Écologie évolutive des populations structurées

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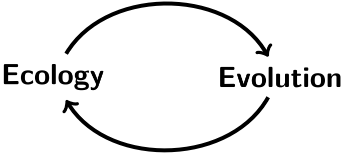
Eco-evolutionary feedback loop



Ecology

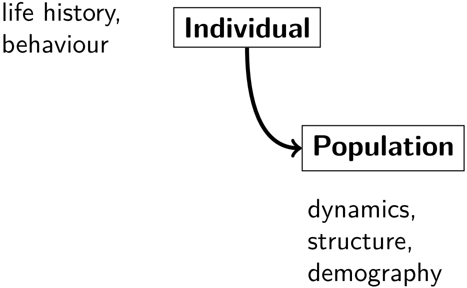
Evolution

Environmental feedback

life history,
behaviour

Individual

Environmental feedback



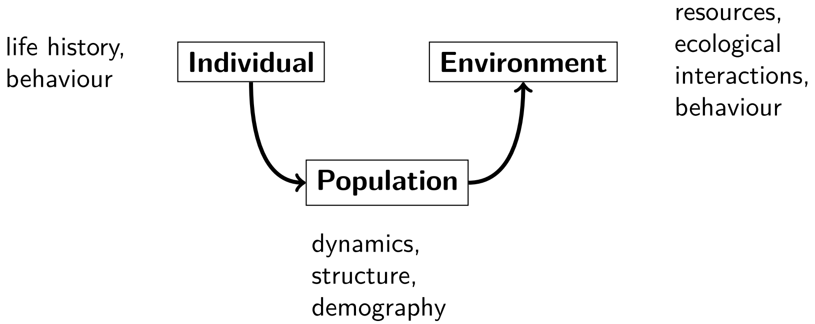
life history,
behaviour

Individual

Population

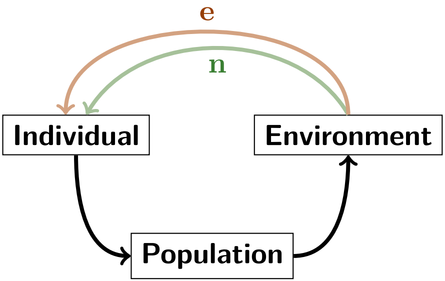
dynamics,
structure,
demography

Environmental feedback



Environment = all the information necessary to compute the reproduction and survival of *individuals*

Environmental feedback



e

n

life history,
behaviour

Individual

Environment

resources,
ecological
interactions,
behaviour

Population

dynamics,
structure,
demography

Environment = all the information necessary to compute the reproduction and survival of *individuals*

- Intrinsic effects (e.g. density of conspecifics)
- Extrinsic effects (e.g. density of resources, predators, prey...)

Prologue – models of eco-evolutionary dynamics

Formalisation

Consider a focal population with N types.

Dynamics of the density of type i:

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = r_i(\mathbf{E})n_i$$

where

$$r_i(\mathbf{E}) = \text{per-capita growth rate of type } i$$

and

$$\mathbf{E} = \text{environment} = \begin{pmatrix} \mathbf{n} \\ \mathbf{e} \end{pmatrix}$$

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External factors

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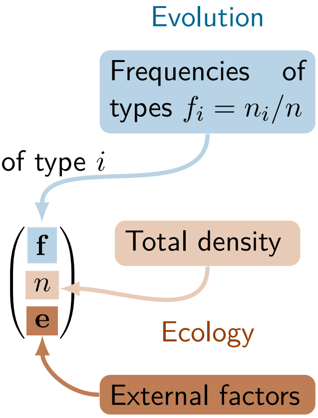

Evolution

Frequencies of types $f_i = n_i/n$

Total density

Ecology

External factors

Eco-evolutionary dynamics

$$\left.\begin{aligned}\frac{\mathrm{d}\mathbf{e}}{\mathrm{d}t} &= \mathcal{D}(\mathbf{E}) \\ \frac{\mathrm{d}n}{\mathrm{d}t} &= \bar{r}(\mathbf{E})n\end{aligned}\right\}\text{Ecology}$$

where

$$\bar{r}(\mathbf{E}) = \sum_i r_i(\mathbf{E})\, f_i$$

is the average per-capita growth rate

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$$\left.\frac{\mathrm{d}f_i}{\mathrm{d}t} = f_i\Big(r_i(\mathbf{E}) - \bar{r}(\mathbf{E})\Big)\right\}\text{Evolution}$$

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Population genetics

Most pop gen studies tend to focus on the **change in frequencies**

$$\frac{\mathrm{d}f_i}{\mathrm{d}t} = f_i \left(r_i(\mathbf{E}) - \bar{r}(\mathbf{E}) \right)$$

and

- either assume the **ecological environment is constant**

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \frac{\mathrm{d}\mathbf{e}}{\mathrm{d}t} = 0$$

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- or assume **specific** forms of **environmental feedback**

Ex 1: $r_i(\mathbf{E}) = m_i - c(n) \;\Rightarrow\; \frac{\mathrm{d}f_i}{\mathrm{d}t} = f_i \left(m_i - \bar{m} \right) = f_i \, s_i$

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Ex 2: $r_i(\mathbf{E}) = m_i c(n) \;\Rightarrow\; \dfrac{\mathrm{d}f_i}{\mathrm{d}t} = f_i\, s_i\, c(n)$

Quantitative genetics

We can also focus on the dynamics of a focal trait, z

The average trait value is then

$$\bar{z} = \sum_i z_i \, f_i$$

with dynamics

$$\begin{aligned} \frac{\mathrm{d}\bar{z}}{\mathrm{d}t} &= \mathsf{Cov}(z, r(\mathbf{E})) \\ &= \boxed{V} \; \boxed{\beta_{zr}} \end{aligned}$$

Environmental feedback will generally affect:

- **the variance $\boxed{V}$ (and the distribution) of the trait**
- **the selection gradient $\boxed{\beta_{zr}}$.**

The Price equation

Now suppose we also consider **mutation**. Consider that

$$r_i(\mathbf{E}) = b_i(\mathbf{E}) - d_i(\mathbf{E})$$

and that mutation occurs with probability μ during reproduction, and that type i may mutate to type j with probability m_{ji}.

Then the change in mean trait takes the form

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \underbrace{\text{Cov}(z, r(\mathbf{E}))}_{\text{Selection}} + \underbrace{\mu\overline{b_i(\mathbf{E})\delta_i}}_{\text{Mutation}}$$

where

$$\text{Cov}(z, r(\mathbf{E})) = \sum_i z_i r_i(\mathbf{E}) f_i - \bar{z}\,\bar{r}(\mathbf{E}), \qquad \text{and} \qquad \delta_i = \sum_j m_{ji} z_j - z_i$$

is the difference between the trait of type i and the mean trait calculated over the mutation distribution.

Some notes on this Price equation

- Explicit dependence on the environment $\mathbf{E}$
- The Price equation needs to be **coupled with equations describing how the environment changes** (e.g. density of the focal species, density of resource or predators, frequencies of the different types, etc.).
- The Price equation **does not provide new information**, but it does allow us to translate pop dynamics into phenotypic change
- **Additional assumptions (weak selection, gaussian distribution of traits)** can be used to make analytical progress by decoupling (to some extent) the dynamics of the mean trait from the environmental dynamics

  Ex: calculating a **selection gradient** from the covariance term of the Price equation.

Change in trait variance

Most treatments stop at the chage in the mean trait.

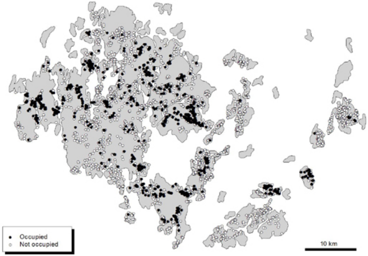
But we can derive Price equations for the change in the other moments of the trait distribution.
Variance dynamics:

$$\begin{aligned}\frac{\mathrm{d}V}{\mathrm{d}t} &= \mathsf{Cov}((z-\bar{z})^2, r(\mathbf{E})) + \text{mutation} \\ &= \mathsf{Cov}(z^2, r(\mathbf{E})) - 2\bar{z}\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} + \text{mutation}\end{aligned}$$

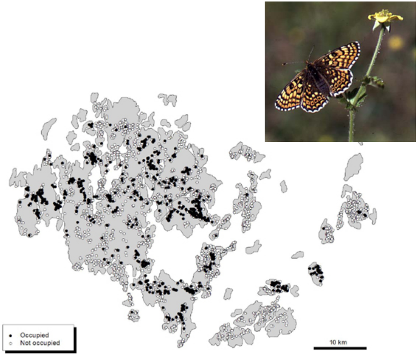
Again this equation is coupled with dynamical equations for $\mathbf{E}$.

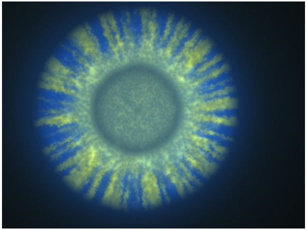
What about population structure?

All natural populations are structured



Spatial structure

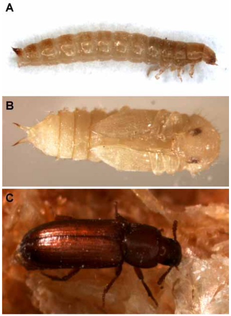




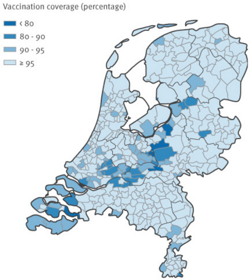
Class structure

Age/size structure

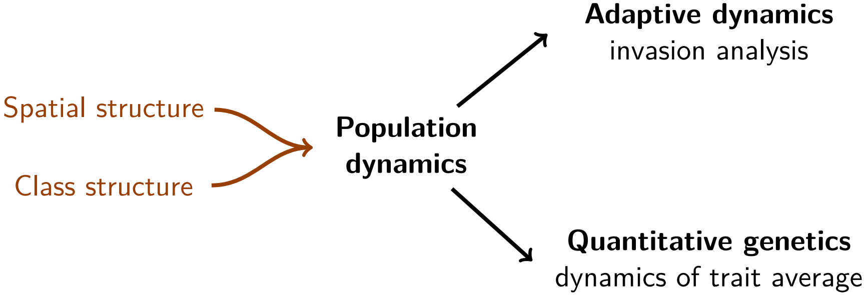
Physical morphs



Developmental stages



Habitat quality



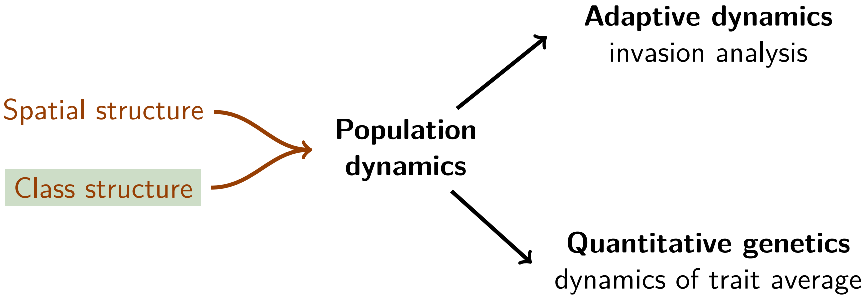
Spatial structure

Class structure

Population dynamics

Adaptive dynamics
invasion analysis

Quantitative genetics
dynamics of trait average



Spatial structure

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Part 1 – Class structure and reproductive value

Environmental heterogeneity and population structure

- Parasites infect **structured** host populations
- Not all hosts have the same **quality** for the parasite

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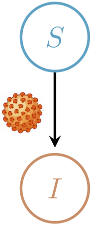

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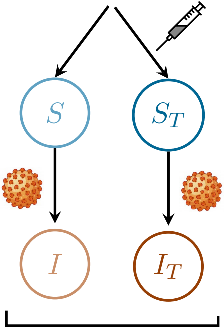

Class structure

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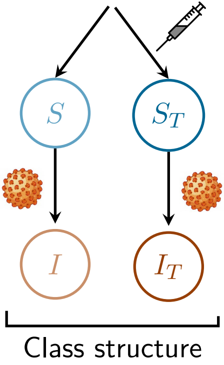


Epidemiological consequences

- Pathogen spread may become more difficult when the frequency of bad-quality hosts increases
- ex: vaccinated or resistant hosts, hosts with fewer contacts with susceptible hosts

Evolutionary consequences

- Two pathogens with the **same genetic background** may have a different **fitness** in high- vs low-quality hosts

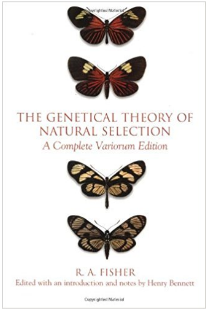
Problem: Can we give an “evolutionary value” to each host class?

We need to take into account this value to extract the effect of **selection** on the change in frequency of a given genotype.

Reproductive value plays this role.

Classical theory of reproductive value

Fisher's definition of reproductive value



THE GENETICAL THEORY OF
NATURAL SELECTION
A Complete Variorum Edition

R. A. FISHER
Edited with an introduction and notes by Henry Bennett

We may ask [...] —To what extent will persons of this age, on the average, contribute to the ancestry of future generations? The question is one of some interest, since the direct action of Natural Selection must be proportional to this contribution. [...] [B]y the analogy of compound interest the present value of the future offspring of persons aged x *is easily seen to be*

$$v_x = v_0 \frac{e^{mx}}{\ell_x} \int_x^\infty e^{-mt} \ell_t b_t dt.$$

Each age group may in this way be assigned its appropriate reproductive value.

Fisher (1930)

Fisher's RV

$$v_x = v_0 \frac{e^{mx}}{\ell_x} \int_x^{\infty} e^{-ma} \ell_a \, b_a da$$

where

- $\ell_a = \exp\left(-\int_0^a d_s \mathrm{d}s\right)$ is the probability to survive up to age a
- d_a is the death rate at age a
- b_a is the birth rate at age a
- m is the population growth rate (Malthusian parameter)

Fisher's RV

$$v_x = v_0 \frac{1}{e^{-mx}\ell_x} \int_x^{\infty} e^{-ma}\ell_a \, b_a da$$

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Fisher's RV

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Fisher's RV

prop. to total number of offspring produced by individuals aged x or more

prop. to density of age-x individuals

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RV as en eigenvector

Assume (linear) population dynamics of the form

$$\mathbf{n}(t+1) = \mathbf{A}\mathbf{n}(t)$$

Provided $\mathbf{A}$ is diagonalisable, the general solution is

$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{u}_i$$

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$c_i = \mathbf{v}_i^\top \mathbf{n}_0$
initial size weighted by left eigenvector

ith eigenvalue of $\mathbf{A}$

Right eigenvector

RV as en eigenvector

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$$\mathbf{n}(t) = \sum_i c_i \lambda_i^t \mathbf{u}_i \qquad \approx c_1 \lambda_1^t \mathbf{u}_1$$

$c_i = \mathbf{v}_i^\top \mathbf{n}_0$
initial size weighted by left eigenvector

ith eigenvalue of $\mathbf{A}$

Right eigenvector

λ_1 = dominant eigenvalue

RV as en eigenvector

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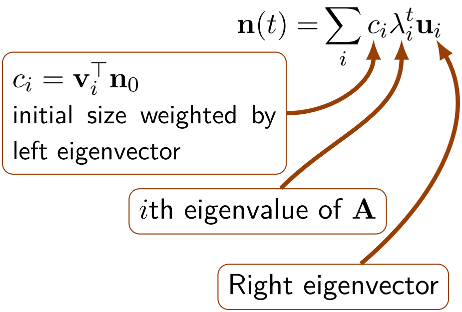

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$c_i = \mathbf{v}_i^\top \mathbf{n}_0$
initial size weighted by left eigenvector

ith eigenvalue of $\mathbf{A}$

Right eigenvector

λ_1 = dominant eigenvalue

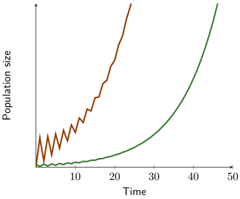
RV = a left eigenvector associated to the dominant eigenvalue of $\mathbf{A}$

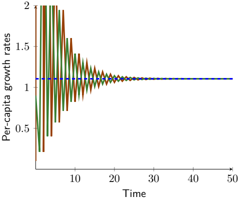
An easy demographic example

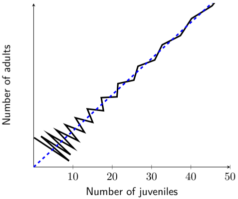
Two-classes: juveniles and adults

$$\begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix} = \begin{pmatrix} 0 & b \\ s_J & s_A \end{pmatrix} \begin{pmatrix} J(t) \\ A(t) \end{pmatrix}$$

- What are the long-term growth rate and class distribution?
  $\Rightarrow \lambda_1$, $\mathbf{u}_1$







- What is the contribution of individuals of different classes to the future population size?
  $\Rightarrow \mathbf{v}_1$

Use in evolutionary game theory

Now suppose a rare mutant appearing in a resident population at equilibrium.

The initial invasion dynamics will be approximately linear, and the invasion fitness is given by the dominant eigenvalue λ of the invasion matrix $\mathbf{A}$.

Use in evolutionary game theory

Now suppose a rare mutant appearing in a resident population at equilibrium.

The initial invasion dynamics will be approximately linear, and the invasion fitness is given by the dominant eigenvalue λ of the invasion matrix $\mathbf{A}$.

For mutations of small phenotypic effect ε, we have the following approximation for the selection gradient:

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\varepsilon} \approx \bar{\mathbf{v}}^{\top} \frac{\mathrm{d}\mathbf{A}}{\mathrm{d}\varepsilon} \bar{\mathbf{u}}$$

where $\bar{\mathbf{v}}$ and $\bar{\mathbf{u}}$ are the RV and class structure in the neutral model at equilibrium (when $\varepsilon = 0$).

The meanings of RV

Demography

Reproductive values give the relative contribution of individuals in a given class to the future of the (stable) population.

Evolution

RV can be viewed as an exchange rate to convert selective effects in different classes into a single currency.

⇒ Measure of how valuable a class is from the point of view of individuals of the focal species

RV in classical theory

Reproductive values are typically assumed to be **constant** and calculated in a stable population.

Some dynamical approaches to RV exist:

- **Crow 1979:** allele-specific, time-dependent RV, for a specific model
- **Tuljapurkar 1989:** RV is an explicit function of time; no connection to evolution
- **Rousset 2004:** RV calculated from a backward recursion; however, only the stationary value in a monomorphic population is of interest for the type of evolutionary questions he considers

Questions

- **What about non-equilibrium or transient dynamics?**
  RV generally computed in exponentially growing or equilibrium populations (asymptotic definition).

- **What about polymorphic populations?**
  Fisher's definition is purely demographic, it is not clear how genetic variation should be handled. Others have defined allele-specific RV (e.g. Crow 1979)

- **Reproductive values: what for?**
  RV contains information about the future we're trying to predict. Is it really a useful concept?

Interlude

Summary so far

Demographic definitions of reproductive value

Relative contribution of individuals in a given class to the future of the population

- Continous age structure (Fisher)

$$v_x = v_0 \frac{1}{e^{-mx}\ell(x)} \int_x^\infty e^{-ma}\ell(a)b(a)\mathrm{d}a$$

- Discrete class structure: left eigenvector of transition matrix

Use in evolutionary biology

Measure of the evolutionary quality of a given class

- Selection gradient (adaptive dynamics)

$$\frac{\mathrm{d}\lambda}{\mathrm{d}\varepsilon} = \bar{\mathbf{v}}^\top \frac{\mathrm{d}\mathbf{A}}{\mathrm{d}\varepsilon} \bar{\mathbf{u}}$$

Next step: a more general theory of RV

Two Price equations for class-structured populations

Basics

Assumptions:

- large population (no demographic stochasticity)
- M clonally reproducing types (polymorphism)
- K discrete classes (but result holds for continuous structure)
- continuous time (but result holds for discrete time)

Notations:

- n_i^k = density of type-i individuals in class k
- $n^k = \sum_{i=1}^{M} n_i^k$ = density of individuals in class k
- $\mathbf{n} = \begin{pmatrix} n^1 & \dots & n^K \end{pmatrix}^\top$ = vector of class densities
- r_i^{jk} = transition rates of i individuals from class k to class j.

Generally, the transition rates r_i^{jk} depend on the environment $\mathbf{E}(t)$ (densities of conspecifics, of competitors, of predators, etc.).

Ecological dynamics of class densities

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}t} = \mathbf{R}(\mathbf{E}(t))\mathbf{n}$$

where $\mathbf{R}$ is the matrix of average transition rates

$$\bar{r}^{jk} = \sum_i r_i^{jk} \frac{n_i^k}{n^k} = \sum_i r_i^{jk} f_i^k$$

f_i^k is the frequency of type-i individuals within class k.

Many population dynamics studies on the field seek to estimate $\mathbf{R}$.

NB: in general, we need another equation for the dynamics of extrinsic factors, but I omit it for simplicity.

Adding the dynamics of frequencies

Full eco-evolutionary dynamics:

$$
\begin{aligned}
\frac{\mathrm{d}\mathbf{n}(t)}{\mathrm{d}t} &= \mathbf{R}(\mathbf{E},t)\mathbf{n}(t) \\
\frac{\mathrm{d}f_i^k(t)}{\mathrm{d}t} &= \sum_j \left(r_i^{kj}(\mathbf{E},t) f_i^j(t) - \bar{r}^{kj}(\mathbf{E},t) f_i^k(t) \right) \frac{f^j(t)}{f^k(t)}
\end{aligned}
$$

where $f^k = n^k/n$ is the frequency of class k.

Can we decouple selection from demography?

Average phenotypic trait

Consider a non-plastic trait z, with value z_i for type i.

- To study evolutionary change, we can look at the dynamics of the mean trait

  $$\bar{z} = \sum_i z_i f_i$$

  where $f_i = n_i/n$ is the frequency of type-i in the population

- We can also calculate this average as

  $$\bar{z} = \sum_k \bar{z}^k f^k$$

  where $\bar{z}^k = \sum_i z_i f_i^k$ is the mean trait in class k and $f^k = n^k/n$ is the frequency of class k

Class-structured Price equation

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \sum_k \underset{k}{\mathsf{cov}} \left(z_i, \sum_j r_i^{jk} \right) f^k \; + \; \sum_k (\bar{z}^k - \bar{z}) \sum_j \bar{r}^{jk} f^k \; + \text{mutation bias}$$

Class-structured Price equation

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \underbrace{\sum_k \operatorname*{cov}_k\left(z_i, \sum_j r_i^{jk}\right) f^k}_{\text{within-class}} + \sum_k (\bar{z}^k - \bar{z}) \sum_j \bar{r}^{jk} f^k + \text{mutation bias}$$

where

$$\operatorname*{cov}_k\left(z_i, r_i^{jk}\right) = \sum_i z_i r_i^{jk} f_i^k - \bar{z}^k \bar{r}^{jk}$$

Class-structured Price equation

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where

$$\underset{k}{\mathsf{cov}}\left(z_i, r_i^{jk}\right) = \sum_i z_i r_i^{jk} f_i^k - \bar{z}^k \bar{r}^{jk}$$

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Now assume negligible mutation rates and that the r_i^{jk} are independent of the type.

Class-structured Price equation

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = 0 f^k + \sum_k (\bar{z}^k - \bar{z}) \sum_j \bar{r}^{jk} f^k + 0$$

Now assume negligible mutation rates and that the r_i^{jk} are independent of the type.

The first and third terms vanish...
... but we if there are phenotypic differentiation between classes ($\bar{z}^k - \bar{z} \neq 0$), we may still observe directional change in the mean trait due to the second term.

Class-structured Price equation

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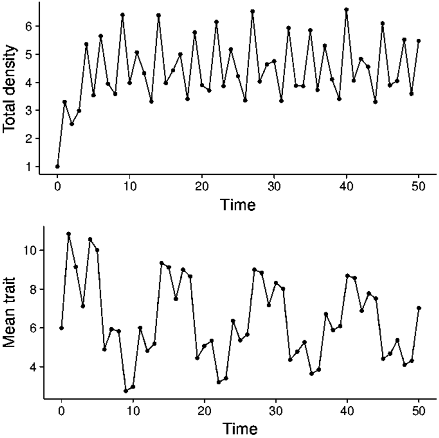
... but we if there are phenotypic differentiation between classes ($\bar{z}^k - \bar{z} \neq 0$), we may still observe directional change in the mean trait due to the second term.
⇒ "passive changes in trait mean" (e.g. Grafen, 2015)

Passive changes in trait mean

Ex: evolution of a trait in an age-structured population (larvae, pupae, adults)



Passive changes in trait mean

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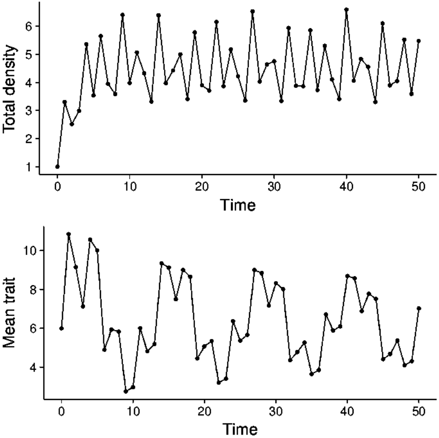

Although the trait fluctuates in time, these changes are NOT due to selection, but to demographic transitions between classes.

How can we get rid of these "passive changes" and extract the signal of natural selection?

The trick is to extend an idea by Fisher and use a **weighted average**:

> *[...] instead of counting all individuals as of equal value in respect of future population, persons of each age are assigned an appropriate value* v_x *[...]*

Let's **assign each individual a class-specific weight** $v^k(t)$. We can then compute the following weighted average:

$$\tilde{z}(t) = \sum_k v^k(t)\bar{z}^k(t)f^k(t) \tag{1}$$

with the normalisation $\sum_k v^k(t)f^k(t) = 1$.

Price equation for a weighted average

Consider the weighted average at time t

$$\tilde{z}(t) = \sum_k c^k(t)\bar{z}^k(t) \qquad \text{where } c^k(t) = v^k(t) f^k(t)$$

The Price equation for the weighted average then takes the form:

$$\boxed{\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sum_k \underset{k}{\mathsf{cov}} \left(z_i, \sum_j v^j r_i^{jk} \right) f^k}$$

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if the c^k's satisfy the following system

$$\frac{\mathrm{d}c^k}{\mathrm{d}t} = c^k \sum_j \bar{r}^{kj}\frac{f^j}{f^k} - \sum_j c^j \bar{r}^{jk}\frac{f^k}{f^j}$$

The two Price equations side by side

With weights unity

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \sum_k \underset{k}{\mathsf{cov}} \left(z_i, \sum_j r_i^{jk} \right) f^k$$

$$+ \sum_k (\bar{z}^k - \bar{z}) \bar{r}^{\bullet k} f^k$$

With the “right” weights

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \sum_k \underset{k}{\mathsf{cov}} \left(z_i, \sum_j v^j r_i^{jk} \right) f^k$$

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Discrete-time result

The discrete-time Price equation for the weighted average is

$$\tilde{z}(t+1) - \tilde{z}(t) = \sum_k \underset{k}{\mathsf{cov}} \left(z_i, \sum_j \; v^j(t+1) \; \frac{w_i^{jk}(t)}{\bar{w}(t)} \right) \; f^k(t)$$

with the following recursion for the class weights

$$c^k(t) = \sum_j c^j(t+1) \frac{\bar{w}^{jk}(t) n^k(t)}{n^j(t+1)}$$

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Biological interpretation of the class weights

Suppose we sample a random gene at some time in the future and want to calculate the probability $c^k(t)$ that its ancestor is in class k at time t when we look backward in the past.

These probabilities satisfy the recursions (Rousset 2004)

$$\begin{aligned} c^k(t) &= \sum_j c^j(t+1) p(k,t|j,t+1) \\ &= \sum_j c^j(t+1) \frac{\bar{w}^{jk}(t) n^k(t)}{n^j(t+1)} \end{aligned}$$

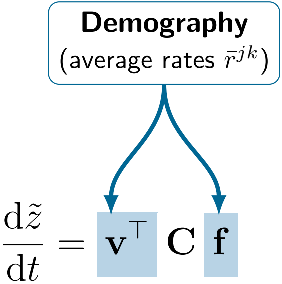
Perhaps more intuitively, $c^k(t)$ measures the (relative) number of future descendants left by genes present in class k at time t
⇒ (class) reproductive value (at time t)

The interplay between demography and selection

Demography and selection

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \ \mathbf{C} \ \mathbf{f}$$

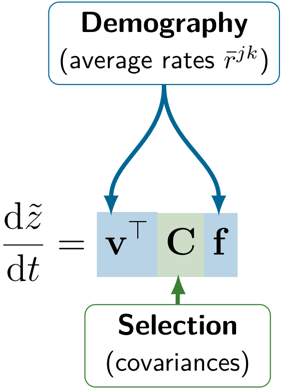
Demography and selection



Demography
(average rates $\bar{r}^{jk}$)

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \, \mathbf{C} \, \mathbf{f}$$

Demography and selection



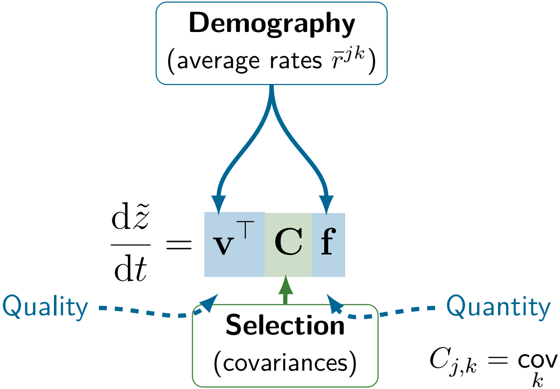
Demography
(average rates $\bar{r}^{jk}$)

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C}\,\mathbf{f}$$

Selection
(covariances)

$$C_{j,k} = \underset{k}{\mathsf{cov}}\left(z_i, r_i^{jk}\right)$$

Demography and selection



Demography

(average rates $\bar{r}^{jk}$)

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C} \, \mathbf{f}$$

Quality

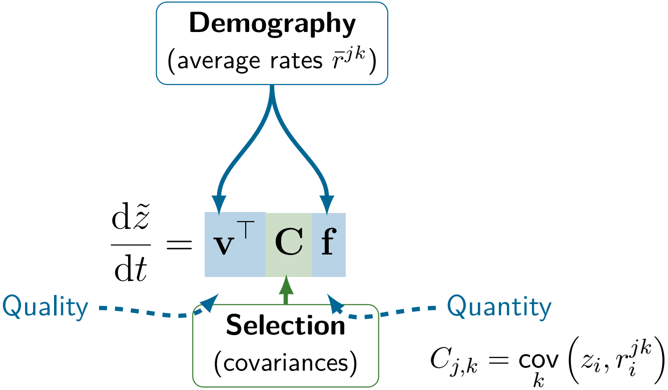
Quantity

Selection

(covariances)

$$C_{j,k} = \operatorname*{cov}_{k}\left(z_i, r_i^{jk}\right)$$

Demography and selection



Demography

(average rates $\bar{r}^{jk}$)

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C}\, \mathbf{f}$$

Selection

(covariances)

$$C_{j,k} = \underset{k}{\mathsf{cov}}\left(z_i, r_i^{jk}\right)$$

Does not depend on any assumption on

- the trait distribution (no weak selection or rare mutant)
- the underlying population and environmental dynamics (non-linear dynamics, density-dependence...)

Dynamical equations for the demographic process

$$\frac{\mathrm{d}\mathbf{f}}{\mathrm{d}t} = \mathbf{R}(\mathbf{E}(t))\mathbf{f} - \bar{r}(t)\mathbf{f} \qquad \text{(forward)}$$

$$\frac{\mathrm{d}\mathbf{v}^\top}{\mathrm{d}t} = -\mathbf{v}^\top\mathbf{R}(\mathbf{E}(t)) + \bar{r}(t)\mathbf{v}^\top \qquad \text{(backward)}$$

where

$$\bar{r}(t) = \frac{1}{n}\frac{\mathrm{d}n}{\mathrm{d}t}$$

is the per-capita growth rate of the total population.

(Similar equations in discrete-time and for continous population structure (ex: age))

Recovering classical results

$$\frac{\mathrm{d}\mathbf{f}}{\mathrm{d}t} = \mathbf{R}(\mathbf{E}(t))\mathbf{f} - \bar{r}(t)\mathbf{f} \qquad \text{(forward)}$$

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Exponential growth

$$\mathbf{R}\mathbf{f} = \bar{r}\mathbf{f}$$

$$\mathbf{v}^\top\mathbf{R} = \bar{r}\mathbf{v}^\top$$

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Exponential growth

$$\mathbf{R}\mathbf{f} = \bar{r}\mathbf{f}$$

$$\mathbf{v}^\top\mathbf{R} = \bar{r}\mathbf{v}^\top$$

Density-dependent populations at equilibrium

$$\mathbf{R}\mathbf{f} = 0$$

$$\mathbf{v}^\top\mathbf{R} = 0$$

Recovering classical results

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We thus recover classical eigenvectors results (e.g. Goodman 1968, Tuljapurkar 1989, Taylor 1990, Caswell 2001)...

Recovering classical results

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$$\mathbf{R}\mathbf{f} = 0$$

$$\mathbf{v}^\top\mathbf{R} = 0$$

We thus recover classical eigenvectors results (e.g. Goodman 1968, Tuljapurkar 1989, Taylor 1990, Caswell 2001)...
... but we don't have to assume a monomorphic population.

Reproductive values for predictive theoretical analyses

Predicting the future

Can we use the weighted Price equation:

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \mathbf{C}\mathbf{f}$$

to make predictions on evolution?

Problem: to calculate $\mathbf{v}(t)$, we need information about the whole future of the population, from t onwards.

Solution: separation of time scales between demography and evolution

Then, we can calculate the reproductive values on the ecological attractor of the population (e.g. fixed point, limit cycle), on which the future is to some extent predictable.

Equilibrium

Classical result of Evolutionary Game Theory
(Taylor 1990, Taylor & Frank 1996, Rousset 2004)

Two traits z_w and $z_m = z_w + \varepsilon$.

For small values of ε (weak selection),

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \boxed{\sigma_{zz}} \; \boxed{\hat{\mathbf{v}}^\top \frac{\mathrm{d}\mathbf{R}_m}{\mathrm{d}\varepsilon} \hat{\mathbf{f}}} + O(\varepsilon^3)$$

where

- $\hat{\mathbf{v}}$ and $\hat{\mathbf{f}}$ are calculated at equilibrium in the monomorphic resident population
- $\mathbf{R}_m$ is the matrix of mutant per-capita growth rates r_m^{jk}.
- σ_{zz} is the trait variance in the population

Periodic attractor

Consider a monomorphic population that has settled on a limit cycle with period T.

For weak selection, the average change in mean trait over one period is approximately proportional to

$$\mathcal{S} = \frac{1}{T}\int_0^T \hat{\mathbf{v}}^\top(t)\frac{\mathrm{d}\mathbf{R}_m(t)}{\mathrm{d}\varepsilon}\hat{\mathbf{f}}(t)\,\mathrm{d}t.$$

The RV and class frequencies are time-dependent and computed on the resident periodic attractor.

(see Part 2 of this lecture)

General quasi-equilibrium argument

Under weak selection, we have a separation of time scales:

- **Slow variables** (Evolution): mean trait $\bar{z}$, frequency of type i
- **Fast variables** (Demography): ecological densities, class frequencies, reproductive values

We can thus use quasi-equilibrium arguments to calculate the short- and long-term change in the slow evolutionary variables.

Reproductive values for retrospective data analyses

A potential application for field studies

Suppose we study a real population for which we know:

- the mean traits in each class $\bar{z}^k(t)$
- the class densities $n^k(t)$
- the average fitnesses $\bar{w}^{jk}(t)$.

We can use this data to compute the reproductive values at each time t.

Plotting the weighted trait average will then give us an estimate of the effect of **natural selection** on the change in mean trait, **after elimination of the passive changes**

Example: a variation on the LPA Tribolium model

Larvae ⟶ Pupae ⟶ Adults

$$\mathbf{W}_i(t) = \begin{pmatrix} 0 & 0 & \phi_3\ e^{-c_{el} n^1(t) - c_{ea} n^3(t)} \\ s_1 +\ \omega \dfrac{z_i}{1+\kappa z_i} & 0 & 0 \\ 0 & s_2\ e^{-c_{pa} n^3(t)} & s_3 \end{pmatrix}$$

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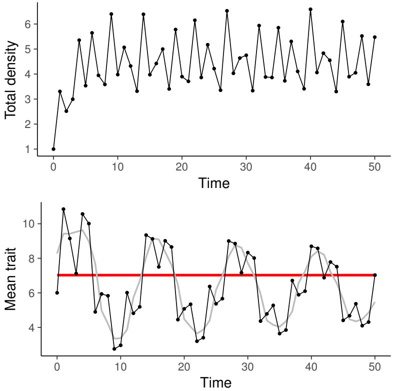
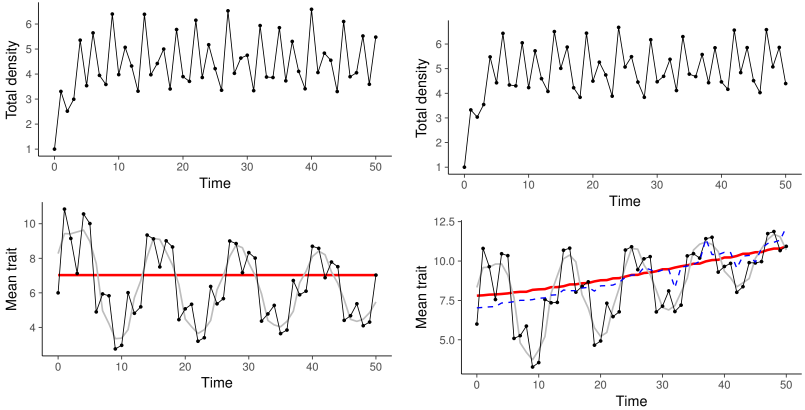
(a) Neutral model ($\omega = 0$)





(a) Neutral model ($\omega = 0$)

(b) Model with selection ($\omega = 0.05$)

What about Fisher's RV?

Continous age structure

We now calculate an average trait value $\tilde{z}$ by weighting each individual with a weight $v(a,t)$ at age a and time t:

$$\tilde{z} = \sum_i z_i \int_0^\infty v(a,t) f(a,t) f_i(a,t) \mathrm{d}a$$

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The dynamics of $\tilde{z}$ can then be written as

$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \underbrace{v(0,t) \int_0^\infty \underset{a}{\mathsf{cov}}(z_i, b_i(a,t))\ f(a,t)\ \mathrm{d}a}_{\text{Production of age-0 individuals}}$$

$$\underbrace{- \int_0^\infty v(a,t)\ \underset{a}{\mathsf{cov}}(z_i, d_i(a,t))\ f(a,t)\ \mathrm{d}a}_{\text{Death of age-}a\text{ individuals}}$$

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if the weights (=RV) satisfy the following PDE

$$\frac{\partial v}{\partial t} + \frac{\partial v}{\partial a} = -\bar{b}(a,t) v(0,t) + \bar{d}(a,t) v(a,t) + \bar{r}(t) v(a,t)$$

and the $f(a,t)$ satisfy an adjoint equation

see also Bacaër & Abdurahman (2008)

Back to Fisher

Asssume **time-independent** birth and death rates $b(a)$ and $d(a)$.

The population is then characterised by a stable growth rate $\bar{r}$, a stable age structure $f(a)$ and a stable distribution of RV $v(a)$, given by:

$$v(a) = v(0)\frac{e^{\bar{r}a}}{\ell(a)}\int_a^{\infty} e^{-\bar{r}s}\ell(s)\bar{b}(s)ds$$

where $\ell(s) = \exp(-\int_0^s \bar{d}(x)\mathrm{d}x)$.

This is Fisher's original definition of RV, but with an explicit dependence on average birth and death rates.

(see also Day et al, Evolution, 2011 for an extension to time-dependent vital rates using a quasi-equilibrium approximation)

Take-home messages for Part 1

- RV-weighting can be used to eliminate **“passive changes in mean trait”** caused by demographic transitions between classes.

- For general ecological scenarios, RV need to be defined:
  - as **time-dependent weights**;
  - at a purely **demographic** level, by averaging vital rates within each class over the distribution of genotypes.

- The individual RV and class frequencies satisfy **coupled dynamical equations** representing the forward and backward ways of looking at population demography.

- Selection is captured by a matrix of **covariances** between the trait and the transition rates

References for Part 1

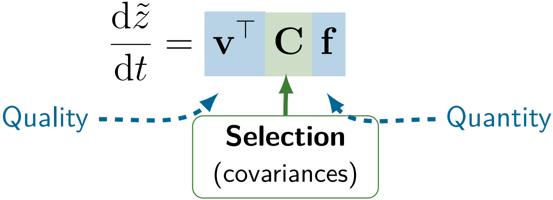
- Lion (2018) *The American Naturalist*
  Theoretical approaches in evolutionary ecology: environmental feedback as a unifying perspective.
- Lion (2018) *The American Naturalist*
  Class structure, demography and selection: reproductive-value weighting in nonequilibrium, polymorphic populations.
- Lion (2018) *J. theor. Biol.*
  From the Price equation to the selection gradient in class-structured populations: a quasi-equilibrium route

... and references therein

Summary so far

We have seen that a good measure of natural selection can be derived using reproductive-value weighting.

The RV-weighted average changes as follows:



$$\frac{\mathrm{d}\tilde{z}}{\mathrm{d}t} = \mathbf{v}^\top \, \mathbf{C} \, \mathbf{f}$$

Quality

Selection
(covariances)

Quantity

For small mutational effect, the RHS yields the selection gradient.

Part 2 – Periodic environmental fluctuations

- One interesting application of time-dependent RVs is when the quality of each class varies over time due to environmental fluctuations.
- In adaptive dynamics, evolution in periodic environments is analysed by calculating the **Floquet exponent** of a rare mutant.
- For class-structured populations, this is often only achievable through **numerical integration**.
- With time-dependent RVs, it is possible to go one step further and have an **analytical expression of the selection gradient**.

General theory

Floquet analysis

For a rare mutant appearing in a resident population on its periodic attractor, the dynamics of the mutant are summarised by a matrix

$$\mathbf{R}_m(\mathbf{E}_w, t)$$

To calculate the invasion fitness, one numerically integrates the following matrix equation:

$$\frac{\mathrm{d}\mathbf{X}}{\mathrm{d}t} = \mathbf{R}_m(\mathbf{E}_w, t)\mathbf{X}$$

over one period $[t_0, t_0 + T]$ with initial condition $\mathbf{X}(t_0) = \mathbf{I}$.

The eigenvalues of $\mathbf{X}(t_0 + T)$ are called the Floquet multipliers. The invasion fitness is then given by the Floquet exponent

$$\rho(z_m, z_w) = \frac{1}{T}\mu$$

where μ is the dominant Floquet multiplier.

Alternative approach

For most realistic models, the Floquet exponent can only be calculated numerically.

I will now show how we can use the idea of reproductive-value weighting to calculate an approximation of the invasion fitness under weak selection.

Dynamics of RV-weighted mutant frequency

Suppose for simplicity that we have only two types: w and m.

Instead of looking at the change in mean trait, we directly track the dynamics of the frequency of the mutant type:

$$\tilde{f}_m(t) = \sum_k v^k(t) f_m^k(t) f^k(t)$$

We obtain:

$$\frac{\mathrm{d}\tilde{f}_m}{\mathrm{d}t} = \sum_j \underbrace{f_m^j(t)(1 - f_m^j(t))}_{\textit{genetic variance}} \sum_k v^k(t) \left(r_m^{kj}(\mathbf{E},t) - r_w^{kj}(\mathbf{E},t)\right) f^j(t)$$

together with

$$\frac{\mathrm{d}n^k}{\mathrm{d}t} = \sum_j \bar{r}^{kj}(\mathbf{E},t)\, n^j(t)$$

Weak selection

We now write the vital rates as explicit functions of the phenotypes:

$$r_m^{kj}(\mathbf{E},t) = r^{kj}(z_m,\mathbf{E},t)$$

For weak selection ($z_m = z_w + \varepsilon$), we have

$$r^{kj}(z_m,\mathbf{E},t) - r^{kj}(z_w,\mathbf{E},t) = \varepsilon \frac{\partial r^{kj}}{\partial z_m}(z_w,\mathbf{E},t) + O(\varepsilon^2)$$

and

$$\bar{r}^{kj}(\mathbf{E},t) = r^{kj}(z_w,\mathbf{E},t) + O(\varepsilon)$$

Separation of time scales

Fast variables

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}t} = \mathbf{R}_w(\mathbf{E}, t) + O(\varepsilon)$$

The class densities are fast variables and converge towards the resident periodic attractor: $\hat{\mathbf{n}}(t)$.
Also true of class frequencies and RVs: $\hat{\mathbf{f}}(t)$ and $\hat{\mathbf{v}}(t)$.

Slow variable

In contrast, the RV-weighted mutant frequency is a slow variable:

$$\frac{\mathrm{d}\tilde{f}_m}{\mathrm{d}t} = \varepsilon\, \tilde{f}_m(1 - \tilde{f}_m)\mathcal{S}(t) + O(\varepsilon^2)$$

where

$$\mathcal{S}(t) = \sum_j \sum_k \hat{v}^k(t) \frac{\partial r^{kj}}{\partial z_m}(z_w, \hat{\mathbf{E}}, t)\hat{f}^j(t)$$

Averaging principle

Under weak selection, we can iron out the fluctuations in $\mathcal{S}(t)$. We obtain:

$$\frac{\mathrm{d}\tilde{f}_m}{\mathrm{d}t} = \varepsilon \tilde{f}_m (1 - \tilde{f}_m) \langle \mathcal{S} \rangle + O(\varepsilon^2)$$

The direction of selection is then given by

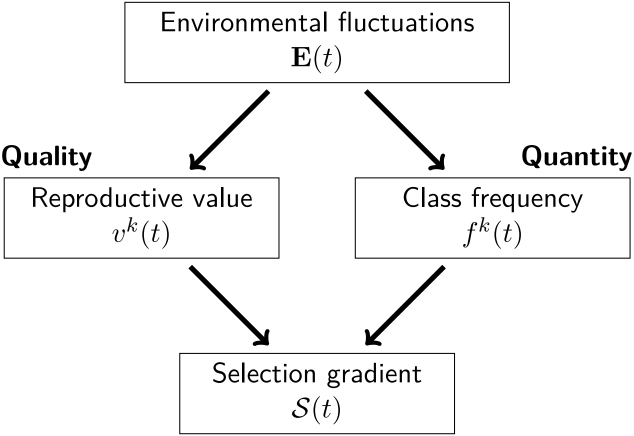
$$\langle \mathcal{S} \rangle = \left\langle \sum_j \sum_k \hat{v}^k(t) \frac{\partial r^{kj}}{\partial z_m}(z_w, \hat{\mathbf{E}}, t) \hat{f}^j(t) \right\rangle$$

(average over one period of the resident attractor)

- Same form as the selection gradient for equilibrium dynamics
- Potential endpoints of evolution are given by the zeros of $\langle \mathcal{S} \rangle$
- "Invasion implies fixation"

  Geritz (2005); Priklopil & Lehmann (2019, class-structured); Cai & Geritz (2020, random environments)

Quantity vs Quality



Environmental fluctuations
$\mathbf{E}(t)$

Quality

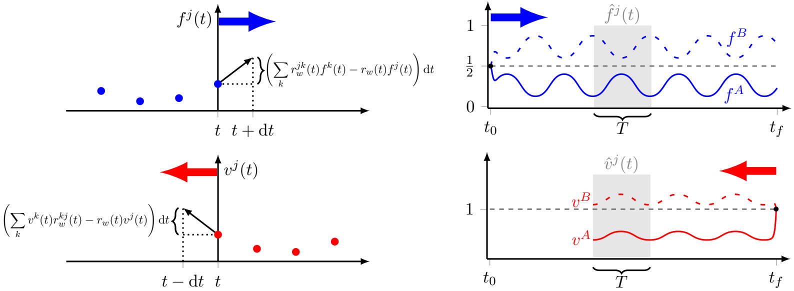
Quantity

Reproductive value
$v^k(t)$

Class frequency
$f^k(t)$

Selection gradient
$\mathcal{S}(t)$

Calculating the class frequencies and reproductive values



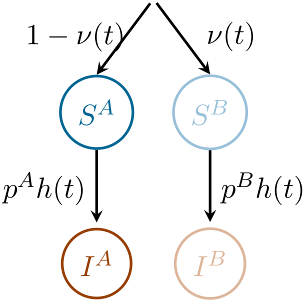
Summary so far...

- The selection gradient for periodic environments can be simply obtained by making the equilibrium selection gradient time-dependent and taking the average over one period [not true for invasion fitness!!]
- Benefit: we retain the biological insightful concept of RV.
- Downside: the calculation of $\hat{v}^k(t)$ and $\hat{f}^k(t)$ is often only possible through numerical integration. [but also true for Floquet approach]

Applications to evolutionary epidemiology

A two-host model

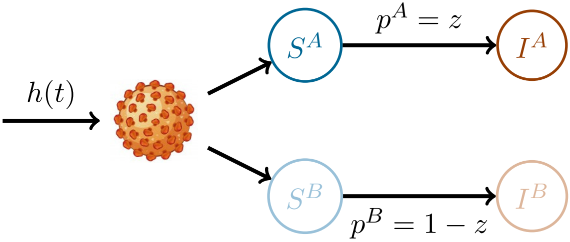
Epidemiological dynamics



$$\frac{\mathrm{d}S^A}{\mathrm{d}t} = b(1-\nu(t)) - dS^A - p^A S^A h(t)$$
$$\frac{\mathrm{d}S^B}{\mathrm{d}t} = b\nu(t) - dS^B - p^B S^B h(t)$$
$$\frac{\mathrm{d}I^A}{\mathrm{d}t} = p^A S^A h(t) - (d+\alpha^A) I^A$$
$$\frac{\mathrm{d}I^B}{\mathrm{d}t} = p^B S^B h(t) - (d+\alpha^B) I^B$$

with $h(t) = \beta^A I^A(t) + \beta^B I^B(t)$ the force of infection and $\nu(t)$ the periodic probability of production of A hosts.

Example 1: evolution of host preference



$h(t)$

S^A

$p^A = z$

I^A

S^B

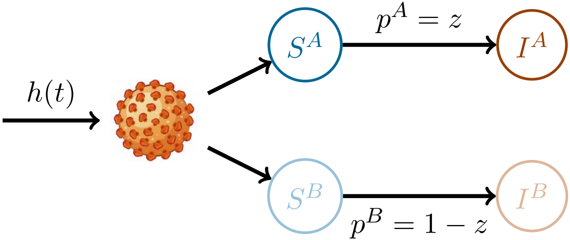
$p^B = 1 - z$

I^B

$\beta^A = \beta^B$

$\alpha^A > \alpha^B$

Example 1: evolution of host preference



$\beta^A = \beta^B$
$\alpha^A > \alpha^B$

Should the pathogen prefer the good or the bad host?

The answer is not obvious because it depends on the availability of each host class, which can fluctuate.

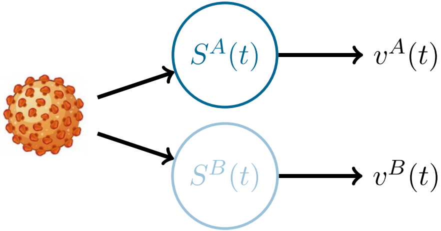
Selection gradient

$$\langle \mathcal{S} \rangle = \beta \left(\left\langle v^A S^A \right\rangle - \left\langle v^B S^B \right\rangle \right)$$

Selection gradient

$$\langle \mathcal{S} \rangle = \beta \left(\left\langle v^A S^A \right\rangle - \left\langle v^B S^B \right\rangle \right)$$

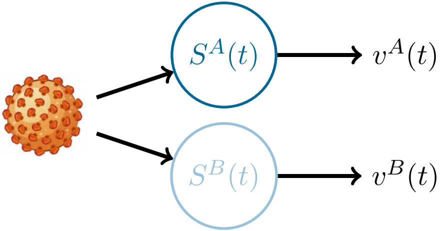
Future reproductive output at time t



Selection gradient

$$\langle \mathcal{S} \rangle = \beta \left(\left\langle v^A S^A \right\rangle - \left\langle v^B S^B \right\rangle \right)$$

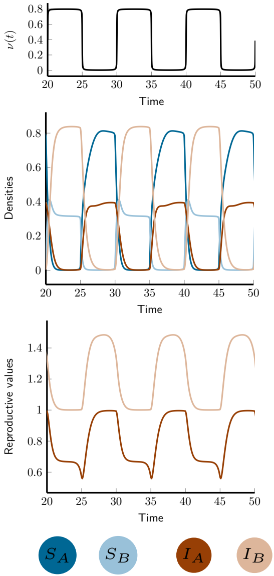
Future reproductive output at time t



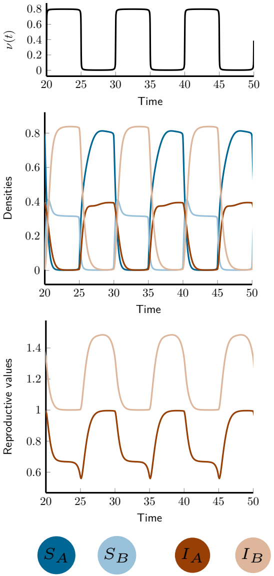
The pathogen will evolve preference for host class A if its average reproductive output is larger in class A than in class B:

$$\left\langle v^A S^A \right\rangle > \left\langle v^B S^B \right\rangle$$

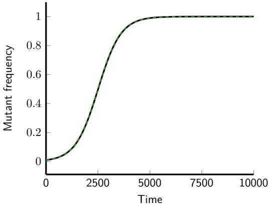
Fast time scale



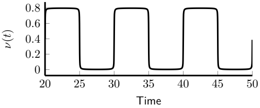
Fast time scale

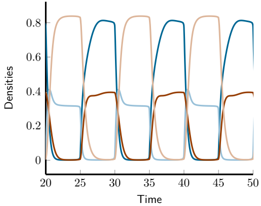


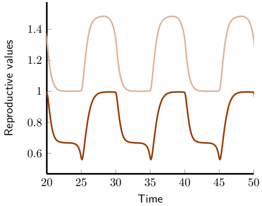
Slow time scale



Fast time scale

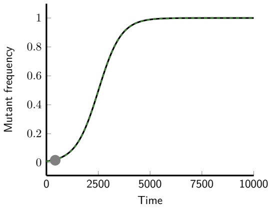




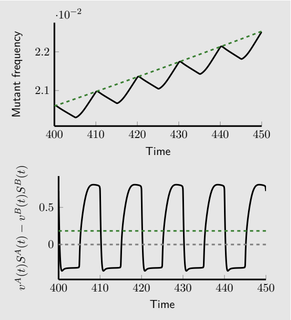


S_A S_B I_A I_B

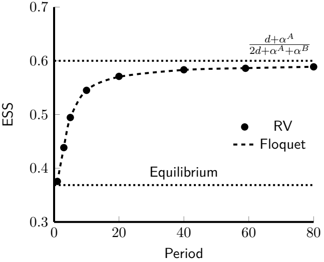
Slow time scale



Let's zoom in:



ESS as a function of period



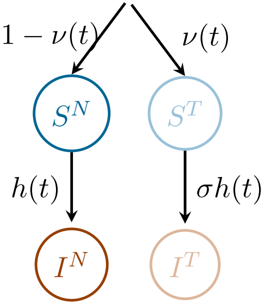
At the ESS:

$$\left\langle v^A S^A \right\rangle = \left\langle v^B S^B \right\rangle$$

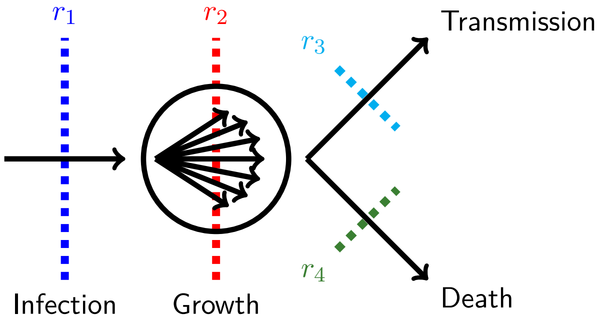
- **When T is small**, ESS is close to prediction of constant model
  $\Rightarrow$ host preference is biased towards the B host, which suffers less from the infection
- **When T is large**, the opposite strategy can be selected
  $\Rightarrow$ host preference is biased towards the host where the pathogen has lower duration of infection.

Example 2: evolution of virulence in response to periodic treatments

Treated hosts (e.g. vaccinated) represent a low-quality habitat for the parasite.



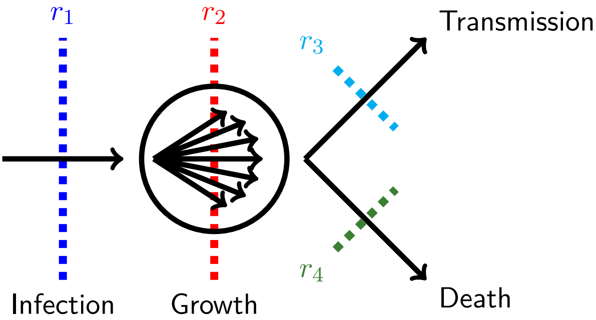
Different types of vaccines



1. Anti-infection vaccine (r_1)
2. Anti-growth vaccine (r_2)
3. Transmission-blocking vaccine (r_3)
4. Anti-virulence vaccine (r_4)

Gandon et al (2001, 2003)

Different types of vaccines



1. Anti-infection vaccine (r_1)
2. Anti-growth vaccine (r_2)
3. Transmission-blocking vaccine (r_3)
4. Anti-virulence vaccine (r_4)

Gandon et al (2001, 2003)

Constant environment

In a constant environment, the selection gradient takes the form

$$\mathcal{S} \approx (1 - c_T) \underbrace{\left[\frac{d + \alpha_N}{\beta_N} \beta'_N(z) - \alpha'_N(z)\right]}_{\mathcal{S}_N} + c_T \underbrace{\left[\frac{d + \alpha_T}{\beta_T} \beta'_T(z) - \alpha'_T(z)\right]}_{\mathcal{S}_T}$$

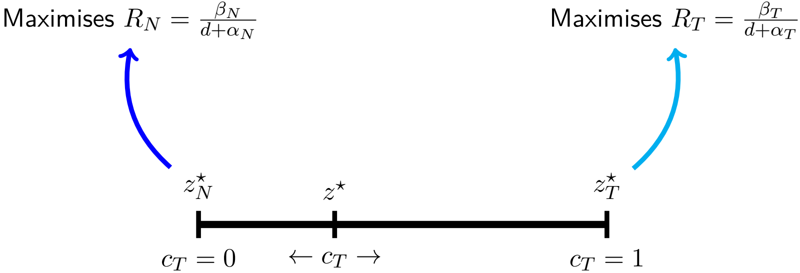
where c_T is the class reproductive value of vaccinated hosts.

Constant environment

In a constant environment, the selection gradient takes the form

$$\mathcal{S} \approx (1 - c_T) \underbrace{\left[\frac{d + \alpha_N}{\beta_N}\beta_N'(z) - \alpha_N'(z)\right]}_{\mathcal{S}_N} + c_T \underbrace{\left[\frac{d + \alpha_T}{\beta_T}\beta_T'(z) - \alpha_T'(z)\right]}_{\mathcal{S}_T}$$

where c_T is the class reproductive value of vaccinated hosts.



Maximises $R_N = \frac{\beta_N}{d+\alpha_N}$

Maximises $R_T = \frac{\beta_T}{d+\alpha_T}$

$z_N^\star$ $z^\star$ $z_T^\star$

$c_T = 0$ $\leftarrow c_T \rightarrow$ $c_T = 1$

Vaccine types and evolution

$$\mathcal{S} \approx (1-c_T)\underbrace{\left[\frac{d+\alpha_N}{\beta_N}\beta'_N(z)-\alpha'_N(z)\right]}_{\mathcal{S}_N}+c_T\underbrace{\left[\frac{d+\alpha_T}{\beta_T}\beta'_T(z)-\alpha'_T(z)\right]}_{\mathcal{S}_T}$$

Anti-transmission vaccine

$$\beta_T=(1-r)\beta_N \qquad \Rightarrow \qquad \mathcal{S}_N=\mathcal{S}_T$$

Hence anti-transmission vaccines have no effect on pathogen life-history traits $(z^\star = z^\star_N)$

Anti-virulence vaccine

$$\alpha_T=(1-r)\alpha_N$$

Vaccines that reduce the short-term effects of virulence in infected hosts should select for higher virulence in the long run.
This effect will be stronger when c_T is large.

Periodic environment

What happens if vaccination coverage fluctuates over time?

Selection gradient

$$\langle \mathcal{S} \rangle \approx (1-\langle c_T \rangle) \underbrace{\left[\frac{d+\alpha_N}{\beta_N} \beta_N'(z) - \alpha_N'(z) \right]}_{\mathcal{S}_N} + \langle c_T \rangle \underbrace{\left[\frac{d+\alpha_T}{\beta_T} \beta_T'(z) - \alpha_T'(z) \right]}_{\mathcal{S}_T}$$

Periodic environment

What happens if vaccination coverage fluctuates over time?

Selection gradient

$$\langle \mathcal{S} \rangle \approx (1-\langle c_T \rangle) \underbrace{\left[\frac{d+\alpha_N}{\beta_N}\beta_N'(z) - \alpha_N'(z)\right]}_{\mathcal{S}_N} + \langle c_T \rangle \underbrace{\left[\frac{d+\alpha_T}{\beta_T}\beta_T'(z) - \alpha_T'(z)\right]}_{\mathcal{S}_T}$$

Anti-transmission vaccine

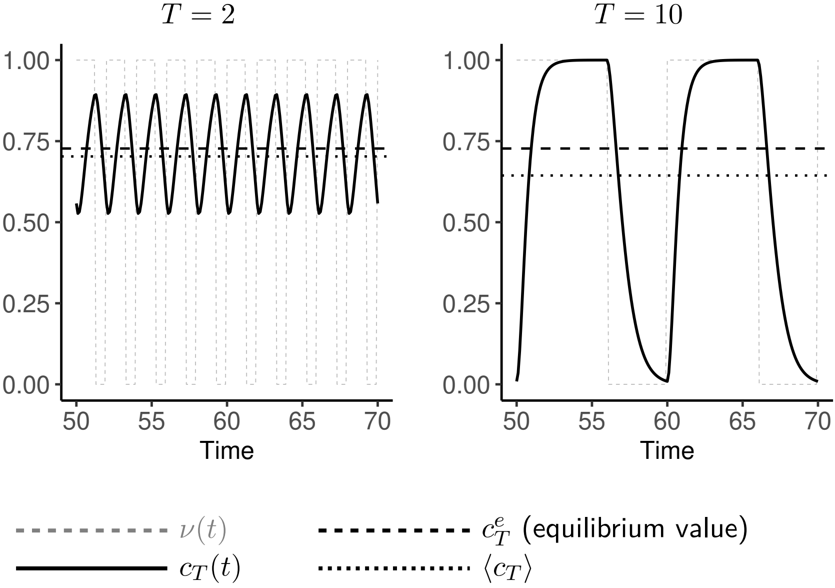
$$\beta_T = (1-r)\beta_N$$

Again, we have $\mathcal{S}_N = \mathcal{S}_T$, and therefore no effect.

Anti-virulence vaccine

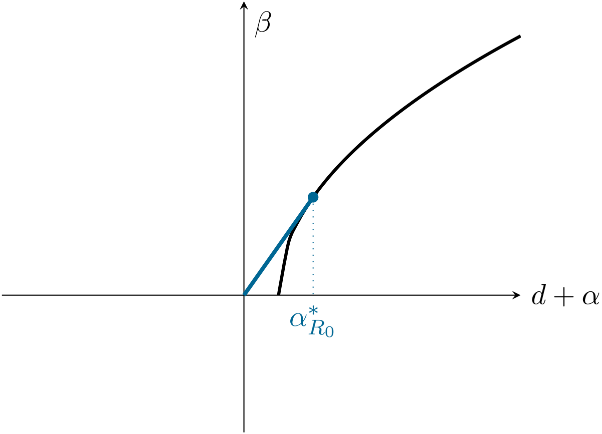
Again, the ESS is somewhere between the optimum for a fully naive population and that of a fully treated population.

But now, the exact position depends only on the **mean class reproductive value of treated hosts**, $\langle c_T \rangle$.


$T = 2$
$T = 10$
1.00
0.75
0.50
0.25
0.00
50
55
60
65
70
Time
$\nu(t)$
$c_T(t)$
c_T^e (equilibrium value)
$\langle c_T \rangle$

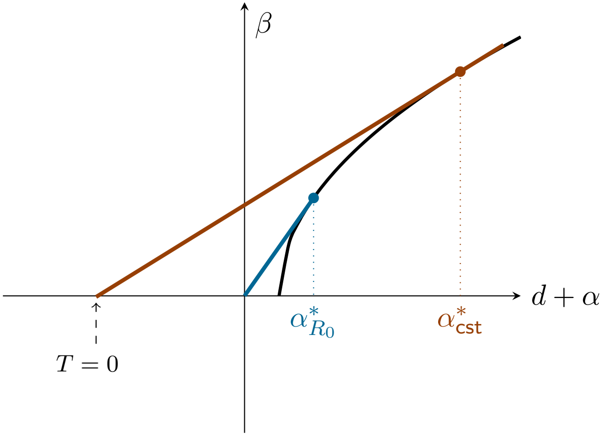
Effect of period on ES virulence

Graphical representation



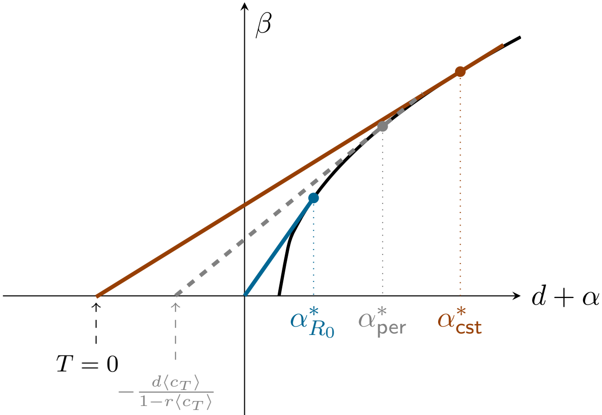
Effect of period on ES virulence

Graphical representation



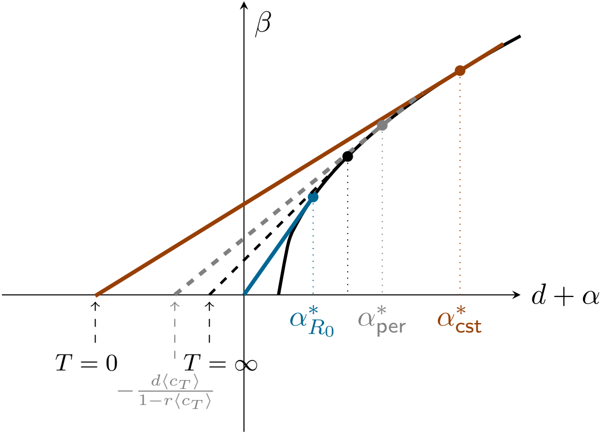
Effect of period on ES virulence

Graphical representation



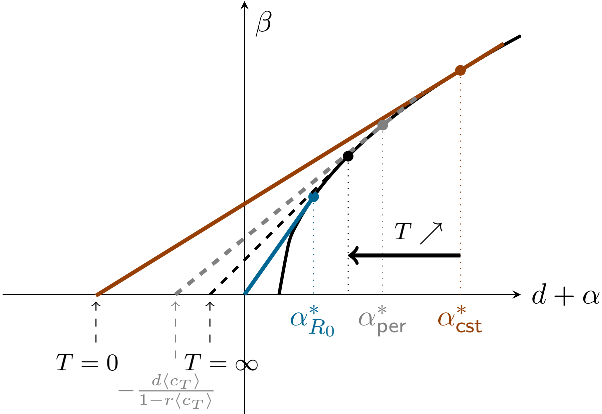
Effect of period on ES virulence

Graphical representation

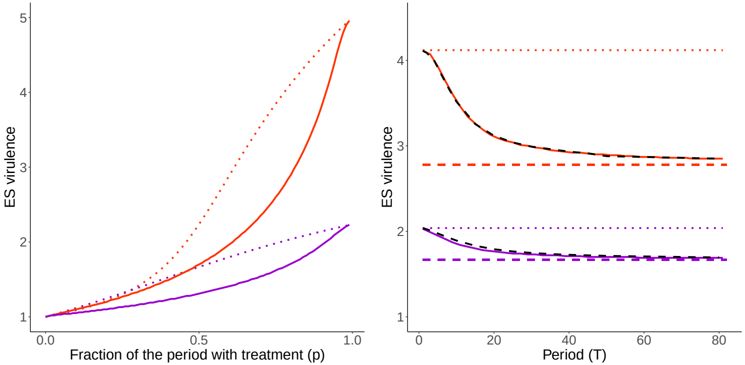


Effect of period on ES virulence

Graphical representation



Effect of period on ES virulence



Fluctuations in vaccination coverage tend to mitigate the negative effects of imperfect vaccines.

Lower bound:

$$\text{for } \beta(z) = \beta_0 \frac{z}{1+z}, \qquad z^\star = \frac{1}{1-pr}$$

Take-home messages for Part 2

- The selection gradient for periodic environments can be simply obtained by making the equilibrium selection gradient time-dependent and taking the average over one period [not true for invasion fitness!!]
- The general approach can be applied to structured epidemiological models with complex dynamics.
- This allows for a direct analytical comparison with equilibrium expressions of the selection gradient.

References

- Walter & Lion (2021) *Proceedings B*
  Epidemiological and evolutionary consequences of periodicity in treatment coverage.
- Lion & Gandon (in press) *Evolution*
  Evolution of class-structured populations in fluctuating environments.

... and references therein

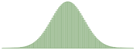
Part 3 – Transient dynamics and polymorphism

Evolutionary ecology

How do ecological processes affect how trait distributions change over time?

Evolutionary ecology

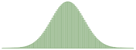
How do ecological processes affect how trait distributions change over time?



Trait distribution

Evolutionary ecology

How do ecological processes affect how trait distributions change over time?



Trait distribution

$V = O(\varepsilon^2)$

Evolutionary ecology

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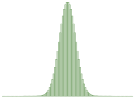

Trait distribution

$V = O(\varepsilon^2)$

Evolutionary ecology

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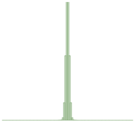


Trait distribution
$V = O(\varepsilon^2)$

Under weak selection (small variance):

$$\begin{aligned}\frac{\mathrm{d}n}{\mathrm{d}t} &= \Phi(n,\bar{z}) + O(\varepsilon)\\ \frac{\mathrm{d}\bar{z}}{\mathrm{d}t} &= V\ S(n,\bar{z}) + O(\varepsilon^3)\\ \frac{\mathrm{d}V}{\mathrm{d}t} &= \dots\end{aligned}$$

cf Abrams et al 1993, Abrams & Matsuda 1997

Separation of time scales

$$\begin{aligned}\frac{\mathrm{d}n}{\mathrm{d}t} &= \overbrace{\Phi(n,\bar{z})}^{\text{Ecological dynamics}} + O(\varepsilon)\\ \frac{\mathrm{d}\bar{z}}{\mathrm{d}t} &= V\;\underbrace{S(n,\bar{z})}_{\text{Selection gradient}} + O(\varepsilon^3)\end{aligned}$$

If the variance is small, $\bar{z}$ is a **slow** variable while n is a **fast** variable.

Separation of time scales

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \Phi(n, \bar{z}) + O(\varepsilon)$$

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = V \; S(n, \bar{z}) + O(\varepsilon^3)$$

Ecological dynamics

Selection gradient

If the variance is small, $\bar{z}$ is a **slow** variable while n is a **fast** variable.

Quasi-equilibrium approximation:
on the slow time scale $\bar{z}$ changes subject to the constraint

$$\Phi(n, \bar{z}) = 0 \qquad \Leftrightarrow \qquad n = \hat{n}(\bar{z})$$

As a result:

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} \approx V \; S(\hat{n}(\bar{z}), \bar{z})$$

Application: Models of character displacement

Slatkin (1979, 1980); Taper & Case (1992)

$$r(z,E(t)) = \rho(z) - \int a(z-y)n(y,t)\mathrm{d}y$$

Taylor approximation:

$$r(z) = \rho(z) - n(t)a(z-\bar{z}) + O(\varepsilon)$$

Application: Models of character displacement

Slatkin (1979, 1980); Taper & Case (1992)

$$r(z, E(t)) = \rho(z) - \int a(z-y)n(y,t)\mathrm{d}y$$

Taylor approximation:

$$r(z) = \rho(z) - n(t)a(z-\bar{z}) + O(\varepsilon)$$

$$\begin{aligned}
\frac{\mathrm{d}n}{\mathrm{d}t} &= \overbrace{\left[\rho(\bar{z}) - n\right] n}^{\Phi(n,\bar{z})} \\
\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} &= V \underbrace{\left[\rho'(\bar{z}) - na'(0)\right]}_{S(n,\bar{z})} \\
\frac{\mathrm{d}V}{\mathrm{d}t} &= V^2 \left[\rho''(\bar{z}) - na''(0)\right]
\end{aligned}$$

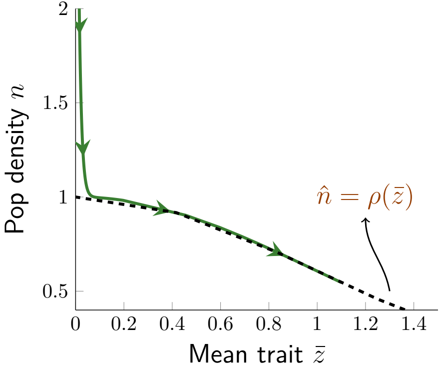
Application: Models of character displacement

Slatkin (1979, 1980); Taper & Case (1992)

$$r(z, E(t)) = \rho(z) - \int a(z-y)n(y,t)\mathrm{d}y$$

Taylor approximation:

$$r(z) = \rho(z) - n(t)a(z-\bar{z}) + O(\varepsilon)$$



$$\frac{\mathrm{d}n}{\mathrm{d}t} = \overbrace{[\rho(\bar{z}) - n]\,n}^{\Phi(n,\bar{z})}$$

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = V\,\underbrace{[\rho'(\bar{z}) - na'(0)]}_{S(n,\bar{z})}$$

$$\frac{\mathrm{d}V}{\mathrm{d}t} = V^2\,[\rho''(\bar{z}) - na''(0)]$$

Hence, for narrow unimodal trait distributions in unstructured populations, we have a good idea of how to proceed.

In this talk, I will examine how this picture is altered by two complications:

- multimodal trait distributions
- population structure

Multimodality and time scales

Densities and trait distribution

Densities

$n(z,t)$	Density of individuals with trait z at time t
$n(t)$	Total density of individuals at time t

$$n(t) = \int n(z,t)\mathrm{d}z$$

Trait distribution

Frequency of individuals with trait z at time t

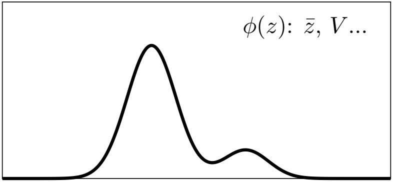
$$\phi(z,t) = \frac{n(z,t)}{n(t)}$$

Our aim is to understand the joint (eco-evo) dynamics of $n(t)$ and $\phi(z,t)$.

Multi-morph decomposition

Classical QG models assume a normal trait distribution

However, trait distributions in nature are not necessarily normal (e.g. skewed, or multimodal).



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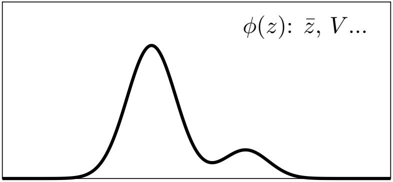
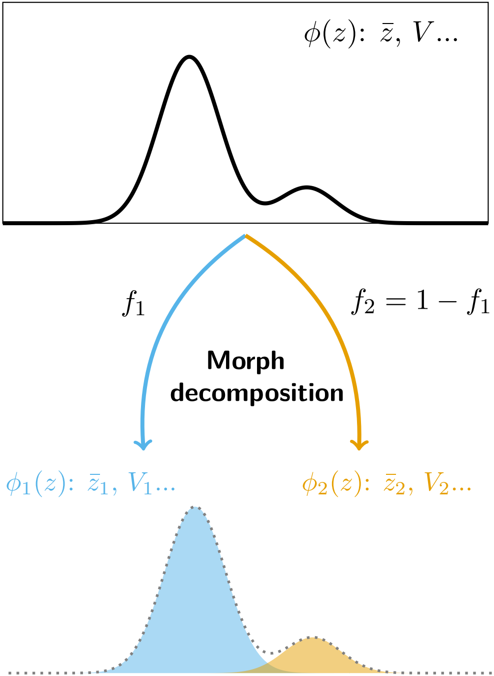


$$\phi(z,t) = \sum_{i=1}^{M} \phi_i(z,t) f_i(t)$$

where

- $\phi_i(z,t)$ is the trait distribution of morph i at time t
- $f_i(t)$ is the frequency of morph i


$\phi(z)$: $\bar{z}$, V...
f_1
$f_2 = 1 - f_1$
Morph decomposition
$\phi_1(z)$: $\bar{z}_1$, V_1...
$\phi_2(z)$: $\bar{z}_2$, V_2...

Moments

Population-level moments ($\phi(z,t)$)

$\bar{z}(t)$	Mean trait value at time t
$V(t)$	Trait variance at time t
$T(t)$	Third central moment at time t
$\vdots$	

Morph moments ($\phi_i(z,t)$)

$\bar{z}_i(t)$	Mean trait value of morph i at time t
$V_i(t)$	Trait variance of morph i at time t
$T_i(t)$	Third central moment of morph i at time t
$\vdots$	

Typically, we consider symmetric morph distributions ($T_i = 0$) but allow for non-symmetric distributions at the pop. level ($T \neq 0$).

Moment closure

If, **at the morph level**, higher-order moments are negligible or can be approximated using moment closure approximations (e.g. Gaussian closure), a morph can be characterised at time t by

- its relative abundance (e.g. its frequency $f_i(t)$)
- its position (e.g. the morph mean $\bar{z}_i(t)$)
- its width (e.g. the morph standard deviation ($\sqrt{V_i(t)}$)

In this talk, I will simply assume Gaussian closure **at the morph level**.

Dynamics

Now that we have statistics to describe the state of the population at a given time, we turn to their dynamics.

⇒ How do the various peaks of the multimodal distribution move and change over time?

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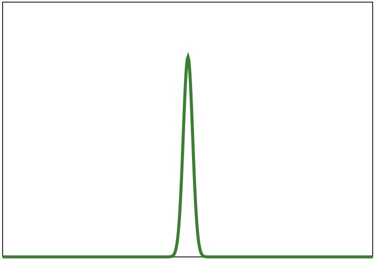

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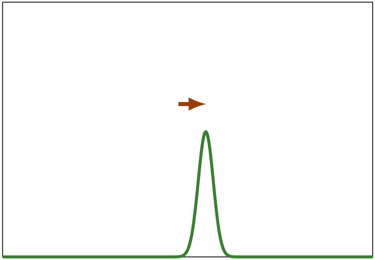

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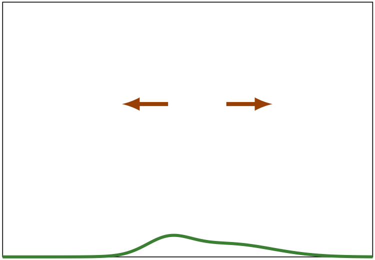

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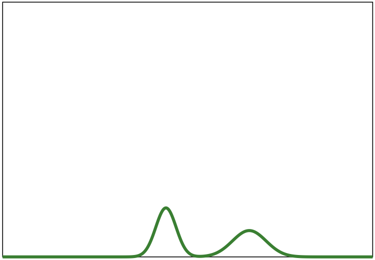

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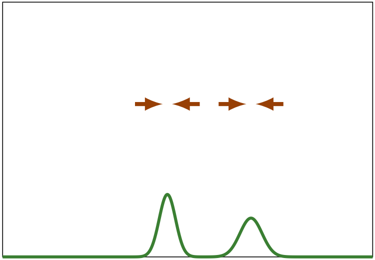

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Population level

$$\frac{\partial n(z,t)}{\partial t} = \ r(z, E(t))n(z,t) \ + \text{mutation}$$

where $E(t)$ is the **environmental feedback**, which captures density-dependence, resource densities, host densities, etc.
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where $E(t)$ is the **environmental feedback**, which captures density-dependence, resource densities, host densities, etc.
(so we may need to couple this equation to other dynamical equations)

Small morph variance approximation

Assume that morph distributions are tightly clustered around their mean

$$\xi_i := z - \bar{z}_i = O(\varepsilon)$$

Taylor-expansion of the vital rates around the morph means:

$$r(z, E(t)) = r(\bar{z}_i) + \xi_i \left.\frac{\partial r}{\partial z}\right|_{z=\bar{z}_i} + \frac{1}{2}(\xi_i)^2 \left.\frac{\partial^2 r}{\partial z^2}\right|_{z=\bar{z}_i} + O(\varepsilon^3)$$

This can be used to derive equations for the dynamics of

- the total density $n(t)$,
- the morph frequencies $f_i(t)$,
- the morph means $\bar{z}_i(t)$,
- the morph variances $V_i(t)$.

Eco-evolutionary dynamics: oligomorphic approximation

$$\frac{\mathrm{d}n}{\mathrm{d}t} = \left(\sum_i r(\bar{z}_i) f_i \right) n + O(\varepsilon)$$

$$\frac{\mathrm{d}f_i}{\mathrm{d}t} = \left(r(\bar{z}_i) - \sum_\ell f_\ell r(\bar{z}_\ell) \right) f_i + O(\varepsilon)$$

$$\frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t} = V_i \left. \frac{\partial r}{\partial z} \right|_{z=\bar{z}_i} + O(\varepsilon^3)$$

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = (V_i)^2 \left. \frac{\partial^2 r}{\partial z^2} \right|_{z=\bar{z}_i} + O(\varepsilon^5)$$

Eco-evolutionary dynamics: oligomorphic approximation

$$\textbf{Fast}\left\{\begin{aligned}\frac{\mathrm{d}n}{\mathrm{d}t} &= \left(\sum_i r(\bar{z}_i) f_i\right) n + O(\varepsilon)\\ \frac{\mathrm{d}f_i}{\mathrm{d}t} &= \left(r(\bar{z}_i) - \sum_\ell f_\ell r(\bar{z}_\ell)\right) f_i + O(\varepsilon)\end{aligned}\right.$$

$$\textbf{Slow}\left\{\begin{aligned}\frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t} &= V_i \left.\frac{\partial r}{\partial z}\right|_{z=\bar{z}_i} + O(\varepsilon^3)\\ \frac{\mathrm{d}V_i}{\mathrm{d}t} &= (V_i)^2 \left.\frac{\partial^2 r}{\partial z^2}\right|_{z=\bar{z}_i} + O(\varepsilon^5)\end{aligned}\right.$$

Separation of time scales

- n and f_i are **fast** variables ($O(1)$ dynamics)
- $\bar{z}_i$ and V_i are **slow** variables ($O(\varepsilon^2)$ and $O(\varepsilon^4)$ dynamics)

Coupling fast and slow evolution

Dynamics of population-level mean trait $\bar{z}$

$$\bar{z} = \sum_i f_i \bar{z}_i$$

Coupling fast and slow evolution

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We have

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = \sum_i \bar{z}_i \frac{\mathrm{d}f_i}{\mathrm{d}t} + \sum_i f_i \frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t}$$

Changes in peak heights

Changes in peak positions

Coupling fast and slow evolution

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Changes in peak heights

Changes in peak positions

With 2 morphs (a wild-type and a mutant), we obtain

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = (\bar{z}_m - \bar{z}_w) f_m (1 - f_m) \Delta r$$

$$+ \sum_i f_i V_i \left. \frac{\partial r}{\partial z} \right|_{\bar{z}_i}$$

where $\Delta r = r(\bar{z}_m) - r(\bar{z}_w)$.

Coupling fast and slow evolution

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = (\bar{z}_m - \bar{z}_w) f_m (1 - f_m) \Delta r$$

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Coupling fast and slow evolution

$$\frac{\mathrm{d}\bar{z}}{\mathrm{d}t} = (\bar{z}_m - \bar{z}_w) f_m (1 - f_m) \Delta r$$

- If the 2 morphs are very different (strong selection), the first line dominates
  $\Rightarrow$ Fast evolution, as in population genetics, scaled by variance $f_m(1-f_m)$ and driven by Δr

Coupling fast and slow evolution

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- If the 2 morphs are similar (weak selection, $\bar{z}_m \approx \bar{z}_w$), the second line dominates
  $\Rightarrow$ Slow evolution, as in AD, QG, scaled by morph variances V_i and driven by selection gradients $\partial r/\partial z$.

Coupling fast and slow evolution

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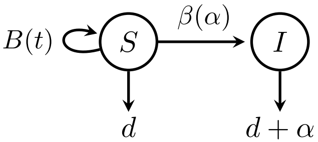
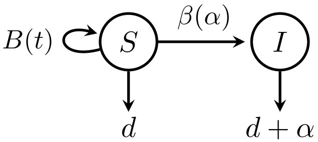
Application: evolution of pathogen virulence



$$r(\alpha) = \beta(\alpha)S(t) - (d+\alpha)$$

Application: evolution of pathogen virulence



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- Trade-off between transmission and virulence

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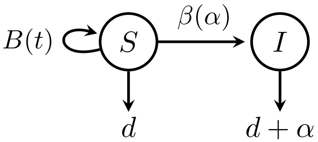

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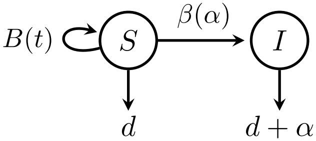

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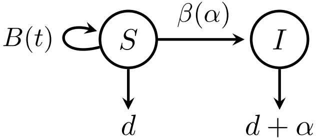

$$r(\alpha) = \beta(\alpha)S(t) - (d+\alpha)$$

- Trade-off between transmission and virulence
- We start with a high density of susceptible hosts ...
- ... a low density of infected hosts (epidemic phase) ...
- ... and different distributions of virulence.

Dynamics of mean virulence

$$\frac{\mathrm{d}I}{\mathrm{d}t} = \left[\bar{\beta}S(t) - (d + \bar{\alpha})\right] I$$

$$\frac{\mathrm{d}\bar{\alpha}}{\mathrm{d}t} = (\bar{\alpha}_m - \bar{\alpha}_w) f_m (1 - f_m) \left[\Delta\beta S(t) - \Delta\alpha\right]$$

$$+ f_m V_m \left[\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|_{\bar{\alpha}_m} S(t) - 1 \right] + (1 - f_m) V_w \left[\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|_{\bar{\alpha}_w} S(t) - 1 \right]$$

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Two limit cases

1. **Small morph variances** $(V_m, V_w \to 0)$
   $\Rightarrow$ Selection favours morph with largest growth rate $(\Delta r > 0)$

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   ⇒ Slow evolution of $\bar{\alpha}_w$ in the direction given by

$$\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|_{\bar{\alpha}_w} S(t) > 1 \qquad \text{with} \quad S(t) \approx \frac{d + \bar{\alpha}_w(t)}{\beta(\bar{\alpha}_w(t))}$$

Dynamics of mean virulence

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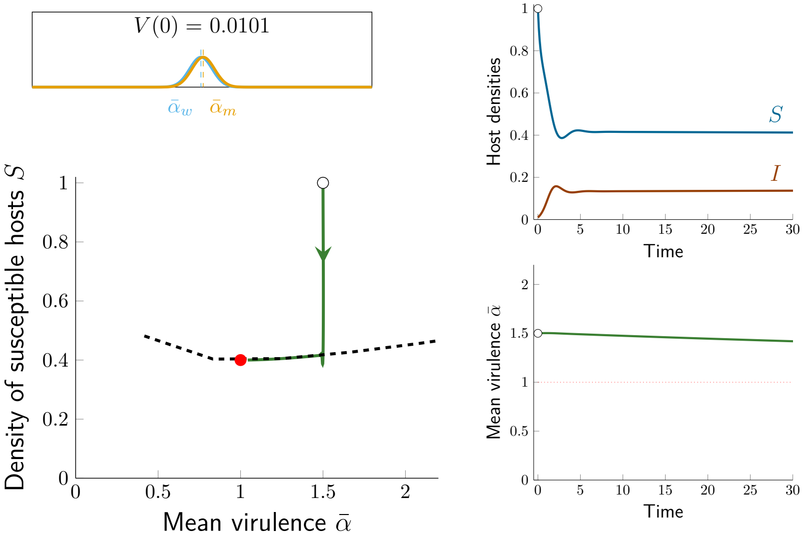
Evolutionary endpoint: $\left.\frac{\mathrm{d}\beta}{\mathrm{d}\alpha}\right|_{\bar{\alpha}_w} = \frac{\beta(\bar{\alpha}_w)}{d + \bar{\alpha}_w}$ (Max. R_0)

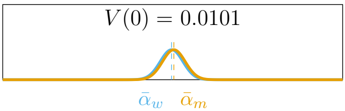
An illustration: evolution of pathogen virulence

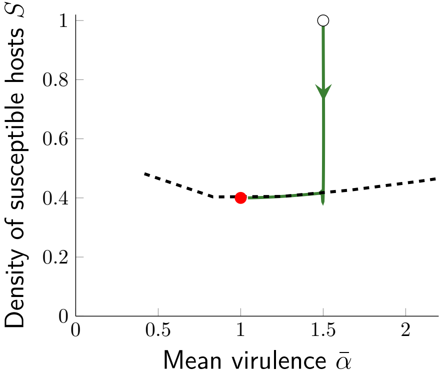


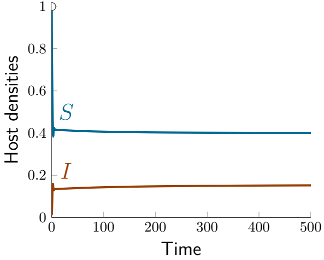
Small variance

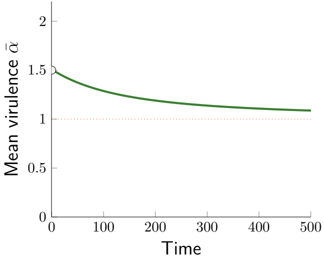
Short time-scale

An illustration: evolution of pathogen virulence





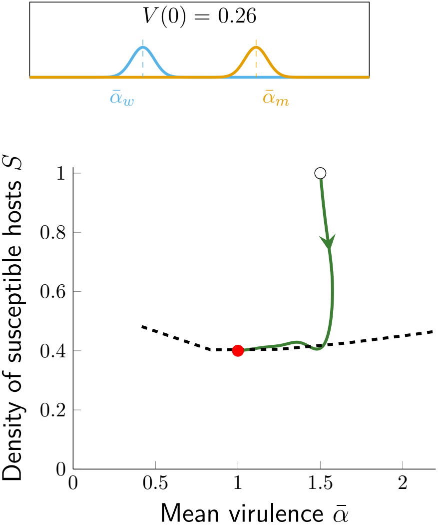




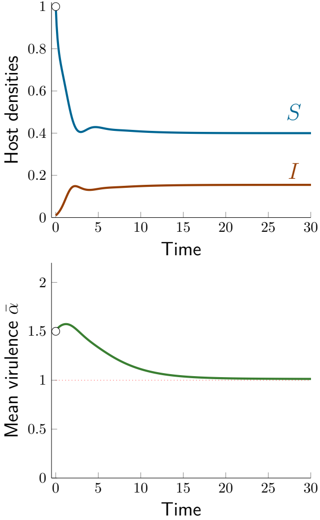
Small variance

Long time-scale

An illustration: evolution of pathogen virulence

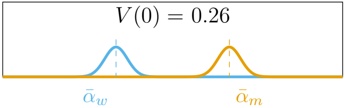


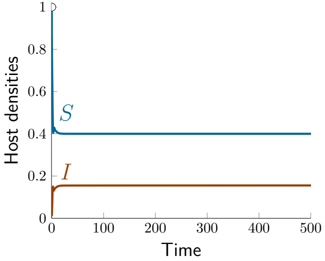
Intermediate variance

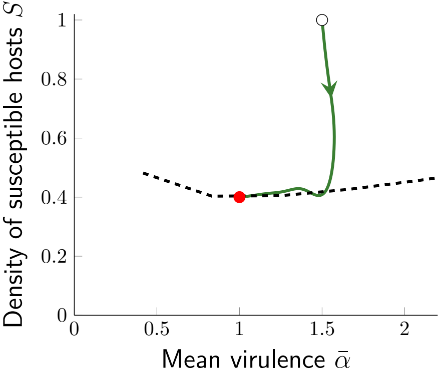


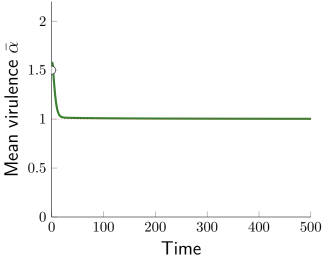
Short time-scale

An illustration: evolution of pathogen virulence





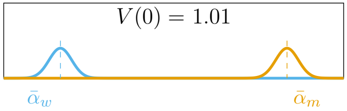


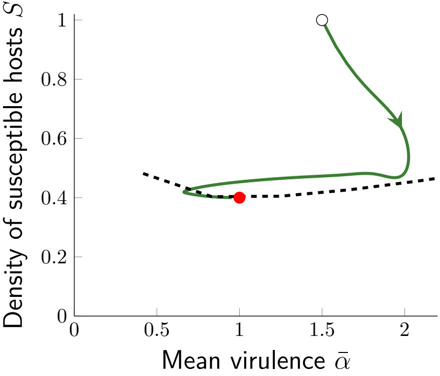


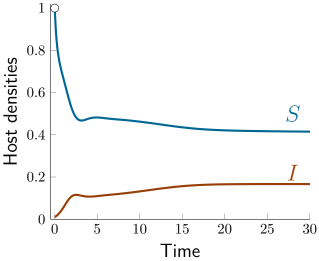
Intermediate variance

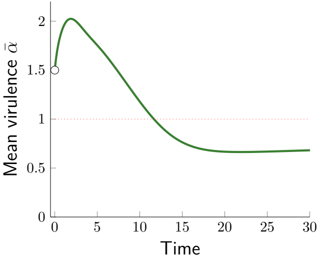
Long time-scale

An illustration: evolution of pathogen virulence





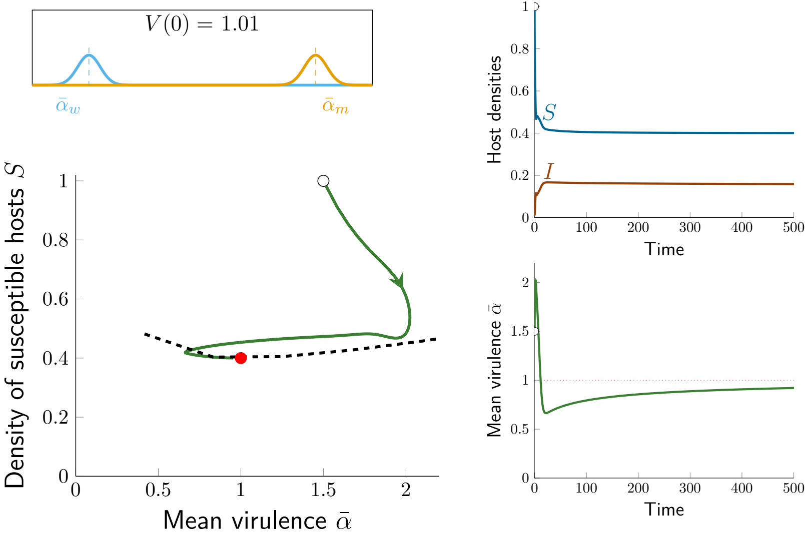




Large variance

Short time-scale

An illustration: evolution of pathogen virulence



Large variance

Long time-scale

Part 4 – What about population structure?

Suppose we now have K classes of individuals.

Densities

$n^k(z,t)$	Density of individuals with trait z in class k at time t
$n^k(t)$	Total density of individuals in class k at time t $n^k(t) = \int n^k(z,t)\mathrm{d}z$
$n(t)$	Total density of individuals at time t, $n(t) = \sum_k n^k(t)$

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$n(t)$ Total density of individuals at time t,
$n(t) = \sum_k n^k(t)$

Distributions

- Class distribution (ecology)

$$f^k(t) = \frac{n^k(t)}{n(t)}$$

- Trait distributions (evolution)

$$\phi^k(z,t) = \frac{n^k(z,t)}{n^k(t)}$$

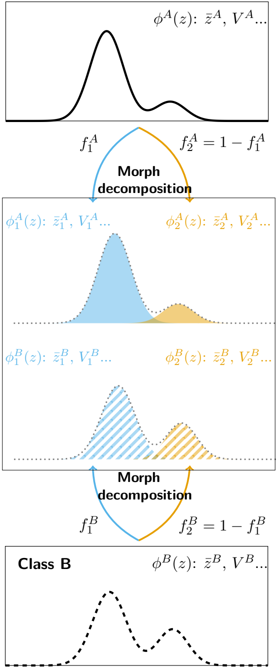
$$\phi(z,t) = \frac{n(z,t)}{n(t)} = \sum_k \phi^k(z,t) f^k(t)$$

Multi-morph decomposition

$$\phi^k(z,t) = \sum_i \phi_i^k(z,t) f_i^k(z,t)$$

where

- $\phi_i^k(z,t)$ is the trait distribution of morph i in class k at time t
- $f_i^k(t)$ is the frequency of morph i in class k


$\phi^A(z)$: $\bar{z}^A$, V^A...
f_1^A
$f_2^A = 1 - f_1^A$
Morph decomposition
$\phi_1^A(z)$: $\bar{z}_1^A$, V_1^A...
$\phi_2^A(z)$: $\bar{z}_2^A$, V_2^A...
$\phi_1^B(z)$: $\bar{z}_1^B$, V_1^B...
$\phi_2^B(z)$: $\bar{z}_2^B$, V_2^B...
Morph decomposition
f_1^B
$f_2^B = 1 - f_1^B$
Class B
$\phi^B(z)$: $\bar{z}^B$, V^B...

Dynamics

Vital rates

We now need to know the transition rates $r^{jk}(z, E(t))$ from class k to class j for individuals with trait z.
These can be collected in a matrix $\mathbf{R}(z)$.

Dynamics

Vital rates

We now need to know the transition rates $r^{jk}(z, E(t))$ from class k to class j for individuals with trait z.
These can be collected in a matrix $\mathbf{R}(z)$.

Small morph variance approximation

Assume that morph distributions are clustered around their means

$$\xi_i^k := z - \bar{z}_i^k = O(\varepsilon)$$

Taylor-expansion of the vital rates:

$$r^{jk}(z, E(t)) = r(\bar{z}_i^k) + \xi_i^k \left. \frac{\partial r}{\partial z} \right|_{z=\bar{z}_i^k} + \frac{1}{2}(\xi_i^k)^2 \left. \frac{\partial^2 r}{\partial z^2} \right|_{z=\bar{z}_i^k} + O(\varepsilon^3)$$

This can be used to derive equations for the dynamics of the total densities $n^k(t)$, morph frequencies $f_i^k(t)$, morph means $\bar{z}_i^k(t)$ and morph variances $V_i^k(t)$.

Dynamics of ecological variables

The densities $n^k(t)$ have the following dynamics

$$\frac{\mathrm{d}\mathbf{n}}{\mathrm{d}t} = \overline{\mathbf{R}}\mathbf{n}$$

where $\overline{\mathbf{R}}$ is the matrix of average vital rates $\bar{r}^{jk}$

$$\bar{r}^{jk} = \sum_i f_i^k r^{jk}(\bar{z}_i^k) + O(\varepsilon^2)$$

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Dynamics of morph frequencies

$$\frac{\mathrm{d}f_i^k}{\mathrm{d}t} = \sum_j \frac{f^j}{f^k} \left(r^{kj}(\bar{z}_i^j) f_i^j - f_i^k \sum_\ell f_\ell^j r^{kj}(\bar{z}_\ell^j) \right) + O(\varepsilon^2)$$

(Class-structured version of the replicator equation)

Morph-specific frequencies: different definitions

It is also useful to introduce the global frequency of morph i

$$f_i = \sum_k f_i^k f^k$$

and the morph frequencies

$$u_i^k = \frac{f_i^k f^k}{f_i}$$

Note the difference:

f_i^k fraction of **morph**-i individuals among all **class**-k individuals

u_i^k fraction of **class**-k individuals among all **morph**-i individuals

Classes: quantity vs. quality

The u morph frequencies have the following dynamics

$$\frac{\mathrm{d}\mathbf{u}_i}{\mathrm{d}t} = \overline{\mathbf{R}}_i \mathbf{u}_i - \bar{r}_i \mathbf{u}_i$$

where

- $\overline{\mathbf{R}}_i$ is the matrix of morph-specific average rates $\bar{r}_i^{jk}$
- $\bar{r}_i = \mathbf{1}^\top \overline{\mathbf{R}}_i \mathbf{u}_i$ is the average growth rate of morph i.

$\Rightarrow$ Measure of class **“quantity”** for a focal morph.

Classes: quantity vs. quality (2)

The following adjoint equation gives the dynamics of the vector of individual reproductive values for morph i

$$\frac{\mathrm{d}\mathbf{v}_i}{\mathrm{d}t} = -\overline{\mathbf{R}}_i \mathbf{v}_i + \bar{r}_i \mathbf{v}_i$$

$\Rightarrow$ Measure of class **“quality”** for a focal morph.

Classes: quantity vs. quality (2)

The following adjoint equation gives the dynamics of the vector of individual reproductive values for morph i

$$\frac{\mathrm{d}\mathbf{v}_i}{\mathrm{d}t} = -\overline{\mathbf{R}}_i \mathbf{v}_i + \bar{r}_i \mathbf{v}_i$$

$\Rightarrow$ Measure of class **“quality”** for a focal morph.

We’ll see that we can use the reproductive values to obtain a lower-dimensional approximation of the dynamics.

Dynamics of morph means and variances

Morph means

$$\frac{\mathrm{d}\bar{z}_i^k}{\mathrm{d}t} = \sum_j \frac{u_i^j}{u_i^k} \left[(\bar{z}_i^j - \bar{z}_i^k) r^{kj}(\bar{z}_i^j) \; + \; V_i^j \left. \frac{\partial r^{kj}}{\partial z} \right|_{z=\bar{z}_i^j} \right] + O(\varepsilon^4)$$

Dynamics of morph means and variances

Morph means

$$\frac{\mathrm{d}\bar{z}_i^k}{\mathrm{d}t} = \sum_j \frac{u_i^j}{u_i^k}\left[(\bar{z}_i^j - \bar{z}_i^k) r^{kj}(\bar{z}_i^j) + V_i^j \left.\frac{\partial r^{kj}}{\partial z}\right|_{z=\bar{z}_i^j} \right] + O(\varepsilon^4)$$

Dynamics of morph means and variances

Morph means

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Morph variances

$$\begin{aligned}\frac{\mathrm{d}V_i^k}{\mathrm{d}t} = \sum_j \frac{u_i^j}{u_i^k} \Bigg[& (V_i^j - V_i^k + (\bar{z}_i^j - \bar{z}_i^k)^2) r^{kj}(\bar{z}_i^j) \\ & + 2(\bar{z}_i^j - \bar{z}_i^k) V_i^j \left.\frac{\partial r^{kj}}{\partial z}\right|_{z=\bar{z}_i^j} \\ & + \frac{1}{2}\left(3(V_i^j)^2 + (\bar{z}_i^j - \bar{z}_i^k)^2 V_i^j - V_i^j V_i^k\right) \left.\frac{\partial^2 r^{kj}}{\partial z^2}\right|_{z=\bar{z}_i^j} \Bigg] + O(\varepsilon^5)\end{aligned}$$

Dynamics of morph means and variances

Morph means

$$\frac{\mathrm{d}\bar{z}_i^k}{\mathrm{d}t} = \sum_j \frac{u_i^j}{u_i^k} \left[(\bar{z}_i^j - \bar{z}_i^k) r^{kj}(\bar{z}_i^j) + V_i^j \left. \frac{\partial r^{kj}}{\partial z} \right|_{z=\bar{z}_i^j} \right] + O(\varepsilon^4)$$

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$$\begin{aligned}\frac{\mathrm{d}V_i^k}{\mathrm{d}t} = \sum_j \frac{u_i^j}{u_i^k} \Bigg[& (V_i^j - V_i^k + (\bar{z}_i^j - \bar{z}_i^k)^2) r^{kj}(\bar{z}_i^j) \\ & + 2(\bar{z}_i^j - \bar{z}_i^k) V_i^j \left. \frac{\partial r^{kj}}{\partial z} \right|_{z=\bar{z}_i^j} \\ & + \frac{1}{2} \left(3(V_i^j)^2 + (\bar{z}_i^j - \bar{z}_i^k)^2 V_i^j - V_i^j V_i^k \right) \left. \frac{\partial^2 r^{kj}}{\partial z^2} \right|_{z=\bar{z}_i^j} \Bigg] + O(\varepsilon^5)\end{aligned}$$

The full dynamics

$$
\begin{aligned}
\frac{\mathrm{d}n^k}{\mathrm{d}t} &= \sum_j \sum_i r^{kj}(\bar{z}_i^j) f_i^j n^j \\
\frac{\mathrm{d}f_i^k}{\mathrm{d}t} &= \sum_j \frac{f^j}{f^k} \left(r^{kj}(\bar{z}_i^j) f_i^j - f_i^k \sum_\ell f_\ell^j r^{kj}(\bar{z}_\ell^j) \right) \\
\frac{\mathrm{d}\bar{z}_i^k}{\mathrm{d}t} &= \sum_j \frac{u_i^j}{u_i^k} \left[(\bar{z}_i^j - \bar{z}_i^k) r^{kj}(\bar{z}_i^j) + V_i^j \left. \frac{\partial r^{kj}}{\partial z} \right|_{z=\bar{z}_i^j} \right] \\
\frac{\mathrm{d}V_i^k}{\mathrm{d}t} &= \sum_j \frac{u_i^j}{u_i^k} \Bigg[(V_i^j - V_i^k + (\bar{z}_i^j - \bar{z}_i^k)^2) r^{kj}(\bar{z}_i^j) \\
&\qquad\qquad + 2(\bar{z}_i^j - \bar{z}_i^k) V_i^j \left. \frac{\partial r^{kj}}{\partial z} \right|_{z=\bar{z}_i^j} \\
&\qquad\qquad + \frac{1}{2} \left(3(V_i^j)^2 + (\bar{z}_i^j - \bar{z}_i^k)^2 V_i^j - V_i^j V_i^k \right) \left. \frac{\partial^2 r^{kj}}{\partial z^2} \right|_{z=\bar{z}_i^j} \Bigg]
\end{aligned}
$$

Projection on RV space

To reduce the dimension of the system, we attempt to aggregate the dynamics at the morph level.

RV-weighted distribution

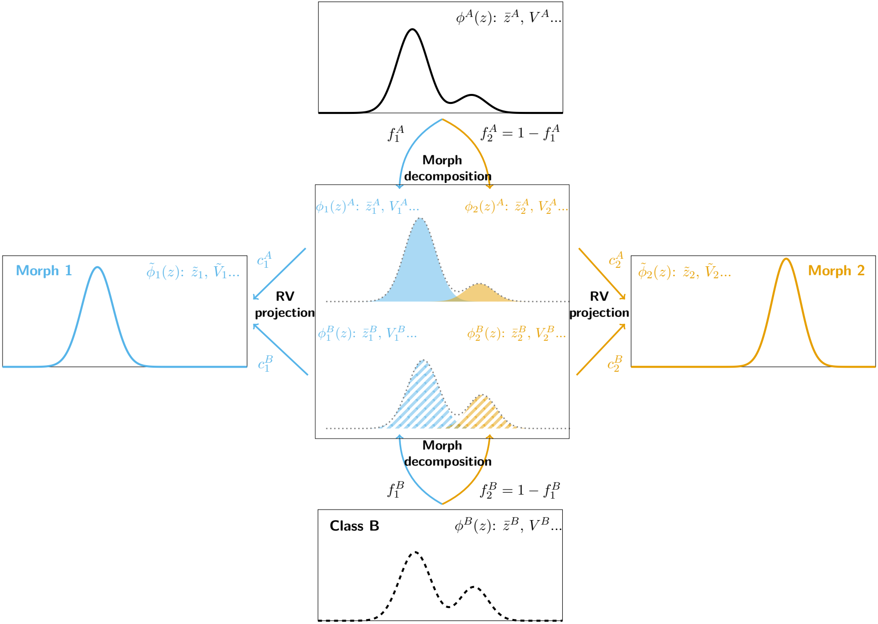
We use the following weighted distribution:

$$\widetilde{\phi}_i(z,t) = \sum_k c_i^k(t)\phi_i^k(z,t)$$

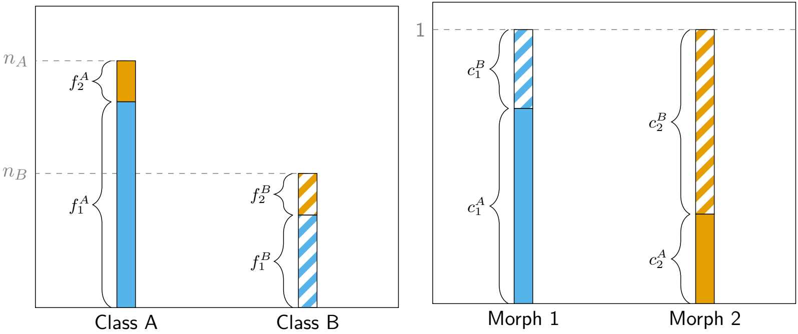
and we derive the dynamics of the moments of this distribution.

The weights are the *class* reproductive values:

$$c_i^k(t) = v_i^k(t)u_i^k(t)$$


$\phi^A(z)$: $\bar{z}^A$, V^A...
f_1^A
$f_2^A = 1 - f_1^A$
Morph decomposition
$\phi_1(z)^A$: $\bar{z}_1^A$, V_1^A...
$\phi_2(z)^A$: $\bar{z}_2^A$, V_2^A...
c_1^A
c_2^A
Morph 1
$\tilde{\phi}_1(z)$: $\tilde{z}_1$, $\tilde{V}_1$...
RV projection
RV projection
$\tilde{\phi}_2(z)$: $\tilde{z}_2$, $\tilde{V}_2$...
Morph 2
$\phi_1^B(z)$: $\bar{z}_1^B$, V_1^B...
$\phi_2^B(z)$: $\bar{z}_2^B$, V_2^B...
c_1^B
c_2^B
Morph decomposition
f_1^B
$f_2^B = 1 - f_1^B$
Class B
$\phi^B(z)$: $\bar{z}^B$, V^B...

A quick illustration



Morph 1 is relatively more abundant within class B ($f_1^B > f_2^B$) but has a lower class reproductive value ($c_1^B < c_2^B$).

Separation of time scales

For small morph variances:

- Fast variables: $n(t)$, $f_i^k(t)$, $u_i^k(t)$, $v_i^k(t)$
- Slow variables: $\widetilde{z}_i(t)$, $\widetilde{V}_i(t)$

Projection on RV space

Fast variables

$$\frac{\mathrm{d}n^k}{\mathrm{d}t} = \sum_j \sum_i r^{kj}(\widetilde{z}_i) f_i^j n^j$$

$$\frac{\mathrm{d}f_i^k}{\mathrm{d}t} = \sum_j \frac{f^j}{f^k} \left(r^{kj}(\widetilde{z}_i) f_i^j - f_i^k \sum_\ell f_\ell^j r^{kj}(\widetilde{z}_\ell) \right)$$

Projection on RV space

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QE approximation

$$\mathbf{0} = \mathbf{R}(\widetilde{z}_i)\mathbf{u}_i = \mathbf{v}_i^\top \mathbf{R}(\widetilde{z}_i)$$

Projection on RV space

Fast variables

$$\frac{\mathrm{d}n^k}{\mathrm{d}t} = \sum_j \sum_i r^{kj}(\widetilde{z}_i) f_i^j n^j$$

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QE approximation

$$\mathbf{0} = \mathbf{R}(\widetilde{z}_i)\mathbf{u}_i = \mathbf{v}_i^\top \mathbf{R}(\widetilde{z}_i)$$

Slow variables

$$\frac{\mathrm{d}\widetilde{z}_i}{\mathrm{d}t} = \widetilde{V}_i \; \mathbf{v}_i^\top \mathbf{S}_i \mathbf{u}_i$$

$$\frac{\mathrm{d}\widetilde{V}_i}{\mathrm{d}t} = 2 \left(\widetilde{V}_i\right)^2 \; \left[\mathbf{v}_i^\top \mathbf{F}_i \mathbf{u}_i + \mathbf{v}_i^\top \mathbf{S}_i (\mathbf{d}_i \circ \mathbf{u}_i) \right]$$

where

$$\mathbf{S}_i = \left.\frac{\partial \mathbf{R}}{\partial z}\right|_{z=\widetilde{z}_i}, \qquad \mathbf{F}_i = \frac{1}{2} \left.\frac{\partial^2 \mathbf{R}}{\partial z^2}\right|_{z=\widetilde{z}_i} \qquad d_i^k = \bar{z}_i^k - \widetilde{z}_i$$

$$\frac{\mathrm{d}\widetilde{z}_i}{\mathrm{d}t} = \widetilde{V}_i \, \mathbf{v}_i^\top \, \left.\frac{\partial \mathbf{R}}{\partial z}\right|_{z=\widetilde{z}_i} \mathbf{u}_i$$

$$\frac{\mathrm{d}\widetilde{V}_i}{\mathrm{d}t} = 2\left(\widetilde{V}_i\right)^2 \, \left[\mathbf{v}_i^\top \, \left.\frac{\partial^2 \mathbf{R}}{\partial z^2}\right|_{z=\widetilde{z}_i} \mathbf{u}_i + \mathbf{v}_i^\top \, \left.\frac{\partial \mathbf{R}}{\partial z}\right|_{z=\widetilde{z}_i} (\mathbf{d}_i \circ \mathbf{u}_i)\right]$$

Application: two-habitat migration-selection models

With two habitats A and B coupled by migration, we have

$$\begin{aligned} r^{AA}(z) &= \rho_A(z) - m_{BA}\,, \\ r^{AB}(z) &= m_{AB}\,, \\ r^{BA}(z) &= m_{BA}\,, \\ r^{BB}(z) &= \rho_B(z) - m_{AB}\,. \end{aligned}$$

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We then have

$$\begin{aligned} \frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t} &= V_i \left[c_i^A \rho'_A(\bar{z}_i) + c_i^B \rho'_B(\bar{z}_i) \right] \\ \frac{\mathrm{d}V_i}{\mathrm{d}t} &= (V_i)^2 \left[c_i^A \rho''_A(\bar{z}_i) + c_i^B \rho''_B(\bar{z}_i) + 2 \frac{\left(c_i^A c_i^B \right)^{3/2}}{\sqrt{m_{AB} m_{BA}}} \left(\rho'_B(\bar{z}_i) - \rho'_A(\bar{z}_i) \right)^2 \right] \end{aligned}$$

where $c_i^A = 1 - c_i^B$ is the class reproductive value of class A for morph i

Example: quadratic fitness functions

$$\rho_k(z) = b - g(z - \theta_k)^2$$

Débarre et al 2013; Meszéna et al 1997;
Mirrahimi & Gandon 2020

$$\begin{aligned}\frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t} &= -2gV_i\left[\bar{z}_i - c_i^A\theta_A - c_i^B\theta_B\right]\\ \frac{\mathrm{d}V_i}{\mathrm{d}t} &= -2gV_i^2\left[1 - \frac{4g}{m}(c_i^A c_i^B)^{3/2}\left(\theta_B - \theta_A\right)^2\right]\end{aligned}$$

where $m = \sqrt{m_{AB}m_{BA}}$

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Implications

1. The morph means stabilise when

$$\bar{z}_i = c_i^A\theta_A + c_i^B\theta_B.$$

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where $m = \sqrt{m_{AB}m_{BA}}$

Implications

1. The morph means stabilise when

$$\bar{z}_i = c_i^A\theta_A + c_i^B\theta_B.$$

2. Selection on morph i is stabilising if

$$4c_i^A c_i^B < \left(\frac{2m}{g}\right)^{2/3}$$

Explicit solutions

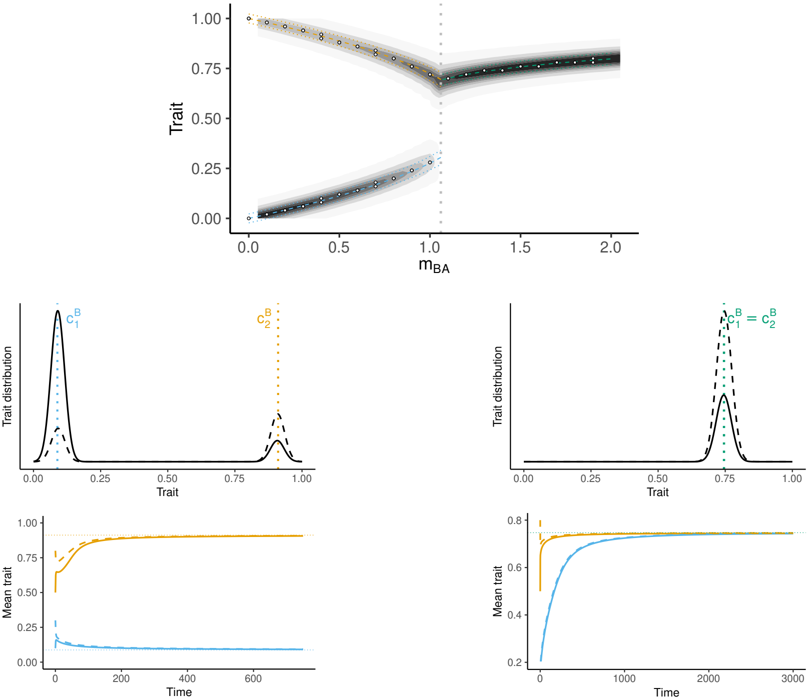
Using the QE relationship for $c_i^B = 1 - c_i^A$:

$$c_i^B = v_i^B u_i^B = \frac{m_{AB}(u_i^B)^2}{m_{BA}(u_i^A)^2 + m_{AB}(u_i^B)^2} = 1 - c_i^A$$

we can calculate the RVs and obtain the equilibrium positions of the two peaks of the bimodal distribution:

$$\bar{z}_1^* = \frac{1}{2} - \frac{1}{2}\sqrt{1 - \frac{4m_{AB}m_{BA}}{g^2}} = 1 - \bar{z}_2^*$$

as previously found (Débarre et al 2013; Mirrahimi & Gandon 2020).


Trait
1.00
0.75
0.50
0.25
0.00
0.0
0.5
1.0
1.5
2.0
m_{BA}
Trait distribution
c_1^B
c_2^B
0.00
0.25
0.50
0.75
1.00
Trait
Trait distribution
$c_1^B = c_2^B$
0.00
0.25
0.50
0.75
1.00
Trait
Mean trait
1.00
0.75
0.50
0.25
0.00
0
200
400
600
Time
Mean trait
0.8
0.6
0.4
0.2
0
1000
2000
3000
Time

Mutation-selection-migration balance

If mutation is unbiased, we obtain

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = -2gV_i^2\left[1 - \frac{4g}{m}(c_i^A c_i^B)^{3/2}\,(\theta_B - \theta_A)^2\right] + c_i^A V_M^A + c_i^B V_M^B$$

where V_M^k is the mutational variance in habitat k.

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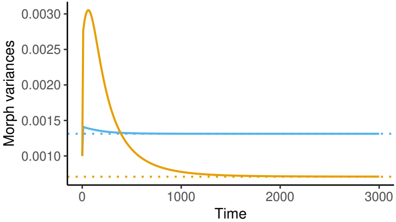
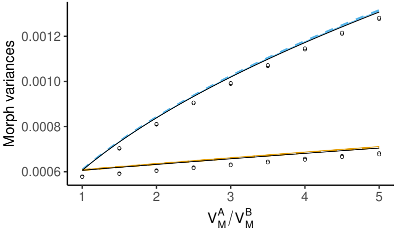


The equilibrium morph variances are

$$V_i^* = \sqrt{\frac{c_i^A V_M^A + c_i^B V_M^B}{2g\left[1 - \frac{4g}{m}(c_i^A c_i^B)^{3/2}\right]}}$$



Extension to competition models

$$\rho_A(z) = b - g(z-\theta_A)^2 - n^A \int a(z-y)\phi^A(y)\mathrm{d}y$$

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Dynamics of morph means:

$$\frac{\mathrm{d}\bar{z}_i}{\mathrm{d}t} = V_i \left[-2g(\bar{z}_i - (c_i^A\theta_A + c_i^B\theta_B)) - \sum_j e_j a'(\bar{z}_j - \bar{z}_i) \right]$$

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Take-home messages for Parts 3 and 4

- This method can be used to analyse the interplay of ecological and evolutionary dynamics
  - over different time scales (e.g. weak vs strong selection)
  - in class-structured populations
- This approach bridges the gap between Adaptive dynamics and Quantitative genetics:
  - non-normal trait distributions
  - ecological feedbacks and disruptive selection
  - non-zero standing variation
  - mutation-selection balance (to some extent)
- Reproductive values provide a useful tool to simplify the dynamics of polymorphic and structured populations.

References for Parts 3 and 4

- Sasaki & Dieckmann (2011) *J. Math. Biol.*
  Oligomorphic dynamics for analyzing the quantitative genetics of adaptive speciation
- Lion, Boots & Sasaki (in press) *American Naturalist*
  Multi-morph eco-evolutionary dynamics in structured populations.

... and references therein

General take-home messages for this course

- A major objective of evolutionary ecology is to understand the **interplay between ecological and evolutionary dynamics over different time scales**.
- I have tried to show how **reproductive value** can be seen as a **unifying concept** when analysing structured population models.
- For **biologists**, reproductive value has a straightforward interpretation as the **quality** of a focal class of individuals.
- For **mathematicians**, reproductive value weighting provides a useful way to **simplify the dynamics of the moments** of the trait distribution.
- It would be interesting to see how this connects with mathematically rigorous formalisations, such as those using Hamilton-Jacobi equations.