

When does evolution Optimise?

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## Observations:

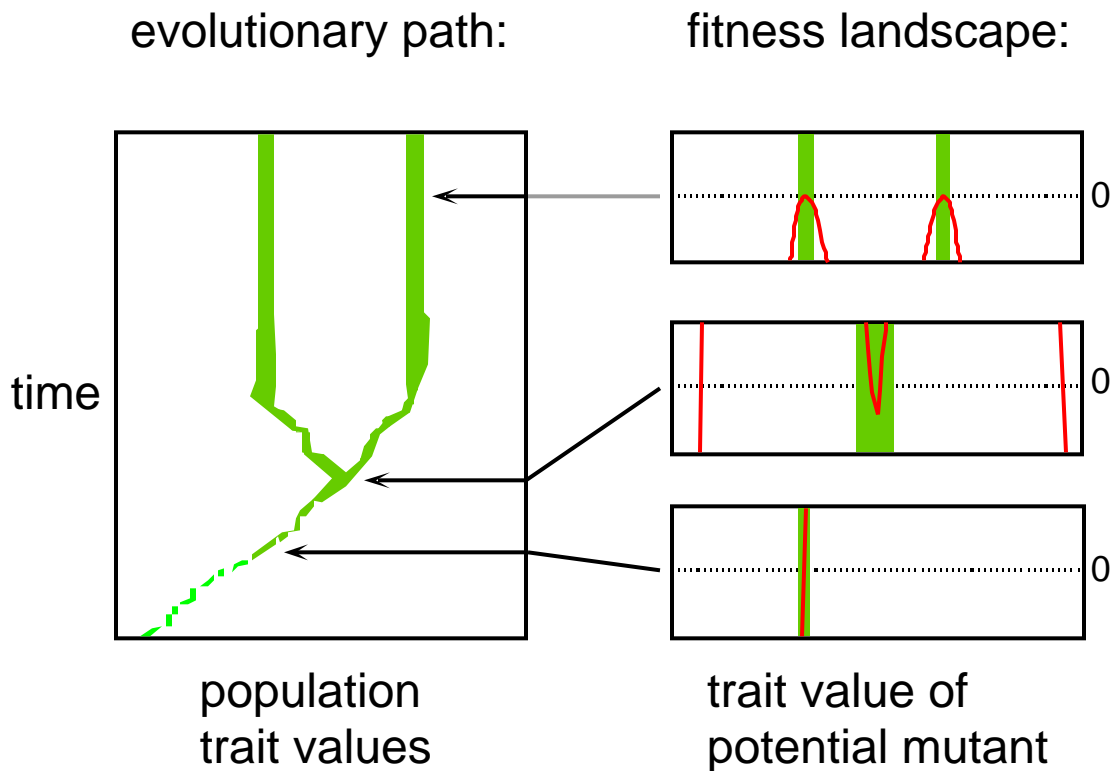
1. Biological theorising is often done in terms of optimisation models
2. The quantity optimised customarily is supposed to be a “fitness measure”
3. Two commonly used demographically based fitness measures are
  - the intrinsic rate of natural increase  $r$ ,
  - and
  - the mean lifetime offspring production  $R_0$
  - (usually, but mistakenly, called basic reproductive rate as it is not a rate but a ratio)
4. Some others are
  - the rate of energy gain
  - and
  - the carrying-capacity  $K$

However, . . . . .

# PROBLEM WITH OPTIMISATION:

**implicit assumption that  
the fitness landscape is constant**

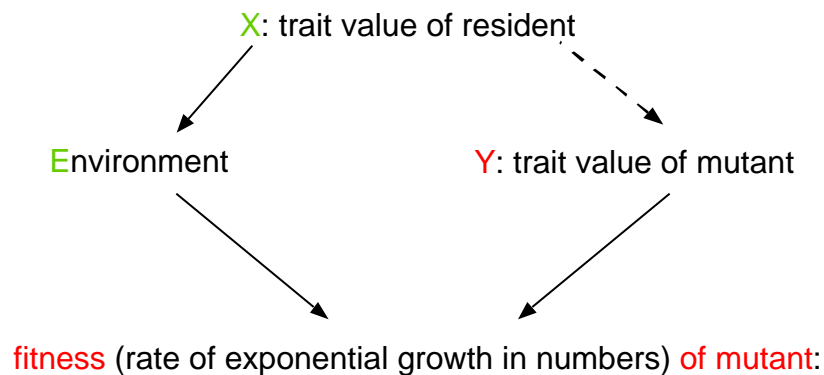
no diversification !



## Questions:

1. Under what conditions can evolution be conceived as optimising?
  2. What does the optimisation principle look like in each case?
  3. In particular, when is the quantity to be optimised  $r$  or  $R_0$ ?
  4. Does all this attention to logical rigor make a difference?
- 

## Setting the stage: the steps of evolution



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

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

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### Convention:

Whenever I say / write

“all  $E$ ”

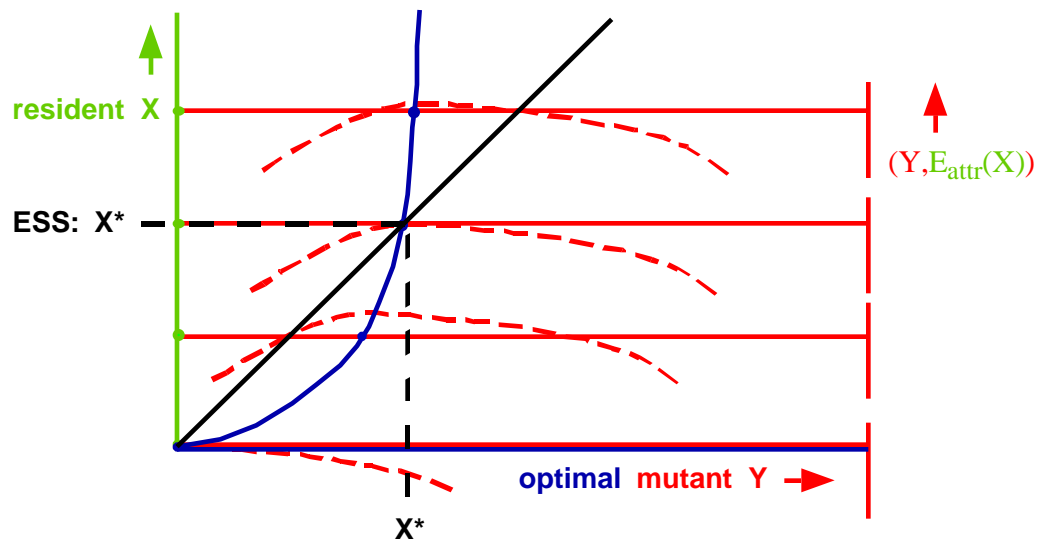
I mean

“all  $E$  that can occur as  $E_{\text{Attr}}(X)$  for some  $X$ ”.

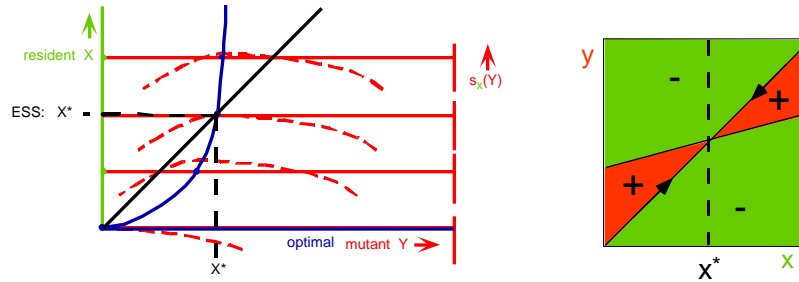
## ESS argument:

- (1) Calculate for each  $E_{\text{attr}}(X)$  the fitness  $(Y, E_{\text{attr}}(X))$  for all potential trait values  $Y$ .
- (2) Determine for each trait value the mutant which maximises  $(Y, E_{\text{attr}}(X))$ . The result is a function  $Y_{\text{opt}}(X)$ .
- (3) Vary  $X$  to find an evolutionarily unbeatable value  $X^*$ , i.e., an  $X^*$  such that

$$Y_{\text{opt}}(X^*) = X^*.$$



- (4) Ascertain that the set of trait values  $X_0$  from which  $X^*$  is approximated with non-zero probability through a sequence  $X_0, X_1, X_2, \dots$ , such that
- $$(X_{i+1}, E_{\text{attr}}(X_i)) > 0,$$
- is sufficiently large to warrant consideration of  $X^*$  as a potential evolutionary trap.



## Remarks:

(i) For the first type of ESS calculation we may replace  $s_x(Y)$  by any function, say  $f(X,Y)$ , such that for each  $X$

$$f(X,Y) \text{ and } s_x(Y)$$

are monotonically related as functions of  $Y$ .

(ii) For all ESS calculations we may replace  $s_x(Y)$  by any function, say  $g(X,Y)$ , such that

$$\text{sign } s_x(Y) = \text{sign } g(X,Y)$$

(iii) When the community dynamics always has a global point attractor

$$\text{sign } \ln(R_0(E_{\text{attr}}(X),Y)) = \text{sign } s_x(Y)$$

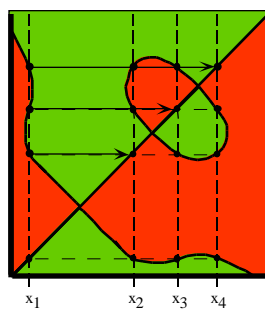
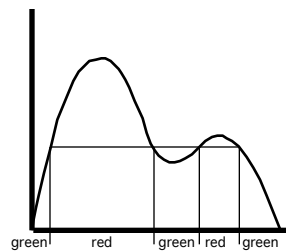
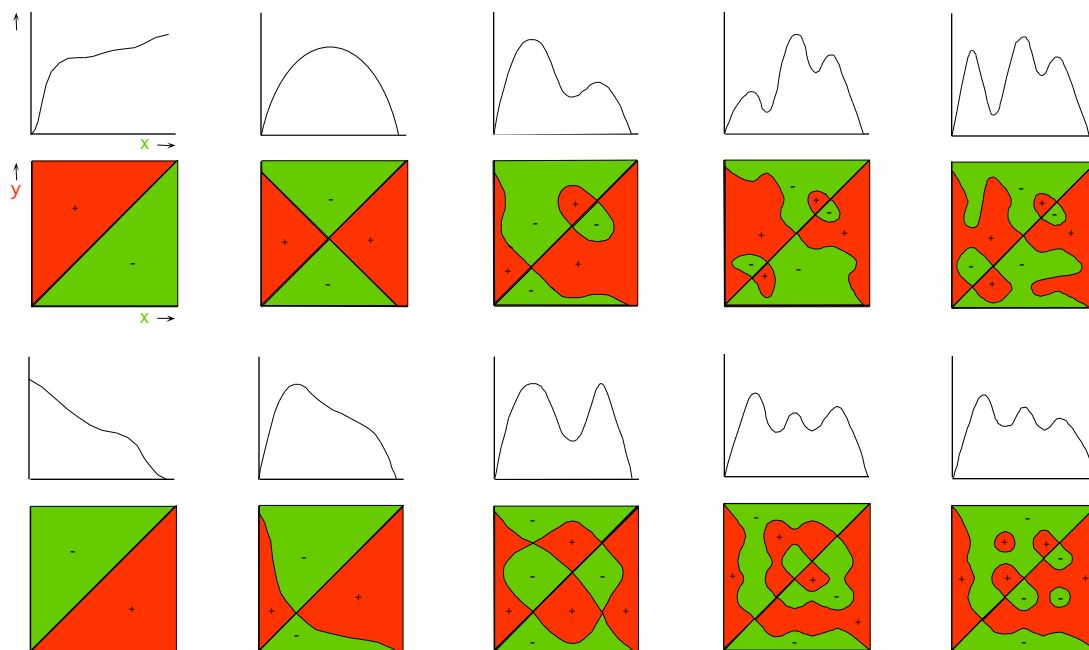
## Questions:

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- ➔ 1. Under what conditions can evolution be conceived as optimising?
  2. What does the optimisation principle look like in each case?
  3. In particular, when is the quantity to be optimised  $r$  or  $R_0$ ?
  4. Does all this attention to logical rigor make a difference?

## Definition:

- \* We shall call a function  $f$  of  $X$  to the real numbers with the property that evolution maximises  $f$  for any constraint on  $X$  an *optimisation principle*.
- 

Some sign structures of  $\rho(y, E_{attr}(x))$  that support an optimisation principle:



## Convergence:

An Optimisation Principle  
is  
a Lyapunov function for the substitution process

But

a Lyapunov function for the substitution process  
is not necessarily  
an optimisation principle.

Optimisation Principles are derived as properties of  
families of models:  
ecology plus trait space  
plus all possible constraints on the trait space

Lyapunov functions are properties of a single model:  
ecology plus trait space.

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## Questions:

1. Under what conditions can evolution be conceived as optimising?
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## HEURISTICS (i)

“Being more “efficient” increases your fitness  
in any relevant environment.”

## HEURISTICS (ii)

“Evolution minimises the availability  
of a **limiting** resource”

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### Definition:

- \* We shall call a function  $f$  of  $X$  to the real numbers with the property that evolution maximises  $f$  for any constraint on  $X$  an

*optimisation principle.*

- And we shall call a function  $f$  of  $E$  to the real numbers with the property that evolution minimises  $f(E_{\text{attr}}(X))$  for any constraint on  $X$ , a

*pessimisation or Verelendungs principle.*

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HEURISTICS: Let  $f$  (X) be a prospective optimisation principle:

Then we expect by analogy of heuristics (i) that  $f$  can be written as

$$f(X,E) = g(f(X),E),$$

with  $g$  increasing in its first argument, i.e.  $g(x_1, E) > g(x_2, E)$  if  $x_1 > x_2$ .

The knowledge that only the sign of  $f$  matters lets us modify this to

$$\text{sign } f(X,E) = \text{sign } g(f(X),E).$$



### Definition:

\* We shall say that

*the trait vector acts  
effectively one-dimensionally & monotonically*

whenever there exists a function  $f$  of  $X$  to the real numbers such that

$$\text{sign } f(X,E) = \text{sign } f(X),$$

for some function  $f$  which increases in its first argument.

\* We shall say that

*the environment acts  
effectively one-dimensionally & monotonically*

whenever there exists a function  $f$  of  $E$  to the real numbers such that

$$\text{sign } f(X,E) = \text{sign } f(X),$$

for some function  $f$  which increases in its second argument.

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### Example:

*Assume that we only need to deal with constant environments, i.e., the community can always be assumed to be in a population dynamical equilibrium*

Whenever

$$(*) \quad R_0(X,E) = R_0(X,E_V), \quad \text{“V” for “virgin”,}$$

Take

$$R_0 := \ln[R_0], \quad R_0 := \ln[R_0], \quad R_0 := R_0(X,E_V),$$

with  $R_0$  the so-called

*basic reproduction ratio,*

i.e., the lifetime production off offspring.

[(\*) applies i.a. when the trait and the negative effect of the environment act in different life stages.]

Re the concept of “effectively one-dimensionally & monotonically acting environment”:

Any such that

$$\text{sign}(X, E) = \text{sign}(X, (E)),$$

with increasing in its second argument,

can be interpreted as a

*measure of environmental quality,*

as perceived through the physiology of our individuals.

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### **Propositions:**

- 1: Models in which the trait vector acts effectively one-dimensionally & monotonically have an optimisation principle, **and vice versa.**
- 2: Models in which the environment acts effectively one-dimensionally & monotonically have an optimisation principle, **and vice versa.**
- 3: For any optimisation principle there exists **a matched pessimisation principle,** and vice versa.

## Examples (from evolutionary epidemiology):

I: density of infectives      S: density of susceptibles

Population equations:

$$dI/dt = [ \beta S - \gamma - d(S,I) ] I \quad dS/dt = [ b - d(S,I) - \beta I ] S$$

with  $d(S,I) = d_0 + h(S,I)$  and either

(1)  $h(S,I) = \beta S$ , (2)  $h(S,I) = \beta S^2$ , (3)  $h(S,I) = \beta (S + I)$

[in all three models the attractor is always a stable point equilibrium]

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$R_0$  of mutant in given (S,I) background:      nature of feedback loop:

(1)  $R(\beta, \gamma; S, I) = \beta S / [ \gamma + d_0 + \beta S ]$       1 dimensional, monotone

(2)  $R(\beta, \gamma; S, I) = \beta S / [ \gamma + d_0 + \beta S^2 ]$       1-dimensional, non-monotone

(3)  $R(\beta, \gamma; S, I) = \beta S / [ \gamma + d_0 + \beta (S + I) ]$       2-dimensional

## Optimisation principles:

To calculate the optimisation principle for **model (1)** use:

$$R(\beta, \gamma; S, I) = \beta S / [ \gamma + d_0 + \beta S ]$$

$$S^* = (\gamma + d_0) / (\beta - \gamma)$$

Pessimisation principle:

R increases in S, therefore  $S^*$  is minimised

Optimisation principle:

Minimising  $S^*$  means minimising  $(\gamma + d_0) / (\beta - \gamma)$ , i.e., maximising

$$-(\gamma + d_0) / (\beta - \gamma), \quad \text{or} \quad (\beta - \gamma) / (\gamma + d_0), \quad \text{or} \quad \dots$$

### Technical check (i)

To judge the effective dimension / monotonicity of the feedback loop we should compare over the different values of  $(\alpha, \beta)$  the dependence of  $R(\alpha, \beta; S^*(\alpha, \beta), I^*(\alpha, \beta))$  on  $(\alpha, \beta)$  locally around those  $(\alpha, \beta)$  that make  $R(\alpha, \beta; S^*(\alpha, \beta), I^*(\alpha, \beta)) = 1$ .

To show that in **model (2)** the feedback loop is non-monotone we start from:

$$R(\alpha, \beta; S, I) = \frac{S}{[\alpha + d_0 + S^2]}, \quad S^* = \frac{-\alpha - (\alpha^2 - 4(\alpha + d_0))^{1/2}}{2\beta}$$

$R$  depends on  $E = (S, I)$ , and therefore on  $(\alpha, \beta)$ , in a 1-dimensional manner (through  $S$  only).

The maximum of  $R$  as a function of  $S$  lies at  $S^{\max}(\alpha, \beta) = [(\alpha + d_0)/\beta]^{1/2}$ .

Let  $(\alpha, \beta) \in M := \{(\alpha, \beta) \mid S^{\max}(\alpha, \beta) = S^*(\alpha, \beta)\}$ . Then  $R(\alpha, \beta; S^{\max}(\alpha, \beta), I^*(\alpha, \beta)) = 1$ .

( $M$  is a curve in the  $(\alpha, \beta)$ -plane.)

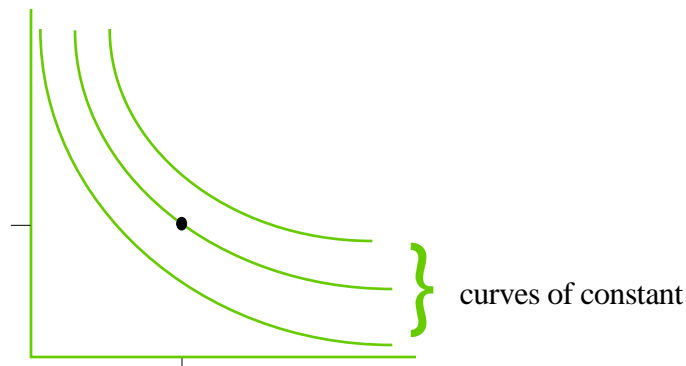
For  $\text{sign} \ln[R(\alpha, \beta; S)]$  to be monotonically related to some  $\phi(E)$

this should be maximal at  $S = S^{\max}(\alpha, \beta)$ .

As  $S^{\max}(\alpha, \beta)$  varies when  $(\alpha, \beta)$  is varied, no single  $\phi$  can do this job.

Let  $\text{sign} \ln[R(\alpha, \beta; S^*(\alpha, \beta), I^*(\alpha, \beta))] = \text{sign} g(\alpha, \beta; \phi(E))$  for some function from  $E$  to the real numbers and a function  $g$  (not necessarily monotone in  $\phi$ ).

Then curves  $(S^*(\alpha, \beta), I^*(\alpha, \beta)) = \phi_0$ , with  $\phi_0$  defined by  $g(\alpha, \beta; \phi_0) = 0$  map into curves  $R(\alpha, \beta; S^*(\alpha, \beta), I^*(\alpha, \beta)) = 1$ .



A curve through a point  $(\alpha, \beta) = (\alpha_0, \beta_0)$  should not change when we change  $(\alpha, \beta)$  in such a manner that the resulting curves still pass through that point.

## Technical check (ii)

To judge the effective dimension / monotonicity of the feedback loop we should compare over the different values of  $(s, I)$  the dependence of  $R(s, I; S^*(s, I), I^*(s, I))$  on  $(s, I)$  locally around those  $(s, I)$  that make  $R(s, I; S^*(s, I), I^*(s, I)) = 1$ .

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To show that in **model (3)** the feedback loop is 2-dimensional we start from:

$$R(s, I; S, I) = \frac{S}{[s + d_0 + (S+I)]}$$

$$I^* = \frac{[(b-d_0)(s) - d_0]}{(s^2 - 2s + 1)}, \quad S^* = \frac{(s + d_0 + I^*)}{(s)}$$

Define curves  $C(s, I)$  in  $(s, I)$ -space by  $R(s, I; S^*(s, I), I^*(s, I)) = 1$ .

If the feedback loop were effectively 1-dimensional, then for all  $(s, I)$  the tangent at  $(s, I) = (s, I)$  to the curve  $R(s, I; S^*(s, I), I^*(s, I)) = 1$  in  $(s, I)$ -space should not vary when  $(s, I)$  moves over  $C$ .

Manipulating partial derivatives shows that this is not the case.

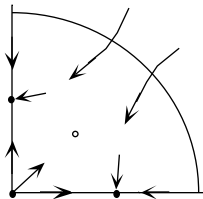
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On 1-dimensional but not necessarily monotonic E

conjecture: PIP is skew symmetric (Stefan Geritz)

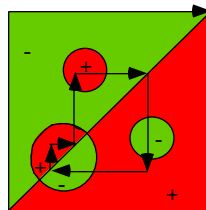
"proof": (a) ++ regions generically are excluded as generically there cannot be an internal population dynamical equilibrium, which should be there by Brouwer's fixed point theorem.

(b) -- regions are also generically excluded as for those configurations there also should be an (unstable) fixed point:



The two boundary fixed points have an open domain of attraction. The complement the community state space is invariant. Remove far away points and the neighbourhood of (0,0). This gives an invariant closed set and therefore a fixed point by Brouwer's theorem.

Skew symmetric PIP that allows Rock Scissors Paper behaviour (Eva Kisdi):



## Questions:

1. Under what conditions can evolution be conceived as optimising?
  2. What does the optimisation principle look like in each case?
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### Assumption:

We only need to deal with

**constant environments,**  
i.e., the community can always be assumed to be in  
**population dynamical equilibrium.**

---

### Proposition:

For constant environments

$$r(X,E) = 0.$$

Moreover,

$$\begin{array}{l} > 0 \\ r(X,E) = 0 \\ < 0 \end{array} \quad \text{if and only if} \quad \begin{array}{l} > 1 \\ R_0(X,E) = 1 \\ < 1, \end{array}$$

allowing the replacement of  $r$  in the ESS recipe by  $\ln[R_0]$ .

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### Definition:

We shall say that

*evolution **just** maximises  $r$ , or  $R_0$ ,*

whenever

$$r(X,E_0), \text{ respectively } R_0(X,E_0),$$

is an optimisation principle **for every choice of  $E_0$ .**

## Proposition:

Evolution just maximises  $r$ , or  $R_0$ ,

### if and only if

it deals with a combination of life histories and ecological embedding such that is possible to write

$$r(X,E) = (r(X, E_0), X),$$

or

$$R_0(X,E) = \exp[ (\ln[R_0 (X, E_0)], X)],$$

respectively,

with  $r$  increasing in its first argument,

and  $E_0$  fixed, but otherwise arbitrary.

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## Examples:

1: Whenever the environment makes itself felt only through an additional death rate  $\mu(E)$ , acting equally on all individuals,  $r(X,E)$  can be expressed as

$$r(X,E) = r(X,E_v) - \mu(E),$$

$E_v$  the virgin environment. Therefore evolution within those confines just maximises  $r$ .

2: Whenever the trait and the environment affect non-overlapping life stages,  $R_0(X,E)$  can be expressed as

$$R_0 (X,E) = (E)R_0 (X,E_v),$$

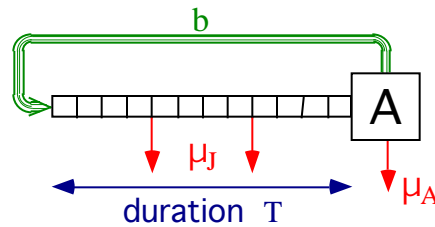
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Example:

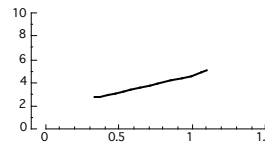


In general: In the Virgin environment:

Length of juvenile period	$T(T_V, E)$	$T_V$ ←	
Juvenile death rate	$\mu_J(E)$	$\mu_{JV}$	
Adult death rate	$\mu_A(E)$	$\mu_{AV}$	
Birth rate (to adults)	$b(T_V, E)$	$b_V(T_V) = (T_V - 1)_+$	

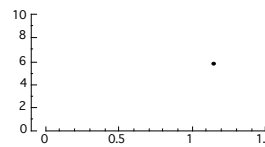
1. E **only** equally additively affects the juvenile and adult mortality rates

maximise  $r$



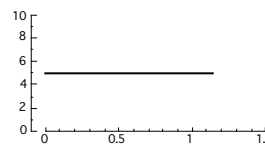
2. E **only** additively affects the adult mortality rate

maximise  $R_0$



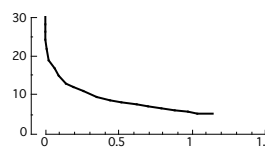
3. E **only** multiplicatively affects the reproduction rate

maximise  $R_0$



4. E **only** additively affects the age at maturation (but not the birth rate)

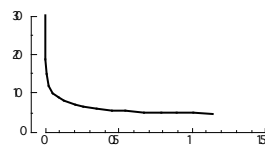
maximise  $R_0$



5. E **only** multiplicatively affects the age at maturation (but not the birth rate)

maximise

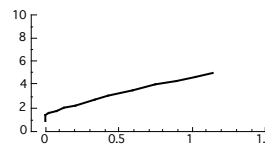
$$T_V^{-1} [\ln(b_V(T_V)) - \ln(\mu_{AV})]$$



6. E **only** additively affects the juvenile mortality rate:

maximise

$$T_V^{-1} [\ln(b_V(T_V)) - \ln(\mu_{AV})]$$



Length of juvenile period  $T^*$  in the field

Field adult mortality  $\mu_A$