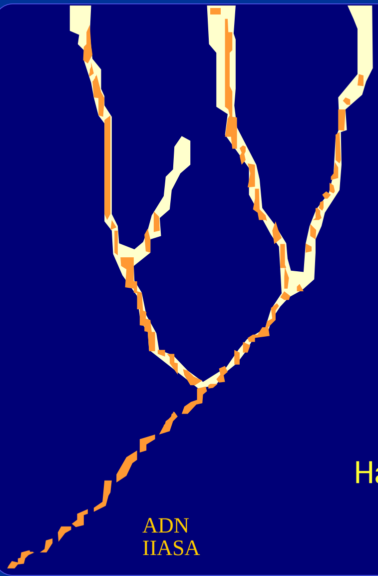

How should we define fitness for general ecological scenarios?

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Preliminary epistemological musings I:

Potential requirements to be fulfilled by a definition:

* correct prediction of time course of single gene substitutions
[for applications to short term evolution, as studied by population geneticists]

* good basis for general adaptive dynamics considerations
[for applications to long term evolution, as studied by evolutionary ecologists (statics) & paleontologists (dynamics)]

If more follows, we are in luck, if not: such is life.

We will have to make compromises!

Candidates

* initial per capita growth rate of rare allele

* probability of invasion by new mutant

[Luckily the two turn out to be connected]

Preliminary epistemological musings II:

Fitness is by necessity a theoretical construct

out in the field there are only organisms that
reproduce their kind almost faithfully and die

Intervening abstractions are necessary:

requires assumptions (to be seen as modelling approximations)

The essential modelling approximations (usually left implicit):

* environments are locally well mixed
  (NB the term environment needs a special definition)
* system sizes are large, but not infinite
* mutations are rare

} evolution behaves fairly deterministically

Fitness is but a very abstracted bookkeeping parameter

NB: all the usual life-history parameters are bookkeeping parameters only

Defining fitness
means considering a relation between bookkeeping parameters

Preliminary epistemological musings III:

Corollary:

It is not possible to measure fitness indirectly
i.e., other than by its effects: gene substitutions.

What one measures then are only components of fitness
i.e., lower order abstractions such as fecundity.

Resulting practical question:

What are the right components in particular instances?

The theory should provide guidelines,
but ultimately the responsibility lies with the field biologist.

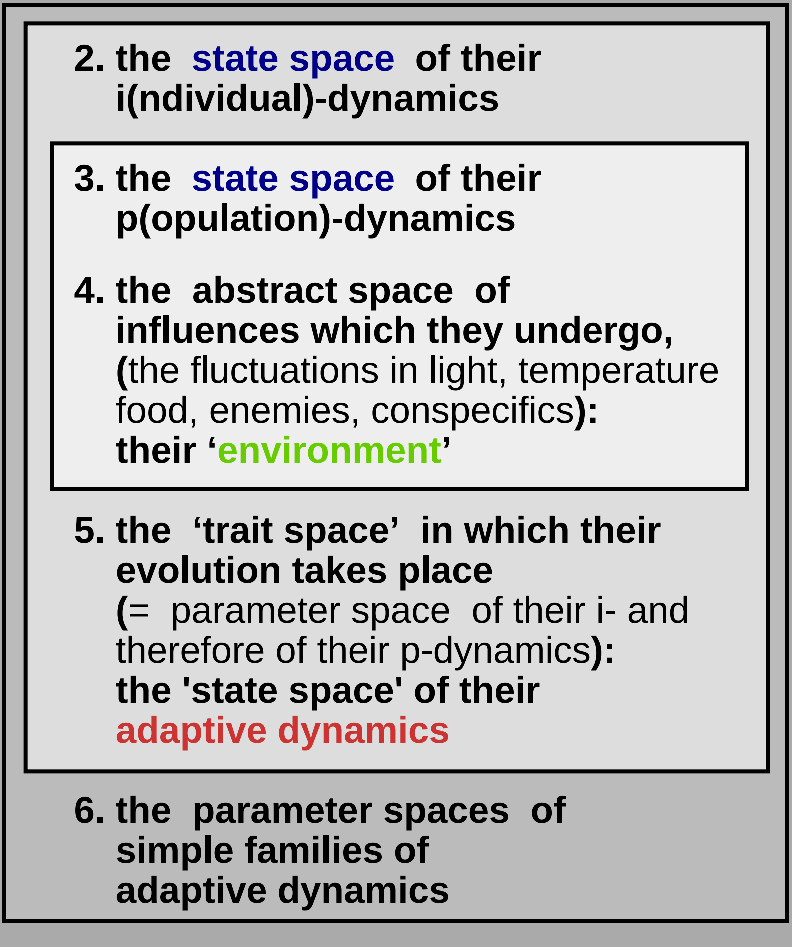
A final point:

The evolutionary fate of more concrete traits of organisms,
e.g., energy intake per unit of time,
or, form of a bone.
is determined by how they map to life history parameters,
and through these, to fitness.

Levels of Abstraction

**illustrated by the spaces that play
a role in adaptive dynamics theory:**

1. the physical space in which the organisms live



2. the state space of their i(ndividual)-dynamics

3. the state space of their p(opulation)-dynamics

4. the abstract space of influences which they undergo,
(the fluctuations in light, temperature food, enemies, conspecifics**):**
their 'environment'

5. the 'trait space' in which their evolution takes place
(= parameter space of their i- and therefore of their p-dynamics**):**
the 'state space' of their adaptive dynamics

6. the parameter spaces of simple families of adaptive dynamics

Under fairly general conditions* we can use the

(vector composed of the) spatial densities
of individuals in the various possible

i(ndividual)-states

as the

p(opulation)-state

in an approximating deterministic population model

(This is the standard assumption underlying most published population models.)

---

*
- local mass action (locally the population output can be approximated by adding the contributions of the individuals in the neighbourhood),
- the numbers of individuals in each neighbourhood over which the environment stays approximately constant are sufficiently large

---

Example:

In discrete time for a finite i-state space and a finite number of well-mixed patches:

$$\mathbf{N}(t+1) = \mathbf{A}(\mathbf{E}(t))\mathbf{N}(t),$$

e.g. together with

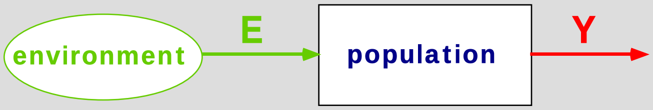
$$\mathbf{E}(t) = \mathbf{H}\mathbf{N}(t),$$

$\mathbf{N}$ a m-vector, $\mathbf{E}$ a k-vector, and $\mathbf{A}$ and $\mathbf{H}$ m×m and k×m matrices respectively.

NB. (course of the) environment: E
condition of the environment: E(t)

The conditional linearity principle

For a given course of the environment
the dynamics of the p-state is linear



NB. (course of the) environment: E
condition of the environment: E(t)

Multiplicative ergodic theorem

Assume for the time being that the environment

(i) is given (e.g. imposed by some experimenter)
(ii) shows no systematic trend, although it may fluctuate (technically: is ergodic)

Let n(t) denote the total population size.
Under fairly general conditions* the limit

$$\lim_{t\to\infty} \frac{1}{t} \ln \frac{n(t)}{n(0)} =: \rho(E)$$

exists.

[Mathematically ρ is known as
the "dominant Lyapunov exponent"
of a "positive linear evolutionary system".]

The appropriate biological term for ρ is "**fitness**"
(of a certain type of individuals in the environment E)

---

* In the example a bound on the components of the A(E(t)) suffices.

Calculating ρ, I:

Without physiological or spatial structure:

(a) Discrete time:
When (i) the generations don't overlap,
(ii) newborns are (stochastically) equal:

$$\rho(E) = \left\langle \ln \langle \text{offspring number} \rangle_{\text{individuals}} \right\rangle_{\text{time}}$$

(b) Continuous time: $\frac{dn}{dt} = r(E(t))n$

Already an average over individuals!

$$\rho(E) = \lim_{t \to \infty} \frac{1}{t} \int_0^t r(E(\tau))d\tau$$

for T-periodic $E(t)$:

$$\rho(E) = \frac{1}{T} \int_0^T r(E(\tau))d\tau$$

Generally: let $\mu\{dE\}$ be the fraction of time that E spends in $\{dE\}$
then

$$\rho(E) = \int_{\mathcal{E}} r(E)\mu\{dE\}$$

Calculating ρ, II:

Constant environments:

(a) Discrete time: $N(t+1) = A(E)N(t)$

$$\boxed{\rho(E) = r(E) = \ln[\text{dominant eigenvalue of } A(E)]}$$

(b) Continuous time: $\frac{dN}{dt} = B(E)\,N$

$$\boxed{\rho(E) = r(E) = \text{dominant eigenvalue of } B(E)}$$

Theorem:

$$\rho(E) \gtrless 0 \quad \text{if} \quad R_0(E) \gtrless 1.$$

where $R_0 \equiv$ average life-time offspring production.

[This can also be expressed as $\operatorname{sign} \ln[R_0] = \operatorname{sign} \rho$.]

Ad calculating ρ:

For larger non-negative matrices A
the quickest way to calculate the dominant eigenvalue
is by an iteration:

- Start with some positive vector M(0), with $\mathbf{1}^T M(0)=1$
- Successively calculate M(t) from

$$\tilde{M}(t+1) = A\,M(t)$$

$$w(t) = \mathbf{1}^T\tilde{M}(t+1), \qquad M(t+1) = \frac{1}{w(t)}\tilde{M}(t+1)$$

- dominant eigenvalue of A $= \lim_{t\to\infty} w(t)$

$$\boxed{\mathbf{1}^T M = \sum_i m_i = |M| = \text{"total population size"}}$$

Calculating ρ, III:

Period T environments:

(a) Discrete time: $N(t+1) = A(E(t))N(t)$

Define

$$\tilde{A}(T) = A(E(0))A(E(1)) \cdots A(E(T-1))$$

(b) Continuous time: $\dfrac{dN}{dt} = B(E(t))\,N$

Calculate $\tilde{A}(T)$ from

$$\frac{d\tilde{A}}{dt} = B(E(t))\tilde{A}, \qquad \tilde{A}(0) = I$$

$$\boxed{\rho(E) = \frac{1}{T}\ln\left[\text{dominant eigenvalue of } \tilde{A}(T)\right]}$$

Calculating ρ, IV:

General fluctuating environments:

Let $M = |N|^{-1}N$, with $|N| = \mathbf{1}^T N$ = total population size

(a) Discrete time: $N(t+1) = A(E(t))N(t)$

Let

$$\tilde{M}(t+1) = A(E(t))M(t)$$

(b) Continuous time: $\frac{dN}{dt} = B(E(t))\,N$

Define $\tilde{M}(t+1)$ by

$$\frac{d\tilde{M}}{d\tau} = B(E(\tau))\,\tilde{M}, \quad \tilde{M}(t) = M(t).$$

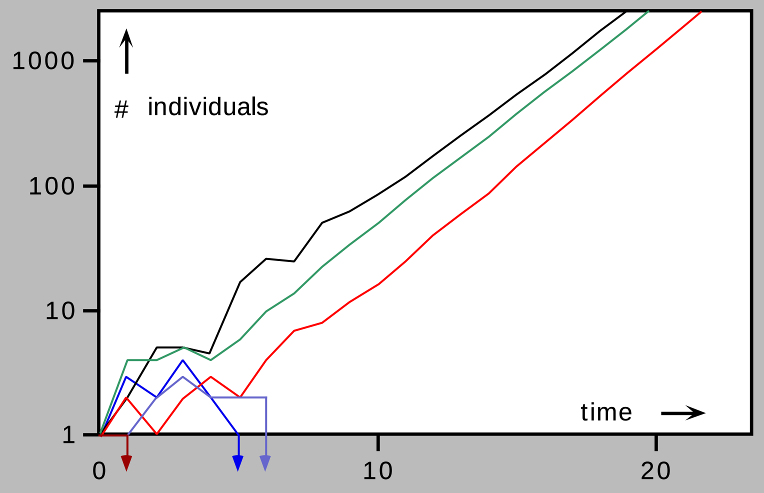
In both cases combine this with

$$w(t) = \mathbf{1}^T\tilde{M}(t+1), \qquad M(t+1) = \frac{1}{w(t)}\tilde{M}(t+1),$$

then

$$\boxed{\rho(E) = \lim_{T\to\infty}\frac{1}{T}\sum_{t=0}^{T-1}\ln[w(t)]}$$

Starting from a single individual I:



In an ergodic environment:

a population starting from a single individual either goes extinct, with probability Q, or "grows exponentially" at a relative rate ρ(E).

Starting from a single individual II:

Let P be probability of invading: $P = 1 - Q$.

* Under very general conditions

$$P > 0 \quad \text{if and only if} \quad \rho(E) > 0.$$

* For constant E and small $\rho(E) > 0$

(i) $$P \approx 2 \ln [R_0(E)] \,/\, \sigma^2$$

with σ^2 a measure for the variability in the life-time offspring production; when everybody is born equal

$$\sigma^2 = \text{Variance [life-time offspring production]}$$

(ii) $$\rho(E) \approx \ln [R_0(E)] \,/\, T$$

with T the mean age of offspring production

Properties of ρ:

(see R Ferrière & M Gatto (1995) Theor Pop Biol **48**: 126-171)

For terminological reasons, concentrate on the discrete time case with finite i-state space and a finite number of well-mixed patches, described by:

$$N(t+1) = A(E(t))N(t)$$

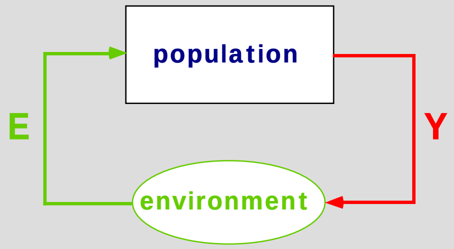
The types are supposed to differ in a trait vector Y.

If all $a_{ij} > 0$: when the a_{ij} are smooth or analytic in Y then so is $\rho(E,Y)$.

[If some a_{ij} can be 0 we may have to be a little more careful: There exist, weird, examples for which $\rho(E,Y)$ is not even continuous in Y despite a smooth dependence of the a_{ij} on Y.]

The real trouble is in the dependence of $\rho(E,Y)$ on E!

In "reality" the loop is closed:



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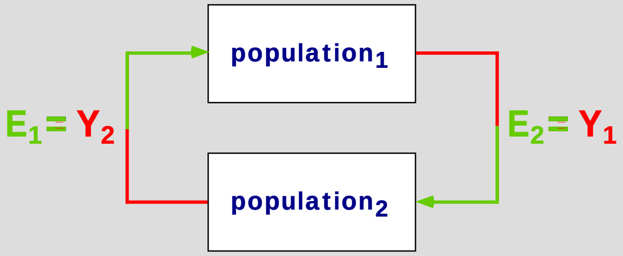


or

.....

Community dynamical attractors I

* In any community model
taking the fysical boundedness of the world into account,
either

- **the c(ommunity)-state goes to some attractor, to which corresponds an environment** E_{attr},

or

- first some types (= species) go extinct, and then the state of the remaining (sub-)community goes to an attractor.

Community dynamical attractors II

An attractor can be

- an equilibrium point,
  for which necessarily E_{attr} is constant,
- a limit cycle,
  for which necessarily E_{attr} regularly oscillates,
- some more complicated object,
  e.g. a strange attractor,
  for which (usually) E_{attr} fluctuates chaotically,

or, if the community dynamics is stochastic,

- a stationary probability distribution for the c-state,
  corresponding to a stationary stochastic E_{attr}.

Community dynamical attractors III

* Whatever the type of the community attractor,

for all species in the community

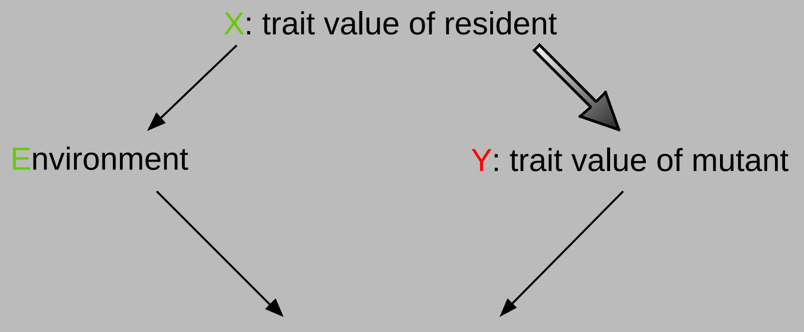
$$\rho_i(E_{attr}) = 0$$

$\Rightarrow$ community **equilibrium points** are characterised by

$$R_{0i}(E_{attr}) = 1$$

(since sign ρ = sign ln $[R_0]$).

Adaptive Dynamics: I the monomorphic case



X: trait value of resident

Environment

Y: trait value of mutant

fitness (rate of exponential growth in numbers) of mutant:

$$s_X(Y) := \rho(E_{attr}(X),Y)$$

* Y has a positive probability to invade into an X community if and only if $s_X(Y) > 0$.

And after that:

* X can be ousted by Y only if $s_Y(X) \le 0$.

Adaptive Dynamics, II polymorphisms:

In (spatially and/or physiologically structured) locally largish populations characterized by trait values (≡ strategies) Y, X, $X_1,\dots, X_n$:

$\rho(E,Y)$: **(fitness)**	asymptotic average rate of relative increase (≡dominant Lyapunov exponent) of Y population in a given ergodic environment E
$E_{attr}(C)$:	the environment "created" by a strategy coalition $C = (X_1,\dots, X_n)$

Implicit presupposition: An $X_1,\dots, X_n$ (plus...) community has a unique global attractor (stationary probability measure on E) with all n strategies present [or else consider local theory only]

$$s_C(Y) := \rho(E_{attr}(C),Y)$$

Example:

Population equations:

$$n_{X_i}(t+1) = a(X_i)\ [f(E(t))]^{-b(X_i)}\ n_{X_i}(t)$$

with

$$E = c(X_1)n_{X_1} + \cdots + c(X_k)n_{X_k} + E_{external}$$

Fitness of Y invader in X population:

$$\rho(Y,E_{attr}) = \langle \ln[a(Y)] - b(Y)\ \ln[f(E_{attr}(t))] \rangle_{time}$$

$$= \ln[a(Y)] - b(Y)\ \langle \ln[f(E_{attr}(t))] \rangle_{time}$$

From setting $Y = X$:

$$0 = \ln[a(X)] - b(X)\ \langle \ln[f(E_{attr}(t))] \rangle_{time}$$

$\Rightarrow$

$$\langle \ln[f(E_{attr}(t))] \rangle_{time} = \ln[a(X)]\ /\ b(X)$$

$\Rightarrow$

$$\rho(Y,E_{attr}) = \ln[a(Y)] - b(Y)\ \ln[a(X)]\ /\ b(X)$$

Example: Lotka-Volterra models

continuous time:

$$\frac{dn_i}{n_i\ dt} = r(x_i)\ [1 - \sum_j a(x_i,x_j)\ n_j\ ]$$

discrete time:

$$\frac{n_i(t+1)}{n_i(t)} = e^{r(x_i)\ [1 - \sum_j a(x_i,x_j)\ n_j\ ]}$$

$\Rightarrow$

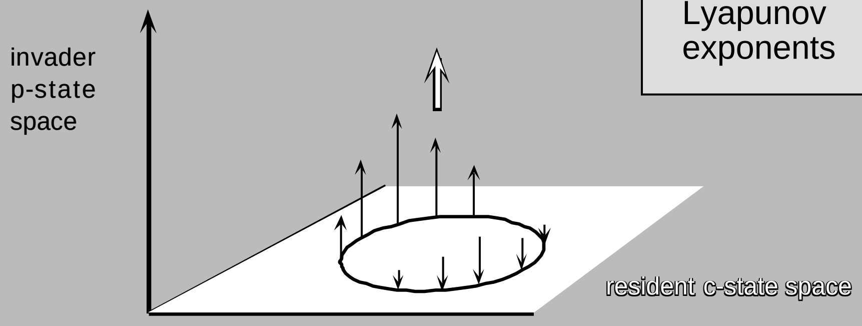
$$s_{x_1,\ldots,x_m}(y) = \rho(y,E_{attr}(x_1,\ldots,x_m))$$

$$= r(y)\ [1 - \sum_j a(y,x_j)\ \bar{n}_j\ ]$$

setting $y = x_i$, $i = 1, \ldots, m$, gives m equations in m unknowns which can be used to calculate the $\bar{n}_j$.

Interpretation:

"transversal"
Lyapunov
exponents



In the community model we linearise around an attractor in the $N_{mut} = 0$ boundary:

tells local behaviour of mutant trajectories

$$\begin{bmatrix} N_{mut}(t+1) \\ N_{res}(t+1)-\hat{N}_{res}(t+1) \end{bmatrix} \approx \begin{bmatrix} \mathbf{A}_{\mathbf{mut}}(E_{res}(t)) & 0 \\ \text{something} & \text{something} \end{bmatrix} \begin{bmatrix} N_{mut}(t) \\ N_{res}(t)-\hat{N}_{res}(t) \end{bmatrix}$$

tells local behaviour of trajectories in pure resident community

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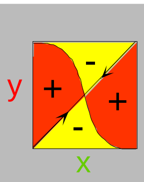
How to calculate PIPs?



Choose successively different values of x.

Let the community dynamics relax to an attractor
(or calculate the c-equilibrium from $R_0\ (x, E_{attr}(x)) = 1$,
plus possibly some other equations relating the components of E).

Use the $E_{attr}(x)$ thus found to calculate $s_x(y) = \rho(E_{attr}(x),y)$,
using the algorithms described previously
for those values of y deemed relevant.

The zero contours of $s_x(y)$ can be calculated using, e.g., a bisection method.

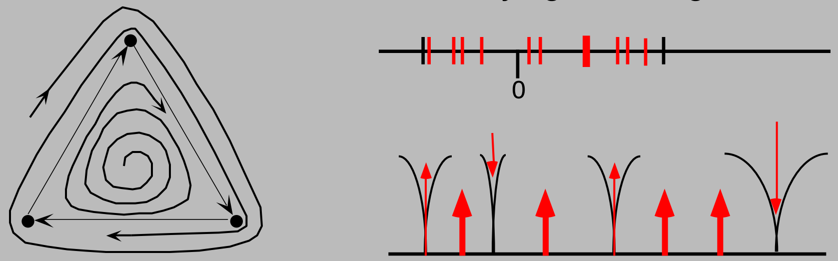
All the time use continuation procedures,
e.g., when increasing x a little,
start the c-dynamics on the previously found attractor.

Repeat the procedure a few times (i) to check the accuracy
(ii) to check for the presence of multiple attractors.

[For point c-equilibria or c-limit cycles it is often possible
to use existing software for numerical bifurcation analysis.]

Problems with E determined by an attractor:

For bounded deterministic c-dynamics perturbed by the smallest possible amount of noise convergence to (so-called ep-chain) attractors is guaranteed.
However, these attractors do not always give an ergodic E.



What is needed is a dense orbit.
Moreover, in chaotic attractors there are other, periodic, orbits, along which one gets different E's and therefore different ρ's: (tranversal) Lyapunov spectrum.

The ρ associated with the dense orbit is called **natural**.

This is the only ρ that persists with (a little) noise.

On "good" attractors

Attractors should be
(i) invariant under (infinitesimally perturbed versions of) the dynamics
(ii) minimal
[an attracting set is minimal if it does not contain a smaller structure of a similar nature]

chain attractors:
attracting sets "when the system is perturbed by infinitesimal noise"
(always exist for bounded c-dynamics)

ep-chain attractors:
as chain attractors, but the noise is not allowed to resurrect extinct types
(the most general types of adaptive dynamics have such attractors for states)

"ordinary" attractors:
attract a set of positive measure
(better: the fraction of ε-neighbourhoods that is attracted goes to 1 for ε → 0;
many chaotic attractors are of this but not the following type)

"strong" attractors:
attract an open neighbourhood,

"good" attractors:
strong attractors of the resident c-dynamics,
that have a transversal Lyapunov spectrum not straddling zero

Gene substitutions I:

If $s_X(Y) > 0$ and $s_Y(X) < 0$,

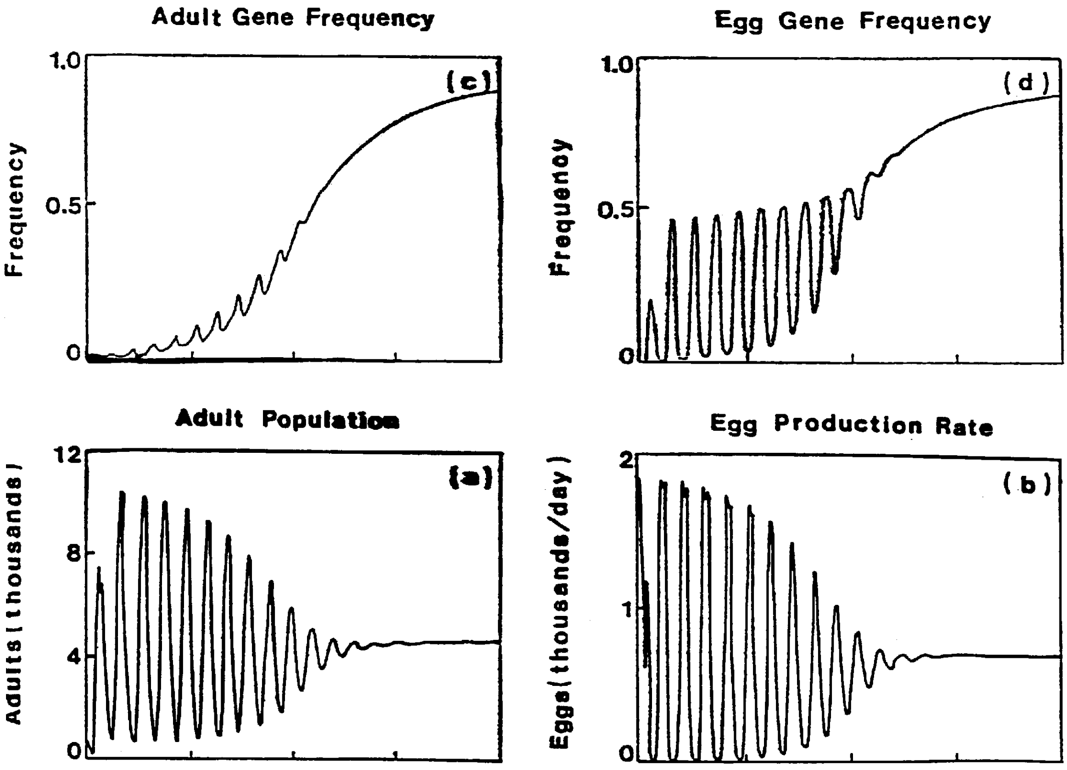
and nothing untowards happens in the interior of the c-state space,

the duration of a substitution

is essentially determined by
the initial and final exponential phases

and therefore by $s_X(Y)$ and $s_Y(X)$.

Example: Gene substitution in Nicholson's blowflies



Gene substitutions II:

Let X not be a c-dynamical bifurcation point, nor close to an evolutionarily singular point.

Moreover let $\varepsilon = |Y-X|$ be sufficiently small.

* Invasion of a "good" c-attractor of X leads to a substitution such that this c-attractor is "inherited" by Y, and

$$s_Y(X) = - s_X(Y) \qquad \text{up to } O(\varepsilon^2).$$

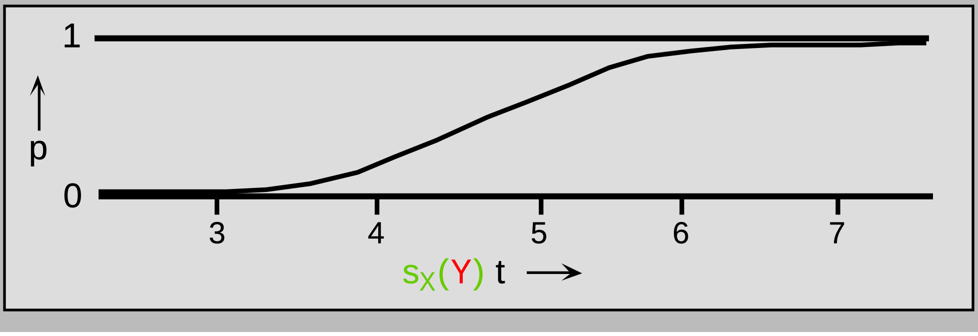
* When an equilibrium point or a limit cycle is invaded, the relative frequency p of Y satisfies

$$\frac{dp}{dt} = s_X(Y)\, p(1-p) \qquad \text{up to } O(\varepsilon^2),$$

(the classical equation for gene frequency change)

[note that $s_X(Y) = O(\varepsilon)$],

while the convergence of the dynamics of the total population densities occurs O(1).



Dimorphisms I:

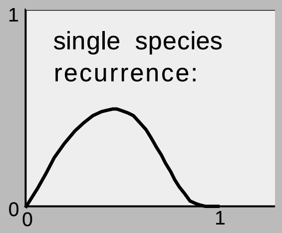
In general, $s_X(Y) > 0$ and $s_Y(X) > 0$ does not guarantee that invasion of X by Y leads to coexistence.

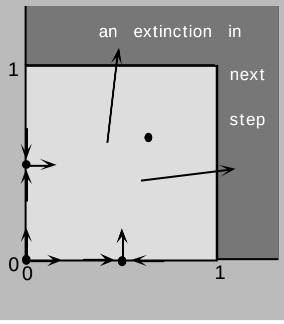
Example:

Consider the following recurrences for two mutualistic populations*

$$n' = R_0^{2+km+(n-1)^{-1}} n \qquad \text{for } 0 \le n < 1$$
$$\quad = 0 \qquad \text{for } 1 \le n$$

$$m' = R_0^{2+kn+(m-1)^{-1}} m \qquad \text{for } 0 \le m < 1$$
$$\quad = 0 \qquad \text{for } 1 \le m,$$





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* These equations may look pretty artificial, but they have all the mathematical properties required of a good population model

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Dimorphisms II:

When in an **ODE** community model

$s_X(Y) > 0$ and $s_Y(X) > 0$,

and both monomorphic attractors are good,

and unique as chain-attractors

then

invasion of X by Y leads to a

protected dimorphism

Dimorphisms III:

Let X not be a c-dynamical bifurcation point.

Moreover let $\varepsilon = |Y-X|$ be sufficiently small,

and let $s_X(Y) > 0$ and $s_Y(X) > 0$

(X is close to an evolutionarily singular point)

and let the monomorphic c-attractors of X and Y be"good"

Then an invasion of X by Y leads to a

"genetically protected" dimorphism

Most distinguishing feature of life

and feature responsible for its special properties (relative to the basic physics and chemistry on which it is superimposed):

(almost faithful) reproduction

This property forms the starting point of adaptive dynamics.

Simplifying assumptions

1. mutation limited evolution 1,2)
2. good local mixing 2)
3. clonal reproduction 2)

4. largish system sizes,
5. "good" c-attractors

6. interior c-attractors unique 3)
7. smoothness of $s_X(Y)$ 3)
8. small mutational steps 3)

---

1) i.e. separated population dynamical and mutational time scales

2) can often be relaxed !

3) only made on some occasions