2)} \end{array}\right]$$

$$\mathbf{M}^{\mathbf{fold}}_{\mathbf{t_1}} = \begin{bmatrix} \frac{w_{(1,1)}.(M_{(1,1)\to(1,1)}+M_{(1,1)\to(1,2)})+w_{(1,2)}.(M_{(1,2)\to(1,1)}+M_{(1,2)\to(1,2)})}{w_{(1,1)}+w_{(1,2)}} & \frac{w_{(2,1)}.(M_{(2,1)\to(1,1)}+M_{(2,1)\to(1,2)})+w_{(2,2)}.(M_{(2,2)\to(1,1)}+M_{(2,2)\to(1,2)})}{w_{(2,1)}+w_{(2,2)}} \\ \frac{w_{(1,1)}.(M_{(1,1)\to(2,1)}+M_{(1,1)\to(2,2)})+w_{(1,2)}.(M_{(1,2)\to(2,1)}+M_{(1,2)\to(2,2)})}{w_{(1,1)}+w_{(1,2)}} & \frac{w_{(2,1)}.(M_{(2,1)\to(1,1)}+M_{(2,1)\to(1,2)})+w_{(2,2)}.(M_{(2,2)\to(1,1)}+M_{(2,2)\to(1,2)})}{w_{(2,1)}+w_{(2,2)}} \end{bmatrix}$$

Folding and Trait Level Analysis

EFP-merging can be extended from states to traits:

- **M** MPPM with trait vector $\boldsymbol{s} = (t_1, t_2)$ can be *folded* over trait t_2 -yielding $\mathbf{M}^{\text{fold}}_{\mathbf{t_1}}$ - by EFP-merging all states sharing the same values for trait t_1.

2 traits, each of size 2

$$\mathbf{M}_{\mathbf{t_1},\mathbf{t_2}} = \left[\begin{array}{cc:cc} M_{(1,1)\to(1,1)} & M_{(2,1)\to(1,1)} & M_{(1,2)\to(1,1)} & M_{(2,2)\to(1,1)} \\ M_{(1,1)\to(2,1)} & M_{(2,1)\to(2,1)} & M_{(1,2)\to(2,1)} & M_{(2,2)\to(2,1)} \\ \hdashline M_{(1,1)\to(1,2)} & M_{(2,1)\to(1,2)} & M_{(1,2)\to(1,2)} & M_{(2,2)\to(1,2)} \\ M_{(1,1)\to(2,2)} & M_{(2,1)\to(2,2)} & M_{(1,2)\to(2,2)} & M_{(2,2)\to(2,2)} \end{array}\right]$$

$$\mathbf{M}^{\text{fold}}_{\mathbf{t_1}} = \begin{bmatrix} \frac{w_{(1,1)}.(M_{(1,1)\to(1,1)}+M_{(1,1)\to(1,2)})+w_{(1,2)}.(M_{(1,2)\to(1,1)}+M_{(1,2)\to(1,2)})}{w_{(1,1)}+w_{(1,2)}} & \frac{w_{(2,1)}.(M_{(2,1)\to(1,1)}+M_{(2,1)\to(1,2)})+w_{(2,2)}.(M_{(2,2)\to(1,1)}+M_{(2,2)\to(1,2)})}{w_{(2,1)}+w_{(2,2)}} \\ \frac{w_{(1,1)}.(M_{(1,1)\to(2,1)}+M_{(1,1)\to(2,2)})+w_{(1,2)}.(M_{(1,2)\to(2,1)}+M_{(1,2)\to(2,2)})}{w_{(1,1)}+w_{(1,2)}} & \frac{w_{(2,1)}.(M_{(2,1)\to(1,1)}+M_{(2,1)\to(1,2)})+w_{(2,2)}.(M_{(2,2)\to(1,1)}+M_{(2,2)\to(1,2)})}{w_{(2,1)}+w_{(2,2)}} \end{bmatrix}$$

General Case

From the permutation of traits σ, we have multidimensional matrix operator $perm_\sigma$,

$\forall \mathbb{A} \in \mathcal{M}_{\mathbf{s}}(\mathbb{R}) \quad perm_\sigma(\mathbb{A})_{i_1,i_2,\ldots,i_n} = \mathbb{A}_{\sigma(i_1,i_2,\ldots,i_n)}$

$\Rightarrow$ corresponding permutation of states σ^*, $\quad \sigma^*(1,\ldots,q) = vec(perm_\sigma(vec_{\mathbf{s}}^{-1}(1,\ldots,q)))$

This allows to generate $\mathbf{M}^{\text{fold}}_{\mathbf{t}\setminus\mathbf{st}} = \underbrace{\mathbf{P}^{\mathbf{BF}}}_{\text{Block-Folding "permutation" matrix}}.(\mathbf{M} \circ \underbrace{\mathbf{W}}_{\text{Ergodic abundance weights}}).\mathbf{P}^{\mathbf{BF}'}$

$\Rightarrow$ ***Folding*, the mechanism constituting *Trait Level Analysis*, is an asymptotically neutral framework that allows to measure the evolutionary and demographic importance of traits**

Overview

1. Introduction
2. Costs of reproduction: concepts and life history model
3. Multitrait Population Projection Models
4. Evolutionary and demographic consequences of physiological costs of reproduction
5. Discussion

The Model

a 3-trait MPPM

- one basic trait: *age*

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*

⇒ encompasses variance in both allocation and acquisition genes

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*
  ⇒ encompasses variance in both allocation and acquisition genes
- one dynamic-heterogeneity trait to model *physiological costs of reproduction* : *parity*

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*

⇒ encompasses variance in both allocation and acquisition genes

- one dynamic-heterogeneity trait to model *physiological costs of reproduction* : *parity*
- The model is an *age-parity-heterogeneity*-MPPM

Features of the *age-parity-heterogeneity*-MPPM

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*

  ⇒ encompasses variance in both allocation and acquisition genes
- one dynamic-heterogeneity trait to model *physiological costs of reproduction* : *parity*
- The model is an *age-parity-heterogeneity*-MPPM

Features of the *age-parity-heterogeneity*-MPPM

- Mutation rate μ: the probability that the offspring is of different genotype than its parent.

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*

  ⇒ encompasses variance in both allocation and acquisition genes
- one dynamic-heterogeneity trait to model *physiological costs of reproduction* : *parity*
- The model is an *age-parity-heterogeneity*-MPPM

Features of the *age-parity-heterogeneity*-MPPM

- Mutation rate μ: the probability that the offspring is of different genotype than its parent.
- We set fertility and survival rates independent from *age a*

The Model

a 3-trait MPPM

- one basic trait: *age*
- one fixed-heterogeneity trait to model *genetic costs of reproduction* : *heterogeneity*

⇒ encompasses variance in both allocation and acquisition genes

- one dynamic-heterogeneity trait to model *physiological costs of reproduction* : *parity*
- The model is an *age-parity-heterogeneity*-MPPM

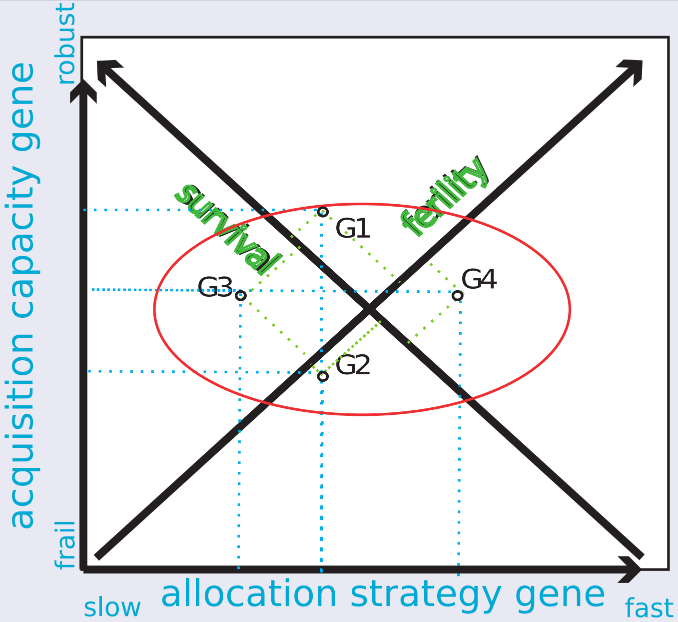
Features of the *age-parity-heterogeneity*-MPPM

- Mutation rate μ: the probability that the offspring is of different genotype than its parent.
- We set fertility and survival rates independent from *age a*
- To distinguish physiological and genetic costs of reproduction, we set vital rates as the product of:

$$vr^{\mathbf{e}}_{a,p,h} = \underbrace{vr^{\mathbf{e}}_{\cancel{a},0,h}}_{\text{zero-parity vital rates} \rightarrow \textbf{genetic costs}} \times \underbrace{\left(1 - \frac{p}{\beta - \alpha + 1}\right)}_{\text{parity effect} \rightarrow \textbf{physiological costs}}$$

The Model

Genotypic map



Features of the *age-parity-heterogeneity*-MPPM

- Mutation rate μ: the probability that the offspring is of different genotype than its parent.
- We set fertility and survival rates independent from *age a*
- To distinguish physiological and genetic costs of reproduction, we set vital rates as the product of:

$$vr^{\mathbf{e}}_{a,p,h} = \underbrace{vr^{\mathbf{e}}_{\cancel{a},0,h}}_{\text{zero-parity vital rates} \rightarrow \textbf{genetic costs}} \times \underbrace{\left(1 - \frac{p}{\beta - \alpha + 1}\right)}_{\text{parity effect} \rightarrow \textbf{physiological costs}}$$

$\Rightarrow$ slow genotypes (like G3) have higher zero-parity survival rate and lower zero-parity fertility rate than fast genotypes (like G4)

$\Rightarrow$ robust genotypes (like G1) have higher zero-parity vital rates than frailer genotypes (like G2)

The Model: MPPM and stochastic model

deterministic structure

- *age* structure : $\omega = 3$ *age*-classes, with $\alpha = 2$ and $\beta = 3$

stochastic structure

MPPM $\mathbf{M^e}$

Zero-parity Leslie matrix for fast genotype g_f, with fertility F and survival s independent from age :

$$\mathbf{M^e}_{g_f,p=0} = \begin{bmatrix} 0 & F & F \\ s & . & . \\ . & s & . \end{bmatrix}$$

The Model: MPPM and stochastic model

deterministic structure

- *age* structure : $\omega = 3$ *age*-classes, with $\alpha = 2$ and $\beta = 3$
- *age* and *parity* structure : there are $\beta - \alpha + 1 = 2$ *parity* classes.

stochastic structure

MPPM $\mathbf{M^e}$

matrix implementing physiological costs for fast genotype g_f (zero-parity rates F and s) :

$$\mathbf{M^e}_{g_f} = \left[\begin{array}{ccc|ccc} 0 & F & F & . & . & \frac{F}{2} \\ s & . & . & . & . & . \\ . & s.(1-F) & . & . & . & . \\ \hline . & . & . & . & . & . \\ . & . & . & . & . & . \\ . & s.F & . & . & . & . \end{array}\right]$$

The Model: MPPM and stochastic model

deterministic structure

- *age* structure : $\omega = 3$ *age*-classes, with $\alpha = 2$ and $\beta = 3$
- *age* and *parity* structure : there are $\beta - \alpha + 1 = 2$ *parity* classes.
- *age-parity-heterogeneity* MPPM w/ 2 genotypes:
  - $\Rightarrow$ a faster genotype (zero-parity rates F and s).
  - $\Rightarrow$ a slower genotype (zero-parity rates $f < F$ and $S > s$).

stochastic structure

MPPM $\mathbf{M^e}$

$$\mathbf{M^e} = \left[\begin{array}{ccc:ccc|ccc:ccc}
0 & (1-\mu).F & (1-\mu).F & \cdot & \cdot & (1-\mu).\frac{F}{2} & 0 & \mu.f & \mu.f & \cdot & \cdot & \mu.\frac{f}{2} \\
s & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & s.(1-F) & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\hdashline
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & s.F & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\hline
0 & \mu.F & \mu.F & \cdot & \cdot & \mu.\frac{F}{2} & \cdot & (1-\mu).f & (1-\mu).f & \cdot & \cdot & (1-\mu).\frac{f}{2} \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & S & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & S.(1-f) & \cdot & \cdot & \cdot & \cdot \\
\hdashline
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\
\cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & S.f & \cdot & \cdot & \cdot & \cdot
\end{array}\right]$$

The Model: MPPM and stochastic model

deterministic structure

- *age* structure : $\omega = 3$ *age*-classes, with $\alpha = 2$ and $\beta = 3$
- *age* and *parity* structure : there are $\beta - \alpha + 1 = 2$ *parity* classes.
- *age-parity-heterogeneity* MPPM w/ 2 genotypes:
  - $\Rightarrow$ a faster genotype (zero-parity rates F and s).
  - $\Rightarrow$ a slower genotype (zero-parity rates $f < F$ and $S > s$).

stochastic structure

- Environmental stochasticity: $\mathbf{M}^{\mathbf{e}}$ is the deterministic structure for env. $\mathbf{e}$. (distribution $\mathcal{D}_{\mathrm{e}}$)

MPPM $\mathbf{M}^{\mathbf{e}}$

$$\mathbf{M}^{\mathbf{e}} = \left[\begin{array}{ccc|ccc|ccc|ccc}
0 & (1-\mu).F & (1-\mu).F & . & . & (1-\mu).\frac{F}{2} & 0 & \mu.f & \mu.f & . & . & \mu.\frac{f}{2} \\
s & . & . & . & . & . & . & . & . & . & . & . \\
. & s.(1-F) & . & . & . & . & . & . & . & . & . & . \\
\hline
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . & . & . & . & . \\
. & s.F & . & . & . & . & . & . & . & . & . & . \\
\hline
0 & \mu.F & \mu.F & . & . & \mu.\frac{F}{2} & . & (1-\mu).f & (1-\mu).f & . & . & (1-\mu).\frac{f}{2} \\
. & . & . & . & . & . & S & . & . & . & . & . \\
. & . & . & . & . & . & . & S.(1-f) & . & . & . & . \\
\hline
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & S.f & . & . & . & .
\end{array}\right]$$

The Model: MPPM and stochastic model

deterministic structure

- *age* structure : $\omega = 3$ *age*-classes, with $\alpha = 2$ and $\beta = 3$
- *age* and *parity* structure : there are $\beta - \alpha + 1 = 2$ *parity* classes.
- *age-parity-heterogeneity* MPPM w/ 2 genotypes:

$\Rightarrow$ a faster genotype (zero-parity rates F and s).

$\Rightarrow$ a slower genotype (zero-parity rates $f < F$ and $S > s$).

stochastic structure

- Environmental stochasticity: $\mathbf{M^e}$ is the deterministic structure for env. **e**. (distribution $\mathcal{D}_\mathrm{e}$)
- Individual stochasticity: Random variable of fertility events is a Bernoulli $\mathcal{F}_{a,p,h} = \mathcal{B}(f_{a,p,h})$,

$\Rightarrow$ full stochastic model : $\left\{\mathbf{M^e}, \mathcal{D}_\mathrm{e}, \mathcal{F}^{\mathbf{e}}_{a,p,h}\right\}$

MPPM $\mathbf{M^e}$

$$\mathbf{M^e} = \left[\begin{array}{ccc:ccc|ccc:ccc}
0 & (1-\mu).F & (1-\mu).F & . & . & (1-\mu).\frac{F}{2} & 0 & \mu.f & \mu.f & . & . & \mu.\frac{f}{2} \\
s & . & . & . & . & . & . & . & . & . & . & . \\
. & s.(1-F) & . & . & . & . & . & . & . & . & . & . \\
\hdashline
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . & . & . & . & . \\
. & s.F & . & . & . & . & . & . & . & . & . & . \\
\hline
0 & \mu.F & \mu.F & . & . & \mu.\frac{F}{2} & . & (1-\mu).f & (1-\mu).f & . & . & (1-\mu).\frac{f}{2} \\
. & . & . & . & . & . & S & . & . & . & . & . \\
. & . & . & . & . & . & . & S.(1-f) & . & . & . & . \\
\hdashline
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & . & . & . & . & . \\
. & . & . & . & . & . & . & S.f & . & . & . & .
\end{array}\right]$$

The Methods

Trait Level Analysis

To measure the evolutionary effects of the costs of reproduction, we use Trait Level Analysis to compare:

- $\mathbf{M}$ the (*age-parity-heterogeneity*)-MPPM implementing physiological and genetic costs of reproduction.
- $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$ the reference Leslie matrix, an *age*-only model without any cost of reproduction.

---

[1] Tuljapurkar, S. D. (1982). Population dynamics in variable environments II. Correlated environments,sensitivity analysis and dynamics. TPB.

[2] Engen, S., Lande, R., Saether, B. E., and Weimerskirch, H. (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models. Mathematical Biosciences

The Methods

Trait Level Analysis

To measure the evolutionary effects of the costs of reproduction, we use Trait Level Analysis to compare:

- $\mathbf{M}$ the (*age-parity-heterogeneity*)-MPPM implementing physiological and genetic costs of reproduction.
- $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$ the reference Leslie matrix, an *age*-only model without any cost of reproduction.

Fitness measures

- fitness components

  ⇒ vital rates and sensitivity analysis (selection gradients)

---

[1] Tuljapurkar, S. D. (1982). Population dynamics in variable environments II. Correlated environments,sensitivity analysis and dynamics. TPB.

[2] Engen, S., Lande, R., Saether, B. E., and Weimerskirch, H. (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models. Mathematical Biosciences

The Methods

Trait Level Analysis

To measure the evolutionary effects of the costs of reproduction, we use Trait Level Analysis to compare:

- **M** the (*age-parity-heterogeneity*)-MPPM implementing physiological and genetic costs of reproduction.
- $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ the reference Leslie matrix, an *age*-only model without any cost of reproduction.

Fitness measures

- fitness components

  ⇒ vital rates and sensitivity analysis (selection gradients)
- **lifetime population** fitness measure λ the **ergodic growth rate**.

⇒ Preserved by folding, but not its sensitivity.

⇒ Environmental and demographic variances and therefore **stochastic growth rate**[1][2] will be affected by costs :

$$\ln \lambda_s \quad \approx \quad \ln \lambda - \left(\frac{1}{2}. \qquad \underbrace{\sigma^2_{\mathrm{e}}}_{\text{environmental variance}} \qquad \right) - \left(\frac{1}{2.N}. \qquad \underbrace{\sigma^2_{\mathrm{d}}}_{\text{demographic variance}} \qquad \right)$$

---

[1] Tuljapurkar, S. D. (1982). Population dynamics in variable environments II. Correlated environments,sensitivity analysis and dynamics. TPB.

[2] Engen, S., Lande, R., Saether, B. E., and Weimerskirch, H. (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models. Mathematical Biosciences

The Methods

Trait Level Analysis

To measure the evolutionary effects of the costs of reproduction, we use Trait Level Analysis to compare:

- $\mathbf{M}$ the (*age-parity-heterogeneity*)-MPPM implementing physiological and genetic costs of reproduction.
- $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$ the reference Leslie matrix, an *age*-only model without any cost of reproduction.

Fitness measures

- fitness components
  - ⇒ vital rates and sensitivity analysis (selection gradients)
- **lifetime population** fitness measure λ the **ergodic growth rate**.
  - ⇒ Preserved by folding, but not its sensitivity.
  - ⇒ Environmental and demographic variances and therefore **stochastic growth rate**[1][2] will be affected by costs :

$$\ln \lambda_s \approx \ln \lambda - \left(\frac{1}{2}.\underbrace{\sigma_{\mathrm{e}}^2}_{\text{environmental variance}}\right) - \left(\frac{1}{2.N}.\underbrace{\sigma_{\mathrm{d}}^2}_{\text{demographic variance}}\right)$$

- **lifetime individual** fitness measure $\mathcal{LRO}$ the **reproductive success**.
  - ⇒ $E(\mathcal{LRO}) = \mathbf{R_0}$ preserved *in this model* by folding
  - ⇒ The effect of the costs on reproductive success will be measurable by their effects on **variance in reproductive success** $\sigma^2_{\mathcal{LRO}}$

$$\sigma^2_{\mathcal{LRO}} = \underbrace{{\sigma^2_{\mathcal{LRO}}}^{sto}}_{E_h(\sigma^2_{h\mathcal{LRO}})=\text{mean variance across genotypes}\leftarrow\textbf{physiological costs}} + \underbrace{{\sigma^2_{\mathcal{LRO}}}^{het}}_{Var_h(\mathbf{R}_{h0})=\text{difference in }\mathbf{R_0}\text{ between genotypes}\leftarrow\textbf{genetic costs}}$$

---

[1] Tuljapurkar, S. D. (1982). Population dynamics in variable environments II. Correlated environments,sensitivity analysis and dynamics. TPB.

[2] Engen, S., Lande, R., Saether, B. E., and Weimerskirch, H. (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models. Mathematical Biosciences

The Methods

Trait Level Analysis

To measure the evolutionary effects of the costs of reproduction, we use Trait Level Analysis to compare:

- $\mathbf{M}$ the (*age-parity-heterogeneity*)-MPPM implementing physiological and genetic costs of reproduction.
- $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$ the reference Leslie matrix, an *age*-only model without any cost of reproduction.

Fitness measures

- fitness components
  - ⇒ vital rates and sensitivity analysis (selection gradients)
- **lifetime population** fitness measure λ the **ergodic growth rate**.
  - ⇒ Preserved by folding, but not its sensitivity.
  - ⇒ Environmental and demographic variances and therefore **stochastic growth rate**[1][2] will be affected by costs :

$$\ln \lambda_s \approx \ln \lambda - \left(\frac{1}{2}. \underbrace{\sigma_{\mathrm{e}}^2}_{\text{environmental variance}}\right) - \left(\frac{1}{2.N}. \underbrace{\sigma_{\mathrm{d}}^2}_{\text{demographic variance}}\right)$$

- **lifetime individual** fitness measure $\mathcal{LRO}$ the **reproductive success**.
  - ⇒ $E(\mathcal{LRO}) = \mathbf{R_0}$ preserved *in this model* by folding
  - ⇒ The effect of the costs on reproductive success will be measurable by their effects on **variance in reproductive success** $\sigma^2_{\mathcal{LRO}}$

$$\sigma^2_{\mathcal{LRO}} = \underbrace{{\sigma^2_{\mathcal{LRO}}}^{sto}}_{E_h(\sigma^2_{h\mathcal{LRO}})=\text{mean variance across genotypes}\leftarrow\textbf{physiological costs}} + \underbrace{{\sigma^2_{\mathcal{LRO}}}^{het}}_{Var_h(\mathbf{R}_{h0})=\text{difference in }\mathbf{R_0}\text{ between genotypes}\leftarrow\textbf{genetic costs}}$$

  - ⇒ $\sigma^2_{\mathcal{LRO}}$ computed via closed form formula for $\mathbf{M}_{\mathbf{a}}^{\mathbf{fold}}$, using **new** formulas for matrix models with **several offspring classes** for $\mathbf{M}_{\mathbf{a,h}}^{\mathbf{fold}}$, and with **Markov chains with rewards** for $\mathbf{M}$.

---

[1] Tuljapurkar, S. D. (1982). Population dynamics in variable environments II. Correlated environments,sensitivity analysis and dynamics. TPB.

[2] Engen, S., Lande, R., Saether, B. E., and Weimerskirch, H. (2005). Extinction in relation to demographic and environmental stochasticity in age-structured models. Mathematical Biosciences

Computation of variance in reproductive success I

Leslie matrix : *age*-structured population

$$\sigma^2_{\mathcal{LRO}} = \alpha_1 = \sum_{i=1}^{n} P_i \left[Var(\mathcal{F}_i) + y^2_{i+1} s_i (1 - s_i) \right],$$

- $\mathcal{F}_i$ is the fertility process at age i of expectation f_i
- s_i the survival rate at age i, $P_i = \Pi_{k=1}^{i-1} s_i$ the probability to survive to age i
- $y(i) = \frac{1}{P_i} \sum_{j=i}^{n} f_j P_j$ the expectation of $\mathcal{LRO}_{\mathrm{i}}$ (remaining reproductive output for an individual aged i)

Computation of variance in reproductive success I

Leslie matrix : *age*-structured population

$$\sigma^2_{\mathcal{LRO}} = \alpha_1 = \sum_{i=1}^{n} P_i \left[Var(\mathcal{F}_i) + y^2_{i+1} s_i (1 - s_i) \right],$$

- $\mathcal{F}_i$ is the fertility process at age i of expectation f_i
- s_i the survival rate at age i, $P_i = \Pi_{k=1}^{i-1} s_i$ the probability to survive to age i
- $y(i) = \frac{1}{P_i} \sum_{j=i}^{n} f_j P_j$ the expectation of $\mathcal{LRO}_\mathrm{i}$ (remaining reproductive output for an individual aged i)

Populations with hidden-heterogeneity trait (several classes of offspring) : *age-heterogeneity* matrix

From

- survival-fertility decomposition of $\mathbf{M} = \mathbf{T} + \mathbf{F}$
- Next-Generation Matrix $\mathbf{R} = \mathbf{F}.(\mathbf{I} - \mathbf{T})^{-1}$ and the sum of its lines $\mathbf{e}_{\mathcal{LRO}}$
- $\mathrm{w}^{\diamond}$ the vector of relative ergodic abundances of offspring states

We get,

$$E(\mathcal{LRO}) = \sum_{h=1}^{het} \mathrm{e}_h^{\mathcal{LRO}} . \mathrm{w}_h^{\diamond}$$

$$\sigma^2_{\mathcal{LRO}} = \underbrace{w_1^{\diamond}.\sigma^2_{\mathcal{LRO}_1} + w_2^{\diamond}.\sigma^2_{\mathcal{LRO}_2}}_{{\sigma^{\mathrm{sto}}_{\mathcal{LRO}}}^2} + \underbrace{w_1^{\diamond}.{\mathrm{e}_{\mathcal{LRO}_1}}^2 + w_2^{\diamond}.{\mathrm{e}_{\mathcal{LRO}_2}}^2 - {\mathrm{e}_{\mathcal{LRO}}}^2}_{{\sigma^{\mathrm{het}}_{\mathcal{LRO}}}^2}$$

Computation of variance in reproductive success II

Populations with dynamic heterogeneity trait: *age-parity-heterogeneity* matrix

Stochastic fertility processes may become dependent on the *output* state

$\Rightarrow$ **Markov Chain with Rewards**[1]

$$\tilde{\mathbf{T}} = \left[\begin{array}{c:c} \mathbf{T} & 0 \\ \hdashline \mathbf{1}' - \mathbf{1}'.\mathbf{T} & 1 \end{array}\right] \qquad \mathbf{Rw^k} = \begin{bmatrix} \dots & \dots & \dots \\ \dots & Rw^k_{i,j} = \mathcal{F}^k_{T:j \to i} & \dots \\ \dots & \dots & \dots \end{bmatrix} = \underbrace{\left[\begin{array}{cccccc:c} . & . & . & . & . & . & 0 \\ 0 & . & . & . & . & . & 0 \\ . & 0 & . & . & . & . & 0 \\ 1 & . & 0 & . & . & . & 0 \\ . & 1 & . & 0 & . & . & 0 \\ . & . & 1 & . & 0 & . & 0 \\ \hdashline f_1 & f_2 & \dots & f_i & . & f_q & 1 \end{array}\right]}_{\text{Bernoulli fertility for } \textit{age-parity} \text{ MPPM}}$$

---

[1] Hatori, H., 1966. On Markov chains with rewards. Kodai Math. Semin. Reports 18.

Computation of variance in reproductive success II

Populations with dynamic heterogeneity trait: *age-parity-heterogeneity* matrix

Stochastic fertility processes may become dependent on the *output* state

$\Rightarrow$ **Markov Chain with Rewards**[1]

$$\tilde{\mathbf{T}} = \left[\begin{array}{c|c} \mathbf{T} & 0 \\ \hline \mathbf{1}' - \mathbf{1}'.\mathbf{T} & 1 \end{array}\right] \qquad \mathbf{Rw^k} = \begin{bmatrix} \dots & \dots & \dots \\ \dots & Rw^k_{i,j} = \mathcal{F}^k_{T:j \to i} & \dots \\ \dots & \dots & \dots \end{bmatrix} = \underbrace{\left[\begin{array}{cccccc|c} . & . & . & . & . & . & 0 \\ 0 & . & . & . & . & . & 0 \\ . & 0 & . & . & . & . & 0 \\ 1 & . & 0 & . & . & . & 0 \\ . & 1 & . & 0 & . & . & 0 \\ . & . & 1 & . & 0 & . & 0 \\ \hline f_1 & f_2 & \dots & f_i & . & f_q & 1 \end{array}\right]}_{\text{Bernoulli fertility for } \textit{age-parity} \text{ MPPM}}$$

$\boldsymbol{\rho_k} = k^{th}$ moment of $\mathcal{LRO}$, indexed on "starting" states, obtained by convergence.

$$\boldsymbol{\rho_1} = \lim_{t \to +\infty} \boldsymbol{\rho_1}(t) \text{ with } \boldsymbol{\rho_1}(t+1) = (\tilde{\mathbf{T}} \circ \mathbf{Rw^1})'.\mathbf{1} + \tilde{\mathbf{T}}.\boldsymbol{\rho_1}(t)$$

$$\boldsymbol{\rho_2} = \lim_{t \to +\infty} \boldsymbol{\rho_2}(t) \text{ with } \boldsymbol{\rho_2}(t+1) = (\tilde{\mathbf{T}} \circ \mathbf{Rw^2})'.\mathbf{1} + 2.(\tilde{\mathbf{T}} \circ \mathbf{Rw^1})'.\boldsymbol{\rho_1}(t) + \tilde{\mathbf{T}}.\boldsymbol{\rho_2}(t)$$

with initial conditions $\boldsymbol{\rho_1}(0) = \boldsymbol{\rho_2}(0) = \mathbf{0}$ ($\circ$ is the Hadamard, termwise, product)

---

[1] Hatori, H., 1966. On Markov chains with rewards. Kodai Math. Semin. Reports 18.

Computation of variance in reproductive success II

Populations with dynamic heterogeneity trait: *age-parity-heterogeneity* matrix

Stochastic fertility processes may become dependent on the *output* state

$\Rightarrow$ **Markov Chain with Rewards**[1]

$$\tilde{\mathbf{T}} = \left[\begin{array}{c|c} \mathbf{T} & 0 \\ \hline \mathbf{1}' - \mathbf{1}'.\mathbf{T} & 1 \end{array}\right] \qquad \mathbf{Rw^k} = \begin{bmatrix} \dots & \dots & \dots \\ \dots & Rw^k_{i,j} = \mathcal{F}^k_{T:j\rightarrow i} & \dots \\ \dots & \dots & \dots \end{bmatrix} = \underbrace{\left[\begin{array}{cccccc|c} . & . & . & . & . & . & 0 \\ 0 & . & . & . & . & . & 0 \\ . & 0 & . & . & . & . & 0 \\ 1 & . & 0 & . & . & . & 0 \\ . & 1 & . & 0 & . & . & 0 \\ . & . & 1 & . & 0 & . & 0 \\ \hline f_1 & f_2 & \dots & f_i & . & f_q & 1 \end{array}\right]}_{\text{Bernoulli fertility for } \textit{age-parity} \text{ MPPM}}$$

$\boldsymbol{\rho}_\mathbf{k} = k^{th}$ moment of $\mathcal{LRO}$, indexed on "starting" states, obtained by convergence.

$$\boldsymbol{\rho}_\mathbf{1} = \lim_{t\rightarrow+\infty} \boldsymbol{\rho}_\mathbf{1}(t) \text{ with } \boldsymbol{\rho}_\mathbf{1}(t+1) = (\tilde{\mathbf{T}} \circ \mathbf{Rw^1})'.\mathbf{1} + \tilde{\mathbf{T}}.\boldsymbol{\rho}_\mathbf{1}(t)$$

$$\boldsymbol{\rho}_\mathbf{2} = \lim_{t\rightarrow+\infty} \boldsymbol{\rho}_\mathbf{2}(t) \text{ with } \boldsymbol{\rho}_\mathbf{2}(t+1) = (\tilde{\mathbf{T}} \circ \mathbf{Rw^2})'.\mathbf{1} + 2.(\tilde{\mathbf{T}} \circ \mathbf{Rw^1})'.\boldsymbol{\rho}_\mathbf{1}(t) + \tilde{\mathbf{T}}.\boldsymbol{\rho}_\mathbf{2}(t)$$

with initial conditions $\boldsymbol{\rho}_\mathbf{1}(0) = \boldsymbol{\rho}_\mathbf{2}(0) = \mathbf{0}$ ($\circ$ is the Hadamard, termwise, product)

$$\mathbf{e}_{\mathcal{LRO}} = \boldsymbol{\rho}_\mathbf{1}$$

$$\boldsymbol{\sigma}^\mathbf{2}_{\mathcal{LRO}} = \boldsymbol{\rho}_\mathbf{2} - \boldsymbol{\rho}_\mathbf{1} \circ \boldsymbol{\rho}_\mathbf{1}$$

---

[1] Hatori, H., 1966. On Markov chains with rewards. Kodai Math. Semin. Reports 18.

Result I: Effects of costs on vital rates

Age-independent organism with physiological costs and genotypic polymorphism...

full (*age,parity,heterogeneity*)-MPPM **M** with

- physiological costs
- two *heterogeneity* classes: a robust genotype and a frail genotype
- **age-independent vital rates**

We extract vital rates from $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$, the Reference Leslie Matrix

Result I: Effects of costs on vital rates

Age-independent organism with physiological costs and genotypic polymorphism...

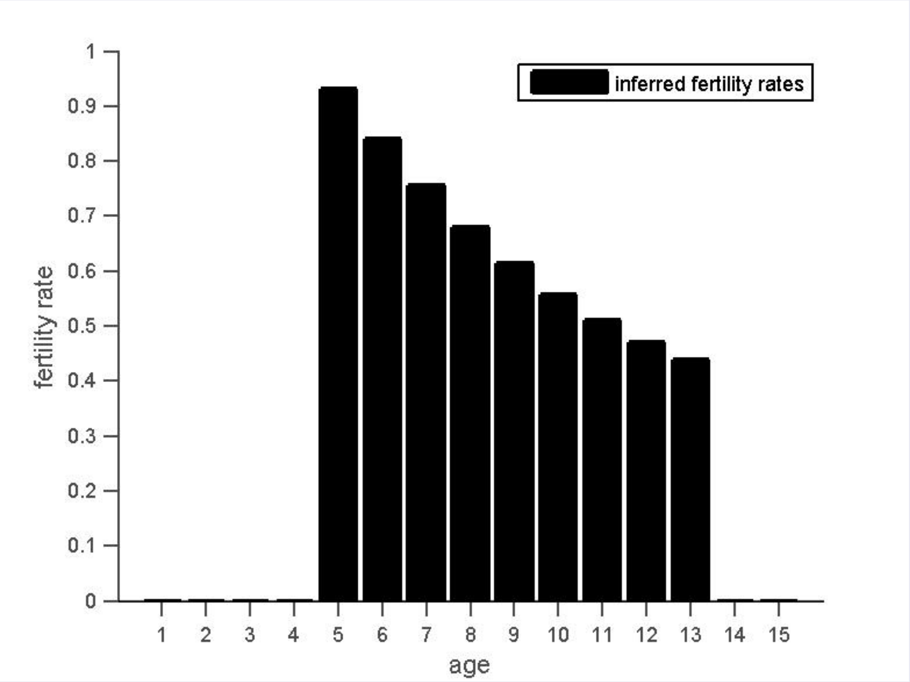
full (*age,parity,heterogeneity*)-MPPM **M** with

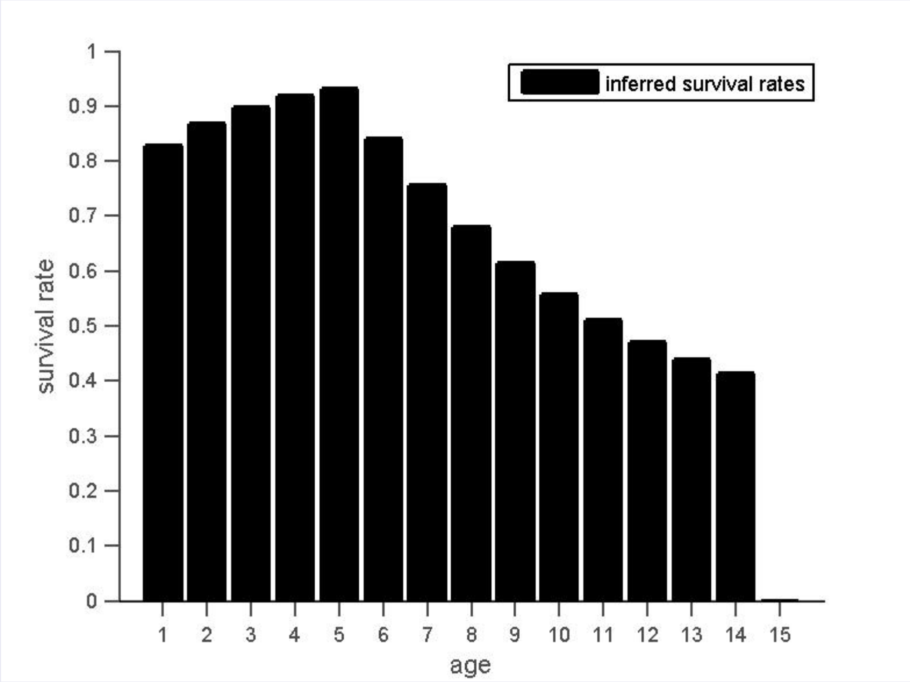
- physiological costs
- two *heterogeneity* classes: a robust genotype and a frail genotype
- **age-independent vital rates**

We extract vital rates from $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$, the Reference Leslie Matrix

⇒ when population considered by **age only**, vital rates **now vary with age** ← transfers of costs

... exhibits familiar vital rates curves when studied by *age* only





Result IIa: Effects of physiological costs of reproduction on selection gradients

Physiological costs reduce selection gradients

- Model is homogeneous age-parity $\mathbf{M}$[1] implementing physiological costs.
- We compare fertility selection gradients - $\frac{\partial \ln \lambda}{\partial \ln f_a}$ - for $\mathbf{M}$ and $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$

---

[1] Model : $\omega = 15$, $\alpha = 5$, zero-parity vital rates are 0.85.

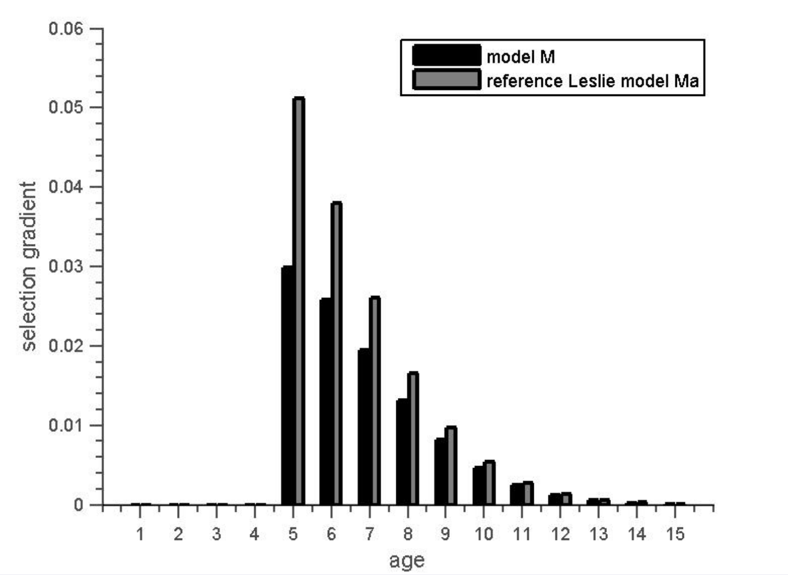
Result IIa: Effects of physiological costs of reproduction on selection gradients

Physiological costs reduce selection gradients

- Model is homogeneous age-parity **M**[1] implementing physiological costs.
- We compare fertility selection gradients - $\frac{\partial \ln \lambda}{\partial \ln f_a}$ - for $\mathbf{M}$ and $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$

⇒ **Physiological costs reduce selection gradients by age**

Fertility selection gradients by age



---

[1] Model : $\omega = 15$, $\alpha = 5$, zero-parity vital rates are 0.85.

Result IIa: Effects of physiological costs of reproduction on selection gradients

Physiological costs reduce selection gradients

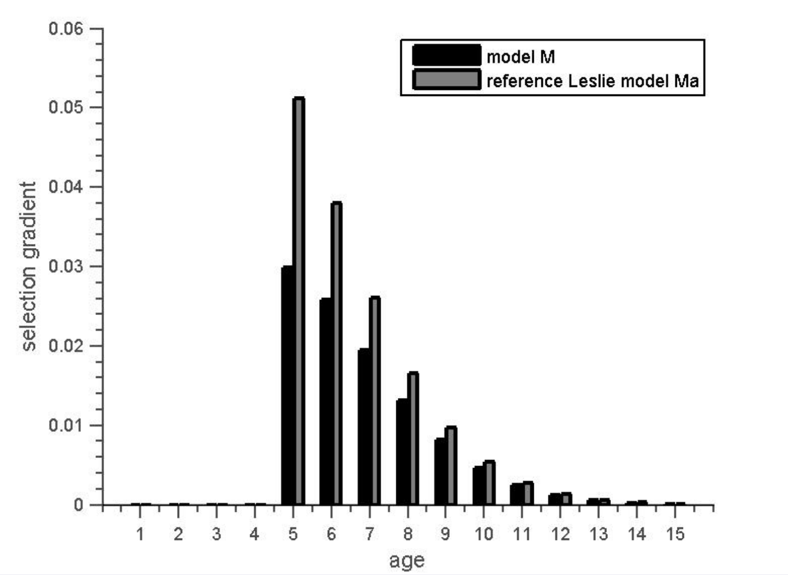
- Model is homogeneous age-parity $\mathbf{M}$[1] implementing physiological costs.
- We compare fertility selection gradients - $\frac{\partial \ln \lambda}{\partial \ln f_a}$ - for $\mathbf{M}$ and $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$

⇒ **Physiological costs reduce selection gradients by age**

⇐ Buffering effect of the costs.

  - "unrealized" fertility events are postponed rather than forfeited.

Fertility selection gradients by age



---

[1] Model : $\omega = 15$, $\alpha = 5$, zero-parity vital rates are 0.85.

Result IIa: Effects of physiological costs of reproduction on selection gradients

Physiological costs reduce selection gradients

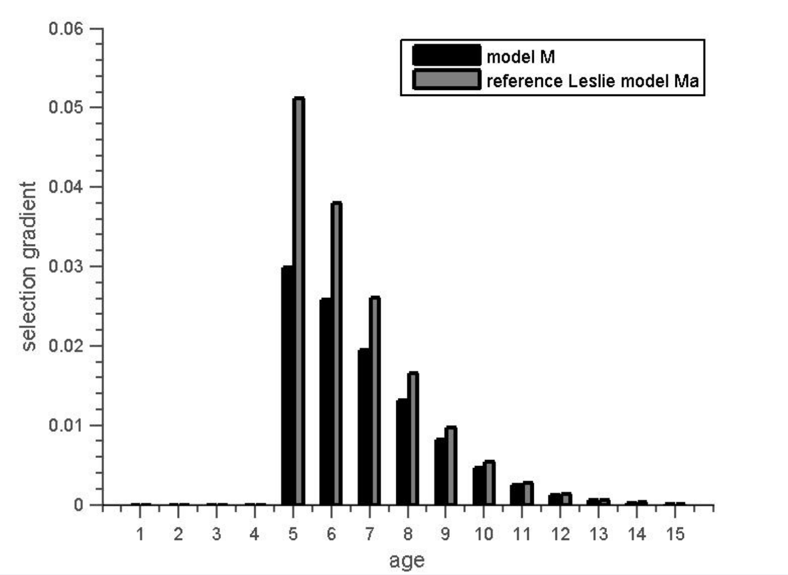
- Model is homogeneous age-parity $\mathbf{M}^1$ implementing physiological costs.
- We compare fertility selection gradients - $\frac{\partial \ln \lambda}{\partial \ln f_a}$ - for **M** and $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$

⇒ **Physiological costs reduce selection gradients by age**

⇐ Buffering effect of the costs.

- "unrealized" fertility events are postponed rather than forfeited.

Fertility selection gradients by age

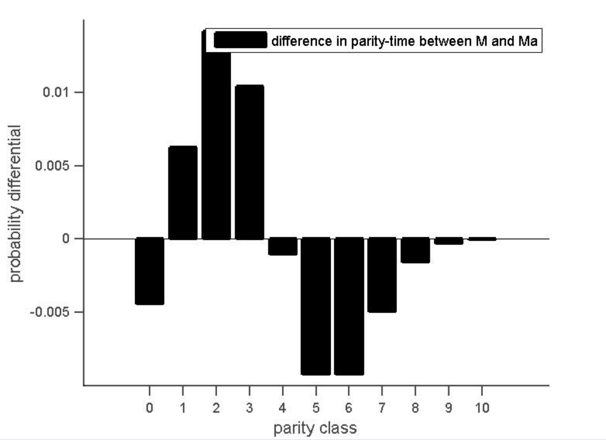


Physiological costs concentrate parity classes

- We compare the stable state abundances of parity classes for **M** and $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$

⇒ Costs of reproduction concentrate parities in the population

Stable state parity abundances distribution



---

[1] Model : $\omega = 15$, $\alpha = 5$, zero-parity vital rates are 0.85.

Result IIb: selection gradients and detectability

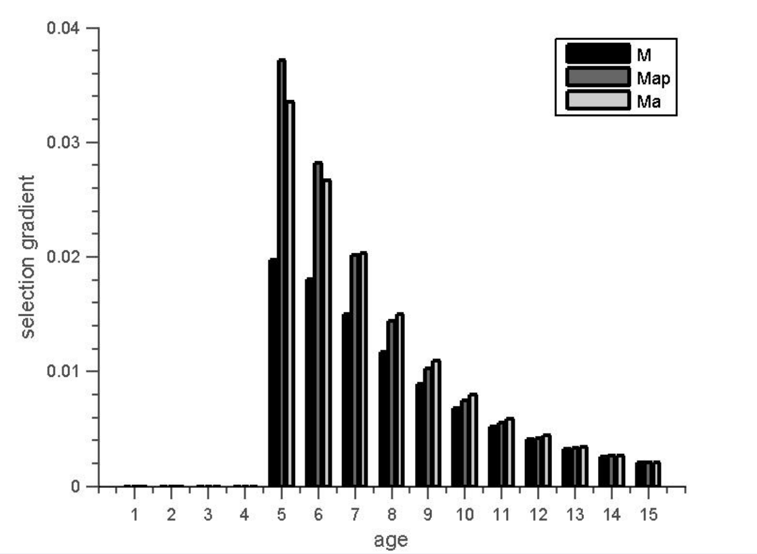
New detectability result

- We add variance in allocation (but no variance in robustness)

⇒ physiological and genetic costs are implemented in **M**

⇒ genotypes have the same fitness

Fertility selection gradients by age



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

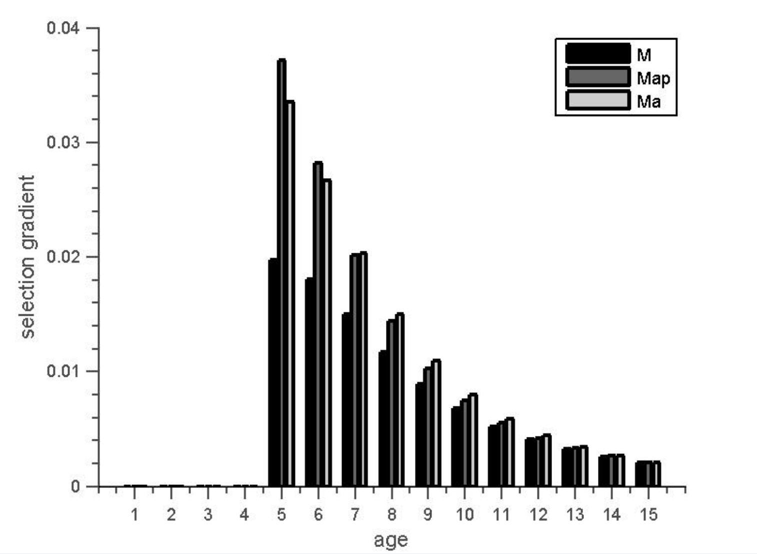
New detectability result

- We add variance in allocation (but no variance in robustness)

  ⇒ physiological and genetic costs are implemented in $\mathbf{M}$

  ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ has still higher selection gradients than $\mathbf{M}$

Fertility selection gradients by age



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

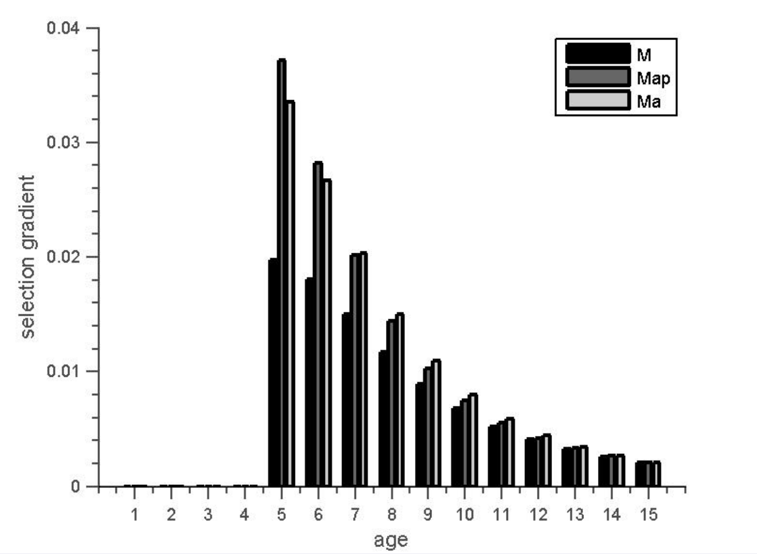
New detectability result

- We add variance in allocation (but no variance in robustness)

  ⇒ physiological and genetic costs are implemented in $\mathbf{M}$

  ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ has still higher selection gradients than $\mathbf{M}$
- But gradients of $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$ are higher still.

Fertility selection gradients by age



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

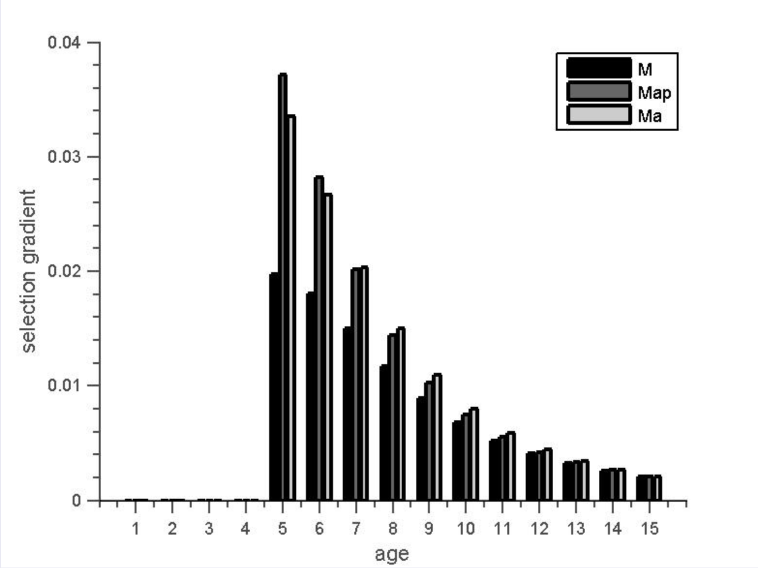
Result IIb: selection gradients and detectability

New detectability result

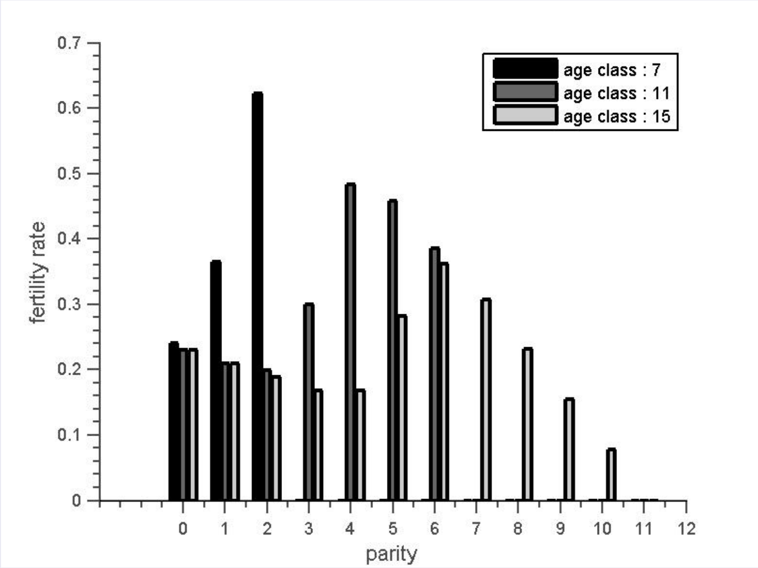
- We add variance in allocation (but no variance in robustness)
  - ⇒ physiological and genetic costs are implemented in $\mathbf{M}$
  - ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ has still higher selection gradients than $\mathbf{M}$
- But gradients of $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$ are higher still.

⇒ When genetic costs are not accounted for, **benefits of reproduction** may emerge instead of **costs**.

Fertility selection gradients by age



Inferred fertility rates by parity for $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

New detectability result

- We add variance in allocation (but no variance in robustness)

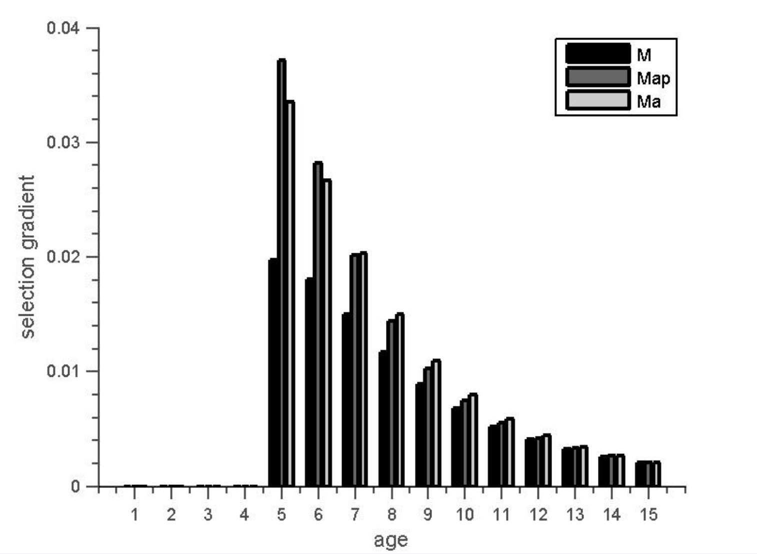
  ⇒ physiological and genetic costs are implemented in $\mathbf{M}$

  ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ has still higher selection gradients than $\mathbf{M}$
- But gradients of $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$ are higher still.

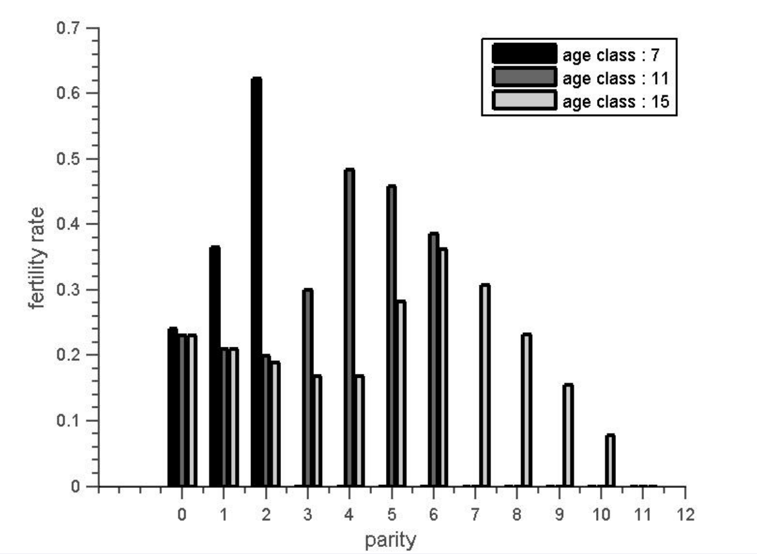
⇒ When genetic costs are not accounted for, **benefits of reproduction** may emerge instead of **costs**.

- This is a new trade-off detectability theorem:

Fertility selection gradients by age



Inferred fertility rates by parity for $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

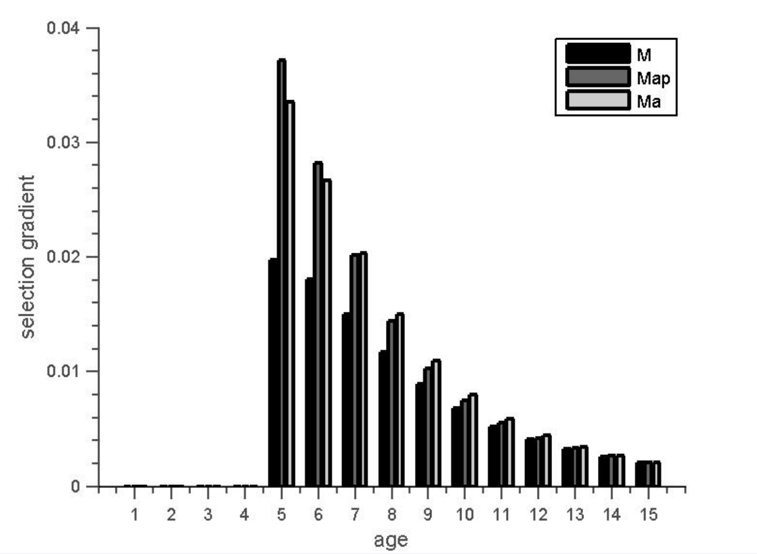
New detectability result

- We add variance in allocation (but no variance in robustness)
  - ⇒ physiological and genetic costs are implemented in **M**
  - ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}_{\mathbf{age}}^{\mathbf{fold}}$ has still higher selection gradients than **M**
- But gradients of $\mathbf{M}_{\mathbf{age},\mathbf{parity}}^{\mathbf{fold}}$ are higher still.

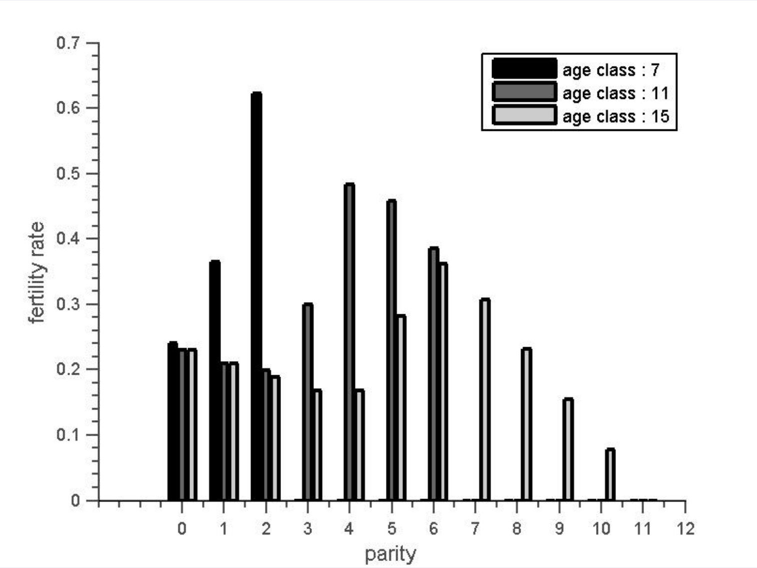
⇒ When genetic costs are not accounted for, **benefits of reproduction** may emerge instead of **costs**.

- This is a new trade-off detectability theorem:
  - In 1986, van Noordwijk and de Jong[1] ⇒ **physiological costs** hidden by allocation variance

Fertility selection gradients by age



Inferred fertility rates by parity for $\mathbf{M}_{\mathbf{age},\mathbf{parity}}^{\mathbf{fold}}$



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

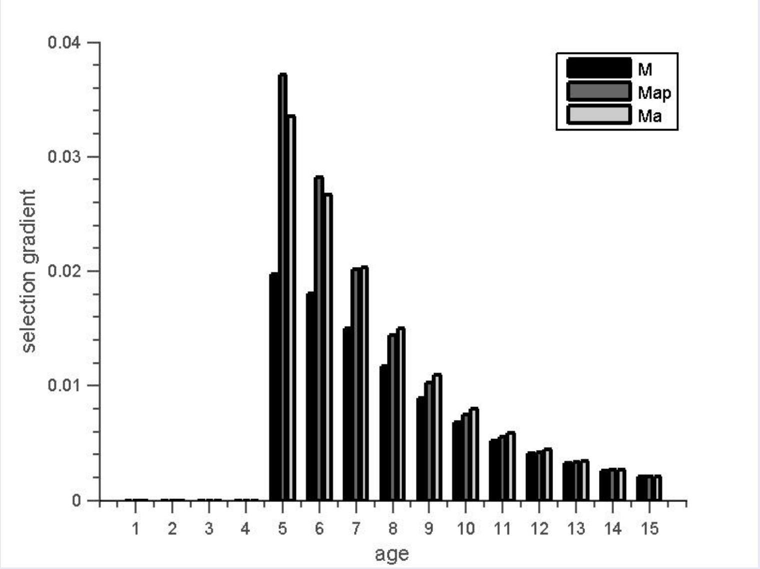
New detectability result

- We add variance in allocation (but no variance in robustness)
  - ⇒ physiological and genetic costs are implemented in $\mathbf{M}$
  - ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}$ has still higher selection gradients than $\mathbf{M}$
- But gradients of $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$ are higher still.

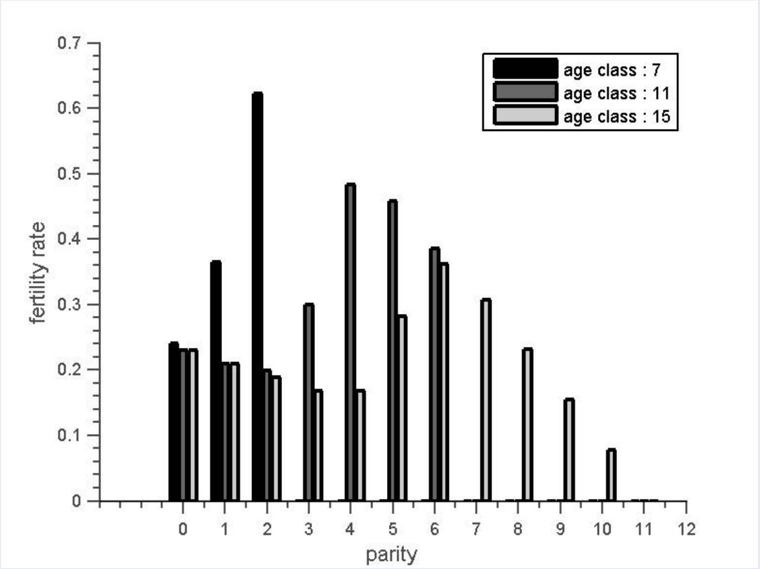
⇒ When genetic costs are not accounted for, **benefits of reproduction** may emerge instead of **costs**.

- This is a new trade-off detectability theorem:
  - In 1986, van Noordwijk and de Jong[1] ⇒ **physiological costs** hidden by allocation variance
  - In 1991, Houle[2] ⇒ detection of **genetic costs** hindered by genetic robustness variance

Fertility selection gradients by age



Inferred fertility rates by parity for $\mathbf{M}^{\mathbf{fold}}_{\mathbf{age,parity}}$



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIb: selection gradients and detectability

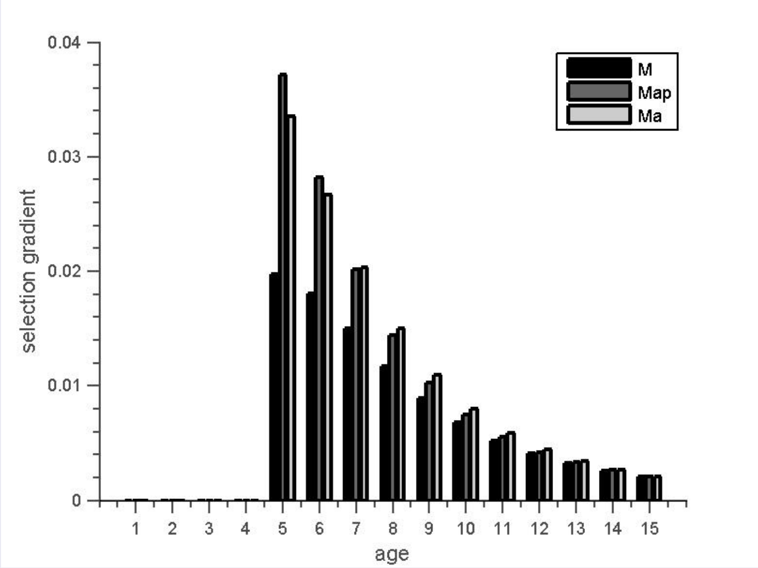
New detectability result

- We add variance in allocation (but no variance in robustness)
  - ⇒ physiological and genetic costs are implemented in $\mathbf{M}$
  - ⇒ genotypes have the same fitness
- Reference Leslie matrix $\mathbf{M}_{\textbf{age}}^{\textbf{fold}}$ has still higher selection gradients than $\mathbf{M}$
- But gradients of $\mathbf{M}_{\textbf{age,parity}}^{\textbf{fold}}$ are higher still.

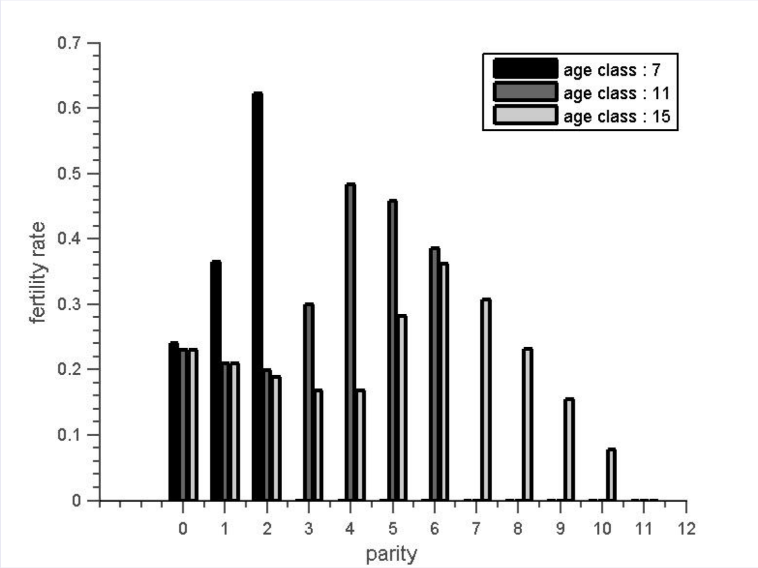
⇒ When genetic costs are not accounted for, **benefits of reproduction** may emerge instead of **costs**.

- This is a new trade-off detectability theorem:
  - In 1986, van Noordwijk and de Jong[1] ⇒ **physiological costs** hidden by allocation variance
  - In 1991, Houle[2] ⇒ detection of **genetic costs** hindered by genetic robustness variance
  - Our result ⇒ detection of **physiological costs** can be blurred by the **genetic costs**

Fertility selection gradients by age



Inferred fertility rates by parity for $\mathbf{M}_{\textbf{age,parity}}^{\textbf{fold}}$



---

[1] van Noordwijk, A. J., de Jong, G. (1986). Acquisition and Allocation of Resources: Their Influence on Variation in Life History Tactics. American Naturalist.

[2] Houle, D. (1991). Genetic covariance of fitness correlates: what genetic correlations are made of and why it matters. Evolution.

Result IIIa: Physiological costs of reproduction reduce $\sigma^2_{\mathcal{LRO}}$

Effects of life history strategy on $\sigma^2_{\mathcal{LRO}}[\mathbf{M}] - \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$

- For **M** implementing physiological costs ,

$$\sigma^2_{\mathcal{LRO}}[\mathbf{M}] < \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$$

---

[1] Model : $\omega = 5$, $\alpha = 1$

Result IIIa: Physiological costs of reproduction reduce $\sigma^2_{\mathcal{LRO}}$

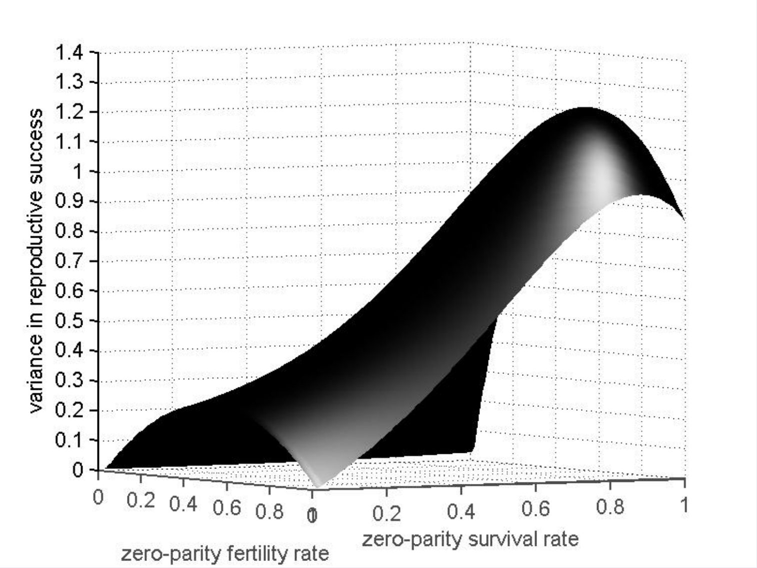
Effects of life history strategy on $\sigma^2_{\mathcal{LRO}}[\mathbf{M}] - \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$

- For **M** implementing physiological costs ,

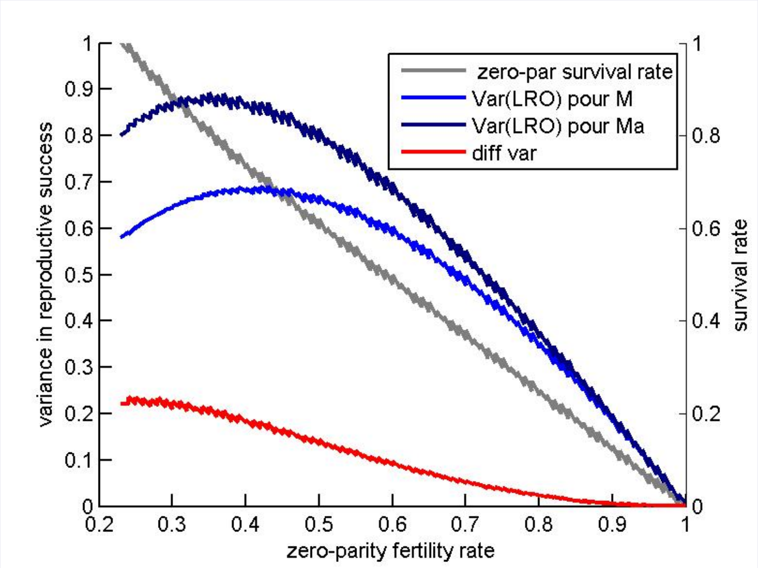
$$\sigma^2_{\mathcal{LRO}}[\mathbf{M}] < \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$$

- $\sigma^2_{\mathcal{LRO}}$ is a function of *allocation* × *acquisition* genotypes :
  $\Rightarrow$ $\sigma^2_{\mathcal{LRO}}$ maximum for central fertility and central/high survival

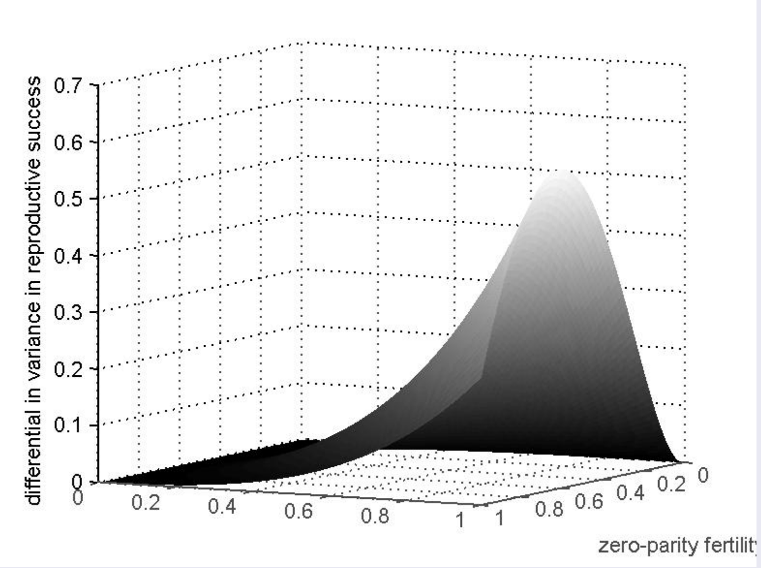
$\sigma^2_{\mathcal{LRO}}$ for Reference Leslie matrix[1]



$\lambda = \mathbf{R_0} = 1$ -isoclines[1]



Effects of costs[1] on $\sigma^2_{\mathcal{LRO}}$



---

[1] Model : $\omega = 5$, $\alpha = 1$

Result IIIa: Physiological costs of reproduction reduce $\sigma^2_{\mathcal{LRO}}$

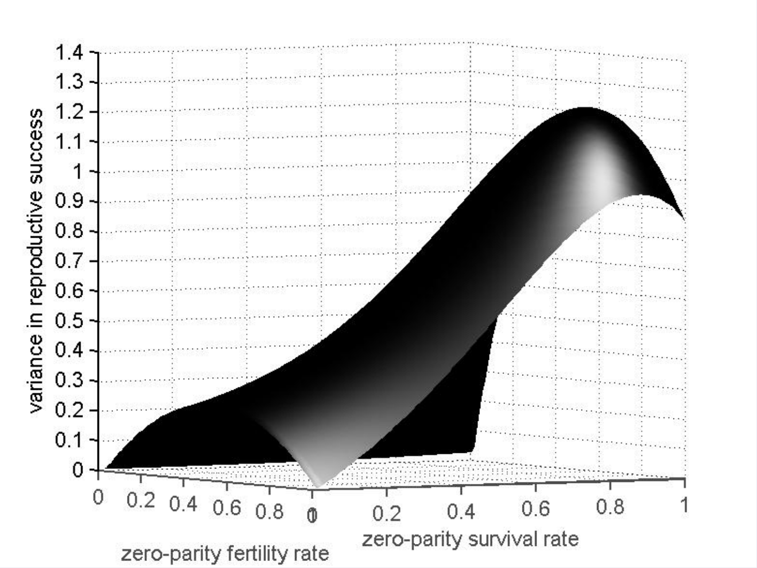
Effects of life history strategy on $\sigma^2_{\mathcal{LRO}}[\mathbf{M}] - \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$

- For **M** implementing physiological costs ,

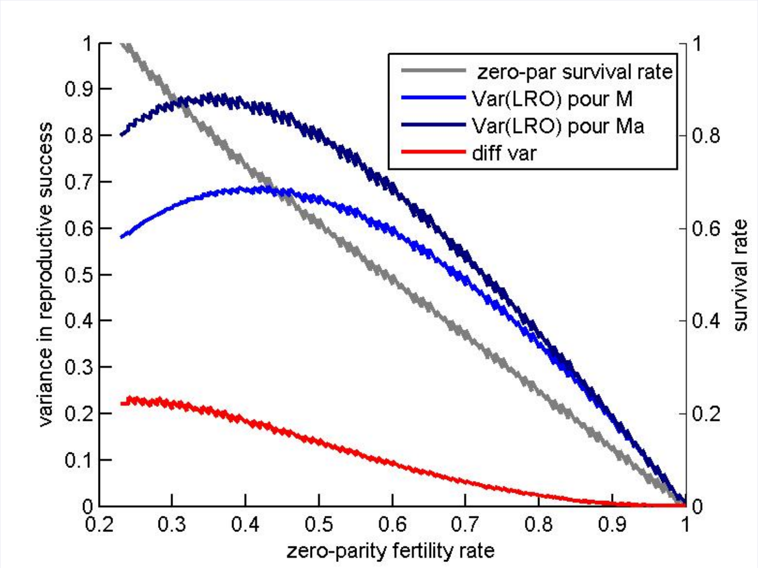
$$\sigma^2_{\mathcal{LRO}}[\mathbf{M}] < \sigma^2_{\mathcal{LRO}}[\mathbf{M}^{\mathbf{fold}}_{\mathbf{age}}]$$

- $\sigma^2_{\mathcal{LRO}}$ is a function of *allocation* × *acquisition* genotypes :
  ⇒ $\sigma^2_{\mathcal{LRO}}$ maximum for central fertility and central/high survival
- $\Delta\sigma^2_{\mathcal{LRO}}$ also a function of the genotypic map but
  ⇒ no buffering effects of the costs for fast/semelparous organisms
  ⇒ the effect keeps increasing as organisms are slower.

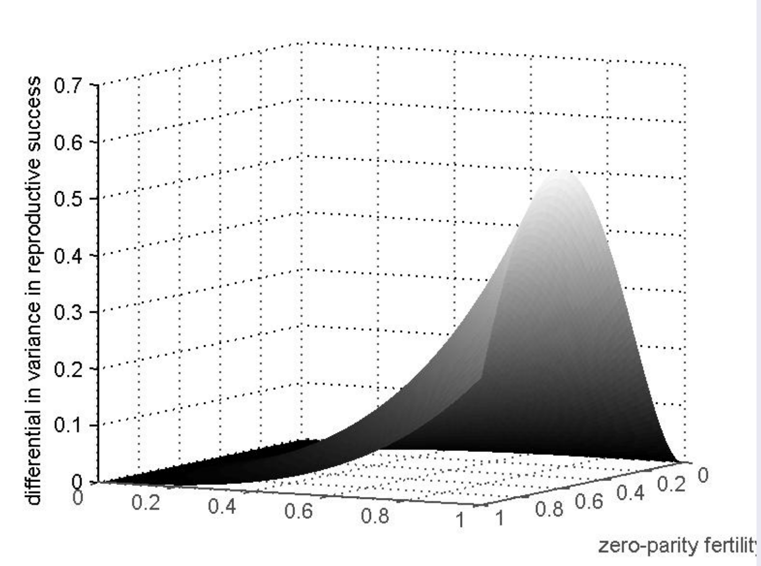
$\sigma^2_{\mathcal{LRO}}$ for Reference Leslie matrix[1]



$\lambda = \mathbf{R_0} = 1$ -isoclines[1]



Effects of costs[1] on $\sigma^2_{\mathcal{LRO}}$



---

[1] Model : $\omega = 5$, $\alpha = 1$

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] ⇒ same selection effectiveness

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] ⇒ same selection effectiveness
- Hill[2] and Engen[3] have shown that for haploid age-structured populations $Ne \approx \frac{N}{\sigma_d^2 . T} \approx \frac{N.\bar{b}.T}{\sigma^2_{\mathcal{LRO}}}$

⇒ We can measure effective selection with *variance-effective selection gradient* $\frac{1}{\sigma^2_{\mathcal{LRO}}} . \frac{\partial \lambda}{\partial f_a}$

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] ⇒ same selection effectiveness
- Hill[2] and Engen[3] have shown that for haploid age-structured populations $Ne \approx \frac{N}{\sigma_d^2 . T} \approx \frac{N.\bar{b}.T}{\sigma_{\mathcal{LRO}}^2}$

⇒ We can measure effective selection with *variance-effective selection gradient* $\frac{1}{\sigma_{\mathcal{LRO}}^2} . \frac{\partial \lambda}{\partial f_a}$

- Physiological costs **decrease** high *variance-effective selection gradients* by age of **fast** organisms
- Physiological costs **increase** low *variance-effective selection gradients* by age of **slow** organisms

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] $\Rightarrow$ same selection effectiveness
- Hill[2] and Engen[3] have shown that for haploid age-structured populations $Ne \approx \frac{N}{\sigma_d^2.T} \approx \frac{N.\bar{b}.T}{\sigma_{\mathcal{LRO}}^2}$

$\Rightarrow$ We can measure effective selection with *variance-effective selection gradient* $\frac{1}{\sigma_{\mathcal{LRO}}^2}.\frac{\partial\lambda}{\partial f_a}$

- Physiological costs **decrease** high *variance-effective selection gradients* by age of **fast** organisms
- Physiological costs **increase** low *variance-effective selection gradients* by age of **slow** organisms

Consequences and possible evolutionary interpretations

- This is one possible answer for the antagonistic pleoitropy riddle of populations structured by age only
  - $\Rightarrow$ fast organisms have high gradients are therefore invaded by ever faster alleles
  - $\Rightarrow$ slow organisms remain slow as their gradients are too small for faster alleles to emerge

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] ⇒ same selection effectiveness
- Hill[2] and Engen[3] have shown that for haploid age-structured populations $Ne \approx \frac{N}{\sigma_d^2.T} \approx \frac{N.\bar{b}.T}{\sigma_{\mathcal{LRO}}^2}$

⇒ We can measure effective selection with *variance-effective selection gradient* $\frac{1}{\sigma_{\mathcal{LRO}}^2} . \frac{\partial\lambda}{\partial f_a}$

- Physiological costs **decrease** high *variance-effective selection gradients* by age of **fast** organisms
- Physiological costs **increase** low *variance-effective selection gradients* by age of **slow** organisms

Consequences and possible evolutionary interpretations

- This is one possible answer for the antagonistic pleoitropy riddle of populations structured by age only

⇒ fast organisms have high gradients are therefore invaded by ever faster alleles

⇒ slow organisms remain slow as their gradients are too small for faster alleles to emerge

- Fast organisms receive little buffering from physiological costs, so their effective gradients remain steep enough to ensure the emergence of alternative alleles and therefore of genetic costs
- Slow organisms are buffered within life trajectories by physiological costs, but their effective gradients are steep enough for faster alleles to emerge if physiological costs do not suffice.

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IIIb: Effects of physiological costs of reproduction on effective size

Demographic variance and effective size

- *Ne* the size of an "ideal" population with same rate of genetic drift[1] ⇒ same selection effectiveness
- Hill[2] and Engen[3] have shown that for haploid age-structured populations $Ne \approx \frac{N}{\sigma_d^2 . T} \approx \frac{N.\bar{b}.T}{\sigma_{\mathcal{LRO}}^2}$

⇒ We can measure effective selection with *variance-effective selection gradient* $\frac{1}{\sigma_{\mathcal{LRO}}^2} \cdot \frac{\partial \lambda}{\partial f_a}$

- Physiological costs **decrease** high *variance-effective selection gradients* by age of **fast** organisms
- Physiological costs **increase** low *variance-effective selection gradients* by age of **slow** organisms

Consequences and possible evolutionary interpretations

- This is one possible answer for the antagonistic pleoitropy riddle of populations structured by age only

⇒ fast organisms have high gradients are therefore invaded by ever faster alleles
⇒ slow organisms remain slow as their gradients are too small for faster alleles to emerge

- Fast organisms receive little buffering from physiological costs, so their effective gradients remain steep enough to ensure the emergence of alternative alleles and therefore of genetic costs
- Slow organisms are buffered within life trajectories by physiological costs, but their effective gradients are steep enough for faster alleles to emerge if physiological costs do not suffice.

⇒ Physiological and Genetic costs buffer stochasticity with different time horizons
⇒ **slow individuals** are mainly buffered by **physiological** costs, and **fast populations** by **genetic** costs

---

[1] Wright, S. (1931). Evolution in mendelian populations. BoMB. [2] Hill, W. G. (1972). Effective size of populations with overlapping generations. TPB.

[3] Engen, S., Lande, R., and Saether, B. E. (2005a). Effective size of a fluctuating age-structured population. Genetics

Result IV: Effects of physiological costs on stochastic growth rate

Costs buffer both stochasticities

We introduce environmental variations.

We can demonstrate formally **physiological costs reduce environmental stochasticity** .

Here we show a simulation:

Result IV: Effects of physiological costs on stochastic growth rate

Costs buffer both stochasticities

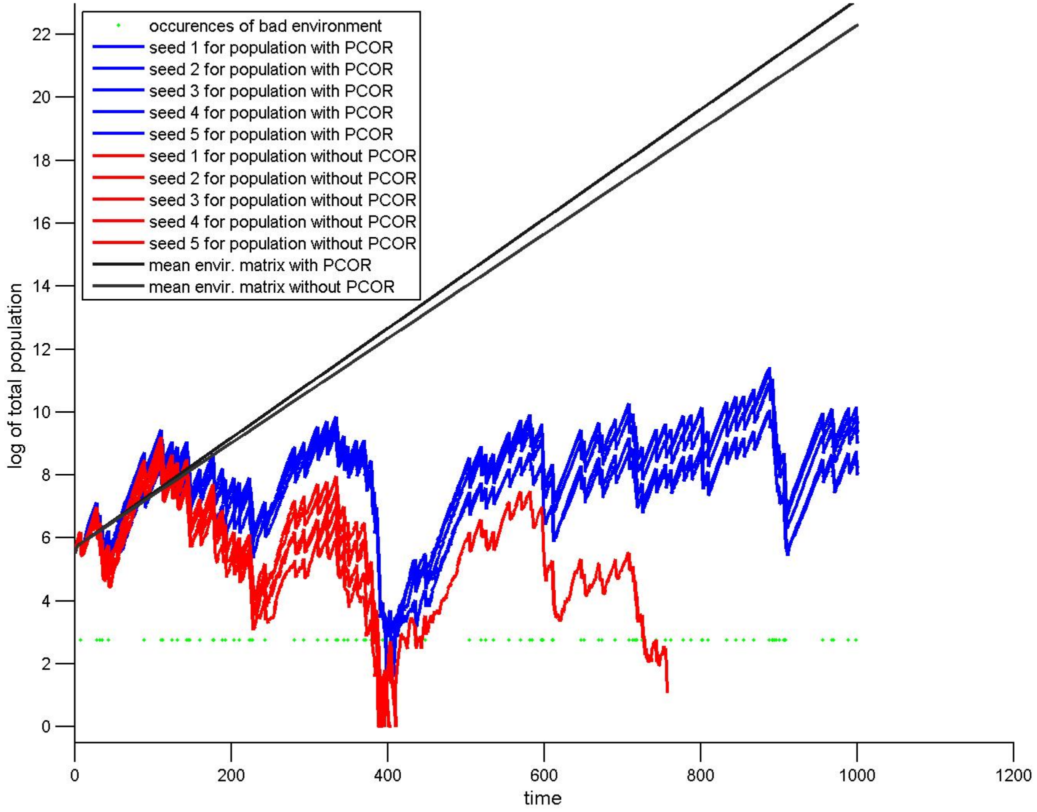
We introduce environmental variations.

We can demonstrate formally **physiological costs reduce environmental stochasticity** .

Here we show a simulation:

- $\mathbf{M_g}$ implements physiological costs
- $\mathbf{M_b}$ same model but with fertility rates at 0
- $\mathbf{M_g^{fold}}$ and $\mathbf{M_b^{fold}}$ evodemo-equivalent models without costs
- Environment is "bad" with prob. $\epsilon = 0.1$ Bernoulli)
- Simulations of 5 pop. with costs and 5 pop. without costs

Projection



Result IV: Effects of physiological costs on stochastic growth rate

Costs buffer both stochasticities

We introduce environmental variations.

We can demonstrate formally **physiological costs reduce environmental stochasticity** .

Here we show a simulation:

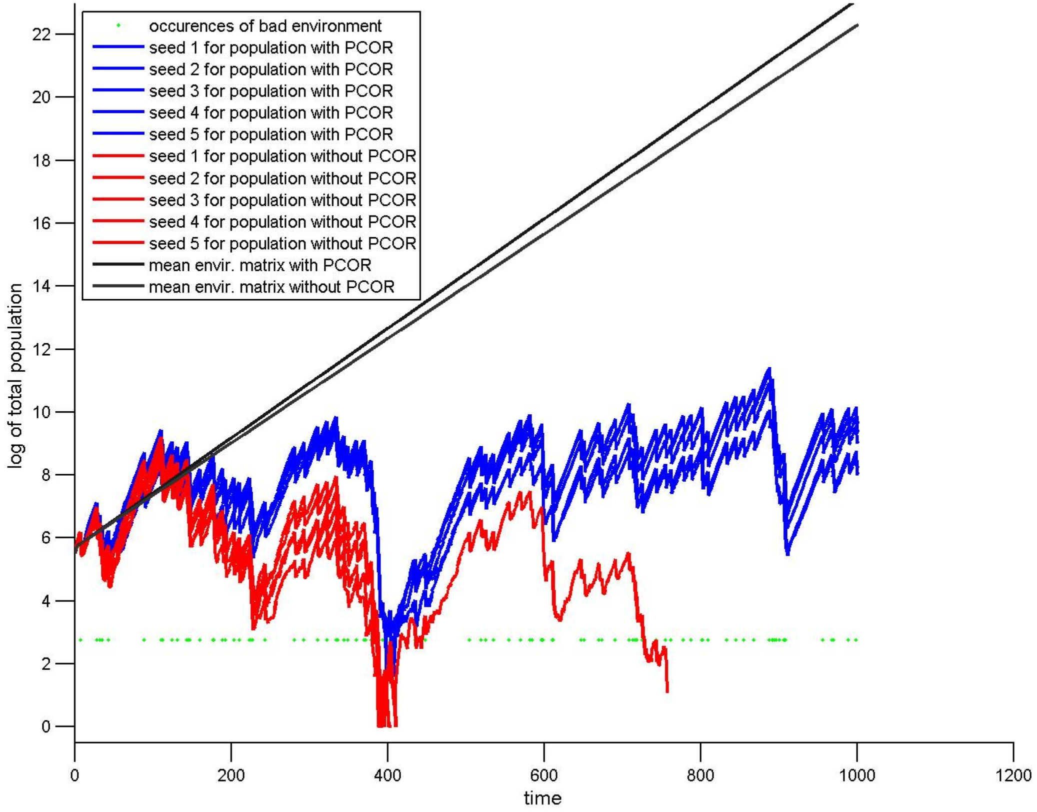
- $\mathbf{M_g}$ implements physiological costs
- $\mathbf{M_b}$ same model but with fertility rates at 0
- $\mathbf{M_g^{fold}}$ and $\mathbf{M_b^{fold}}$ evodemo-equivalent models without costs
- Environment is "bad" with prob. $\epsilon = 0.1$ Bernoulli)
- Simulations of 5 pop. with costs and 5 pop. without costs

- all plotted populations share the same environmental series

⇒ differences between time-steps caused by environmental stochasticity

⇒ differences between populations caused by individual stochasticity

Projection



Overview

Discussion

main results

MPPM methodology and in particular *Trait Level Analysis* has allowed to confirm that:

- Physiological and genetic costs can cohabit. Conjointly they are partly responsible for shaping vital rates curves by age
- Genetic costs hinder detectability of physiological costs
- Forsaking physiological costs leads to overestimation (resp. underestimation) of strength of antagonistic pleiotropy for fast (resp. slow) organisms

⇒ Physiological costs buffer environmental and individual stochasticity of slow individuals.

⇒ Genetic costs buffer environmental variance of fast populations.

Discussion

main results

MPPM methodology and in particular *Trait Level Analysis* has allowed to confirm that:

- Physiological and genetic costs can cohabit. Conjointly they are partly responsible for shaping vital rates curves by age
- Genetic costs hinder detectability of physiological costs
- Forsaking physiological costs leads to overestimation (resp. underestimation) of strength of antagonistic pleiotropy for fast (resp. slow) organisms
  - ⇒ Physiological costs buffer environmental and individual stochasticity of slow individuals.
  - ⇒ Genetic costs buffer environmental variance of fast populations.

Zooming out

- These results hint at the necessity of factoring two traits to model trade-offs ⇒ danger of using one trait only to model life history.
  - ⇒ Using only the best predictor of vital rates may yield appropriate demographic results but evolutionary measures are off.
  - ⇒ In particular, this hints at an important difference between properties of age-structured populations and populations structured by *age only* that should not be confused.
- Multitrait structured demography can develop in many directions: demographic measures, alternative folding methods, development of transient demographic tools

Discussion

main results

MPPM methodology and in particular *Trait Level Analysis* has allowed to confirm that:

- Physiological and genetic costs can cohabit. Conjointly they are partly responsible for shaping vital rates curves by age
- Genetic costs hinder detectability of physiological costs
- Forsaking physiological costs leads to overestimation (resp. underestimation) of strength of antagonistic pleiotropy for fast (resp. slow) organisms
  - ⇒ Physiological costs buffer environmental and individual stochasticity of slow individuals.
  - ⇒ Genetic costs buffer environmental variance of fast populations.

Zooming out

- These results hint at the necessity of factoring two traits to model trade-offs ⇒ danger of using one trait only to model life history.
  - ⇒ Using only the best predictor of vital rates may yield appropriate demographic results but evolutionary measures are off.
  - ⇒ In particular, this hints at an important difference between properties of age-structured populations and populations structured by *age only* that should not be confused.
- Multitrait structured demography can develop in many directions: demographic measures, alternative folding methods, development of transient demographic tools

Other applications of MPPMs/*Trait Level Analysis*

One key extension concerns kinship demography. This new field aims at studying the coevolution of kinship structures and demographic traits. From a modeling perspective this asks :

- how does the demography of a population affects the distribution of kin
- how to implement effects of kin (cooperation/competition) in a demography model

The End

Acknowledgments

I wish to thank my supervisors **Frederic Austerlitz** and **Samuel Pavard** as well as **Evelyne Heyer** heading the lab of Eco-anthropology et Ethnobiology of MNHN/Musée de l'Homme

I deeply thank the **chair MMB** which financed my PhD and in particular **Sylvie Méléard**

I also wish to thank my doctoral school **Frontieres du Vivant**

I am indebted to the members of my thesis advisory committee: **P-H Gouyon**, **Minus v. Baalen**, **V Bansaye** and **J-B André**

And to **Emmanuelle Porcher** for presiding the jury of my PHD defence