Papers for discussion today

1.- **The evolutionary origins of cooperators**. *Science 2004, 306:859-862*.

2.- **On the origin of species by sympatric speciation**. *Nature 1999, 400:354-357*.

Note

All plot files (***mathematica*** .nb) are provided and made in ***Raspberry Pi*** free version.

The Evolutionary Origin of Cooperators and Defectors

Michael Doebeli,[1*] Christoph Hauert,[1†] Timothy Killingback[2]

$x, y \in [0, 1]$ investment strategies

continuous-game *pay-off* functions

collective benefit

Snow Drift $$P(x, y) = B(x + y) - C(x)$$

individual cost

individual benefit

Prisoner's Dilemma $$Q(x, y) = B(y) - C(x)$$

individual cost

payoff

$$P(x, y) = B(x + y) - C(x)$$

replicator dynamics

$$\frac{N_y'}{N_y} = f_y - \bar{f}$$

invasion fitness

$$f_x(y) = P(y, x) - P(x, x)$$

$$s_r(m) \equiv f_x(y) \equiv \frac{N_y'}{N_y} = \overset{\text{mutant payoff}}{P(y, x)} - \underset{\text{resident payoff}}{P(x, x)}$$

invasion fitness

$$f_x(y) = P(y, x) - P(x, x)$$

$$f_x(y) = B(x + y) - C(y) - [B(2x) - C(x)]$$

selection gradient

$$D(x) = \left.\frac{\partial}{\partial y} f_x(y)\right|_{y=x}$$

$$D(x) = \left.\frac{\partial}{\partial y} f_x(y)\right|_{y=x} = B'(2x) - C'(x)$$

x^* singular strategies ?

$$D(x^*) = 0$$

$$D(x^*) = B'(2x^*) - C'(x^*) = 0$$

halts evolutionary dynamics

canonical equation

$$\frac{d}{dt}x(t) = \frac{1}{2}\mu\sigma^2 N^* \cdot \underbrace{\frac{\partial}{\partial y} f_x(y)\Big|_{y=x}}_{D(x)} = 0$$

$$\frac{d}{dx}\, D(x)|_{x=x^*} = 2B''(2x^*) - C''(x^*)$$

$$\frac{d}{dx}\, D(x)|_{x=x^*} ?$$

convergent stable

$$\frac{d}{dx}D(x)\Big|_{x=x^*} < 0$$

attractor

non convergent stable

$$\frac{d}{dx}D(x)\Big|_{x=x^*} > 0$$

repeller

if attractor, evolution converges to x^*

What happens next? Once x^* has been reaced ?

$$\frac{\partial}{\partial y}\left(\frac{\partial}{\partial y} f_{x^*}(y)\right)\Big|_{y=x} = B''(2x^*) - C''(x^*)$$

$$\frac{\partial}{\partial y}\left(\frac{\partial}{\partial y} f_{x^*}(y)\right)\Big|_{y=x} \quad ?$$

Max

$$\frac{\partial}{\partial y}\left(\frac{\partial}{\partial y} f_{x^*}(y)\right)\Big|_{y=x} < 0$$

ESS

Min

$$\frac{\partial}{\partial y}\left(\frac{\partial}{\partial y} f_{x^*}(y)\right)\Big|_{y=x} > 0$$

Branching

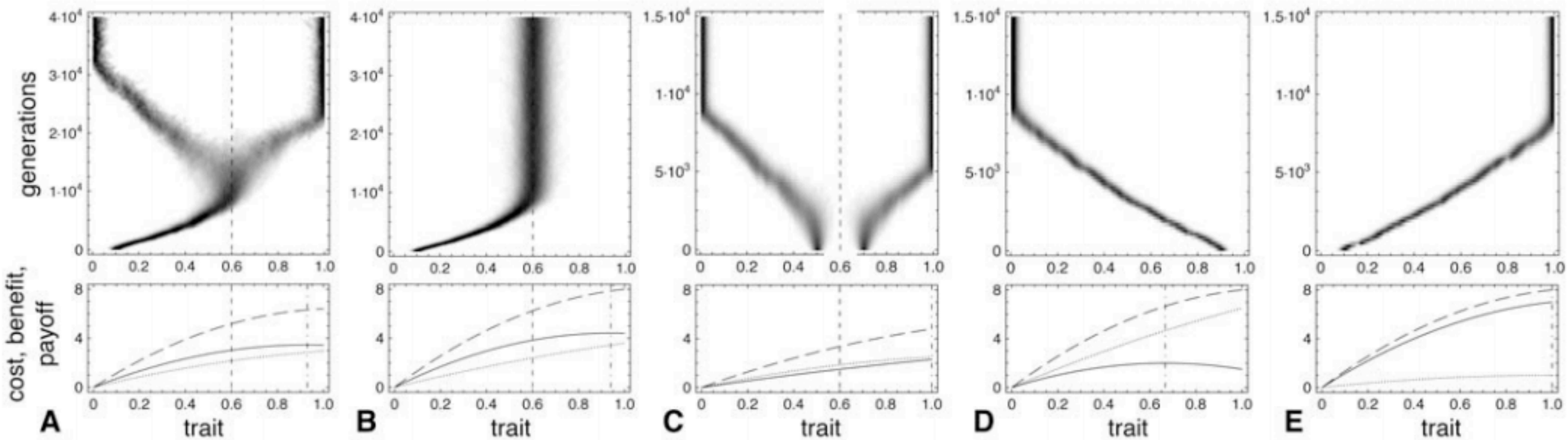
Fig.1

collective benefit

$$P(x, y) = B(x + y) - C(x)$$

Snow Drift

individual cost



$$B(0) = 0$$

$$B(x) = b_2 \cdot x^2 + b_1 \cdot x$$

$$C(0) = 0$$

$$C(x) = c_2 \cdot x^2 + c_1 \cdot x$$

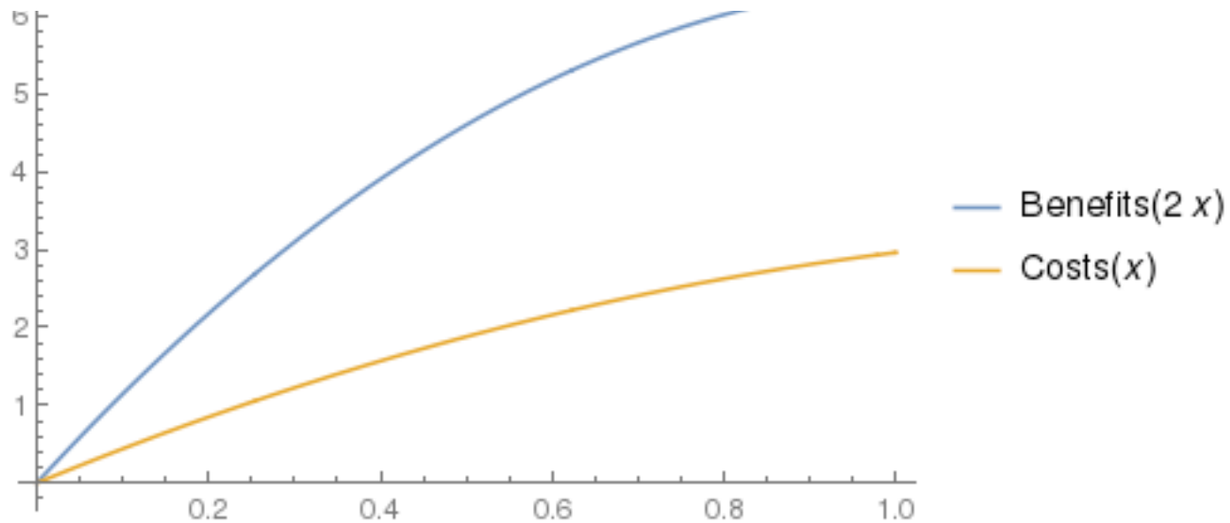
$$c_i, b_i \in \{A, B, C, D, E\}, i = 1, 2$$

```
In[6]:= b1 = 6; c1 = 4.56;

In[76]:= b2 = -1.4; c2 = -1.6;
         Benefits[x_] := b1 * x + b2 * x^2; Costs[x_] := c1 * x + c2 * x^2;

         Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[78]=



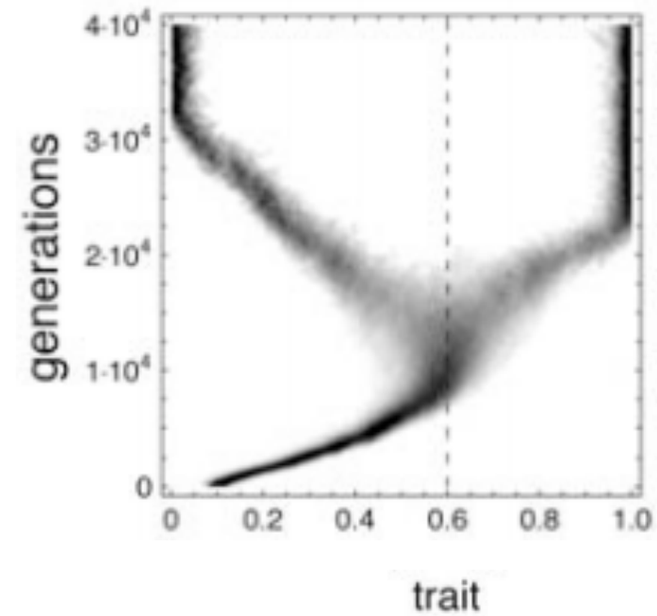
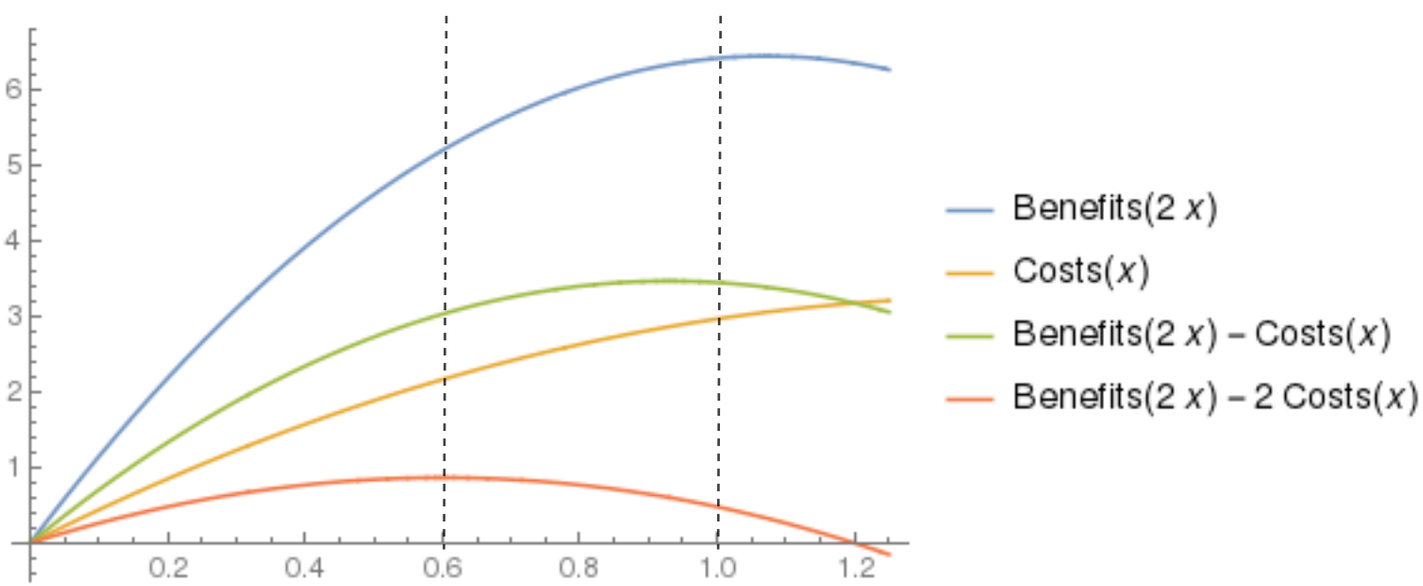


Fig. 1A

```
In[89]:= Plot[{Benefits[2 x], Costs[x], Benefits[2 x] - Costs[x], Benefits[2 x] - 2 * Costs[x]}, {x, 0, 1.25},
          PlotLegends → "Expressions"]
```

Out[89]=

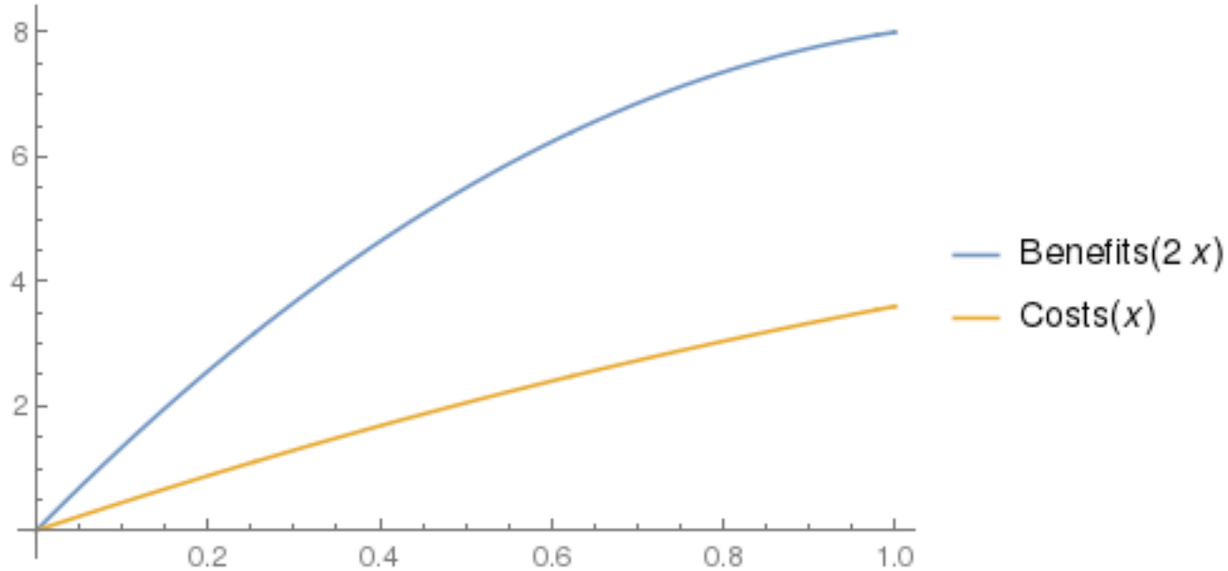


```
In[90]:= b1 = 7; b2 = -1.5; c1 = 4.6; c2 = -1;

In[91]:= Benefits[x_] := b1 * x + b2 * x^2; Costs[x_] := c1 * x + c2 * x^2;

In[92]:= Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[92]=



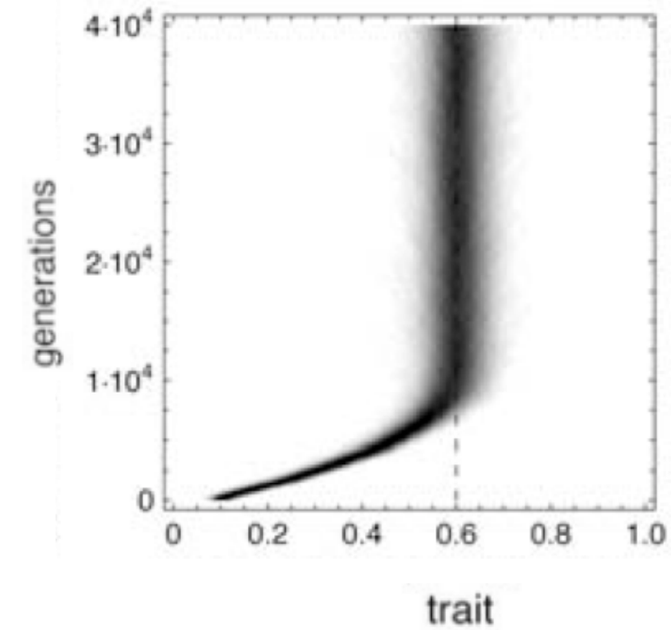
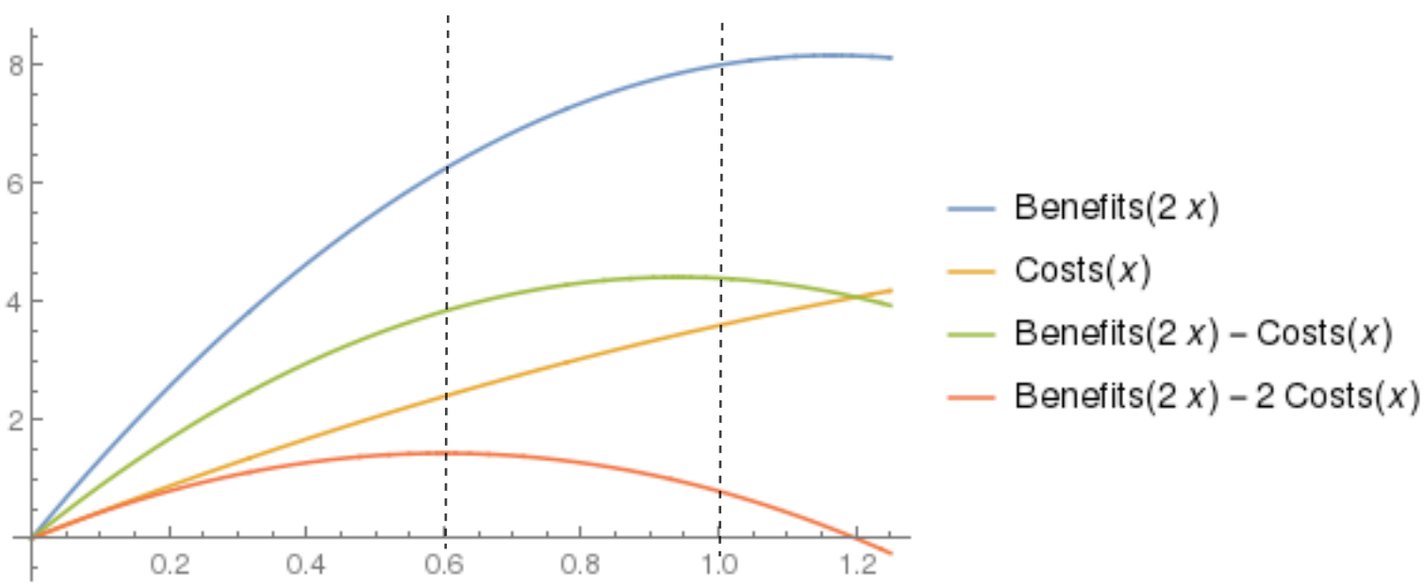


Fig. 1B

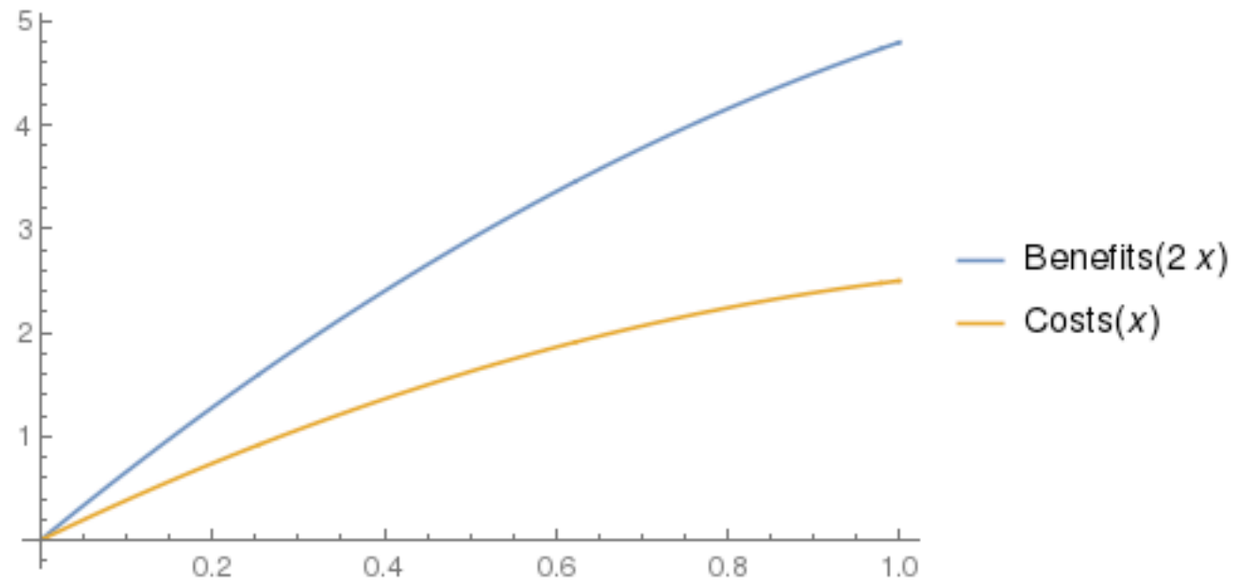
```
In[93]:= Plot[{Benefits[2 x], Costs[x], Benefits[2 x] - Costs[x], Benefits[2 x] - 2 * Costs[x]}, {x, 0, 1.25},
          PlotLegends → "Expressions"]
```

Out[93]=



```
In[94]:= b1 = 3.4; b2 = -0.5; c1 = 4.0; c2 = -1.5;
         Benefits[x_] := b1 * x + b2 * x^2; Costs[x_] := c1 * x + c2 * x^2;
In[96]:= Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[96]=



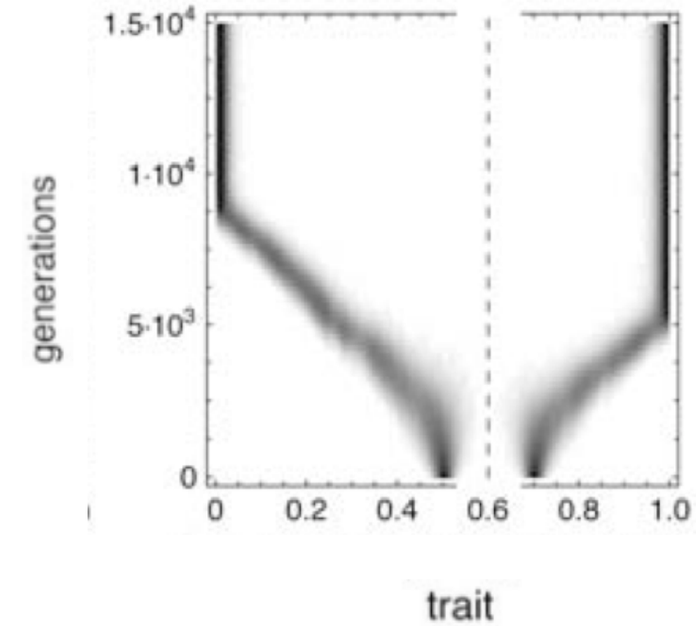
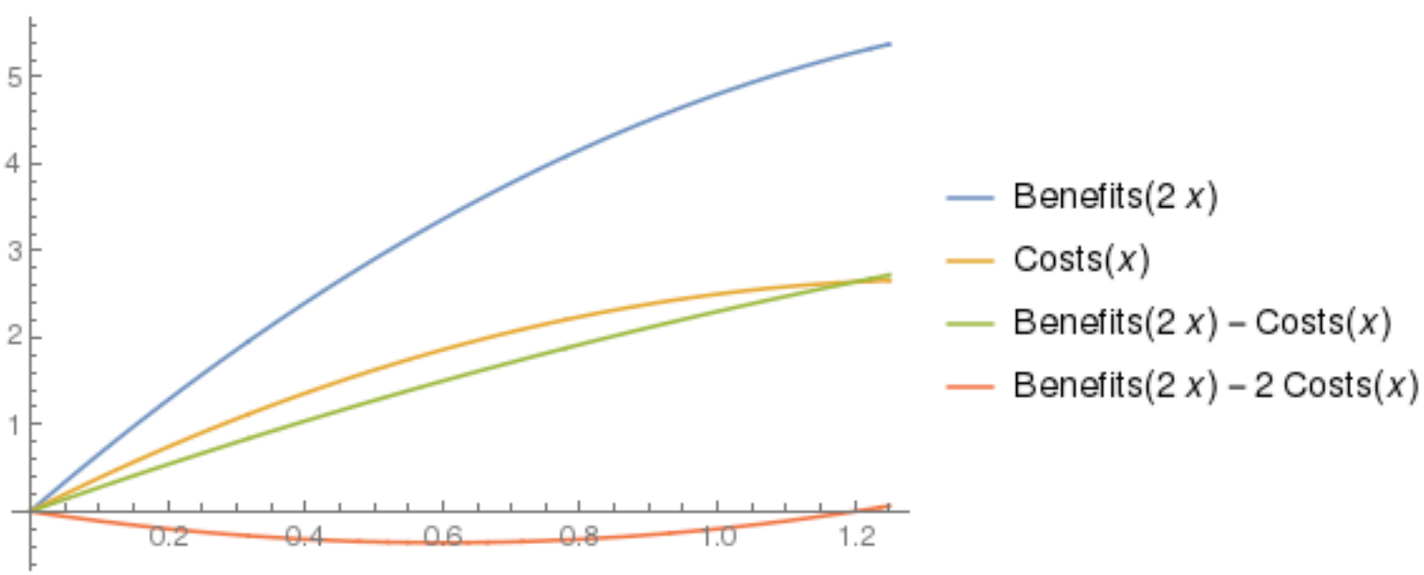


Fig. 1C

```
In[97]:= Plot[{Benefits[2 x], Costs[x], Benefits[2 x] - Costs[x], Benefits[2 x] - 2 * Costs[x]}, {x, 0, 1.25},
          PlotLegends → "Expressions"]
```

Out[97]=

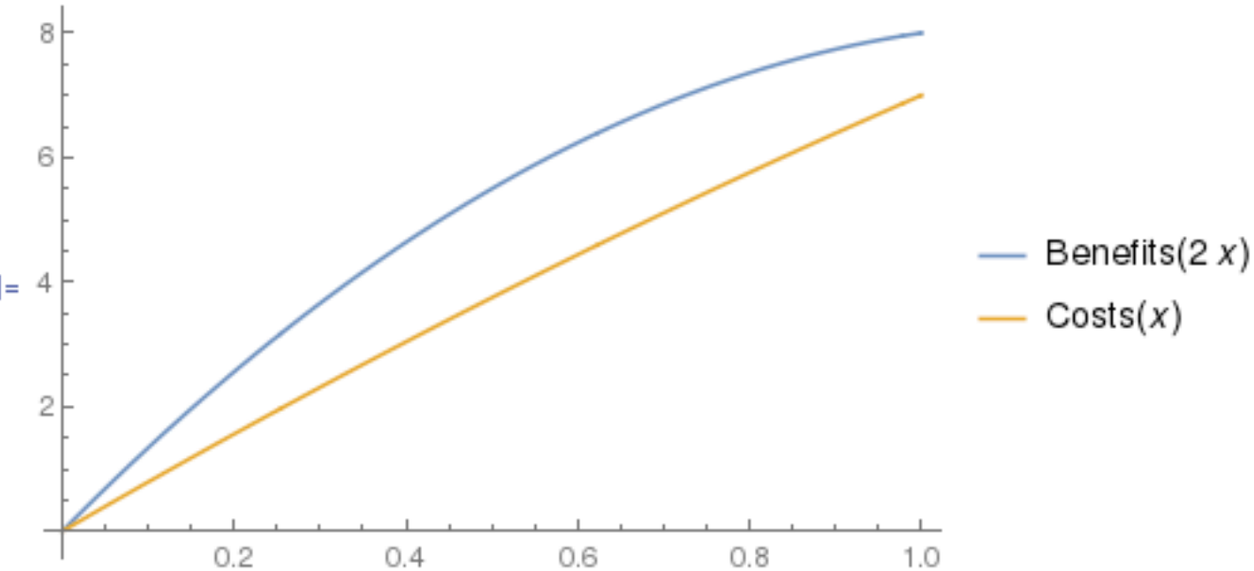


```
In[106]:= b1 = 7; b2 = -1.5; c1 = 8.0; c2 = -1;

In[107]:= Benefits[x_] := b1 * x + b2 * x^2; Costs[x_] := c1 * x + c2 * x^2;

In[108]:= Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[108]=



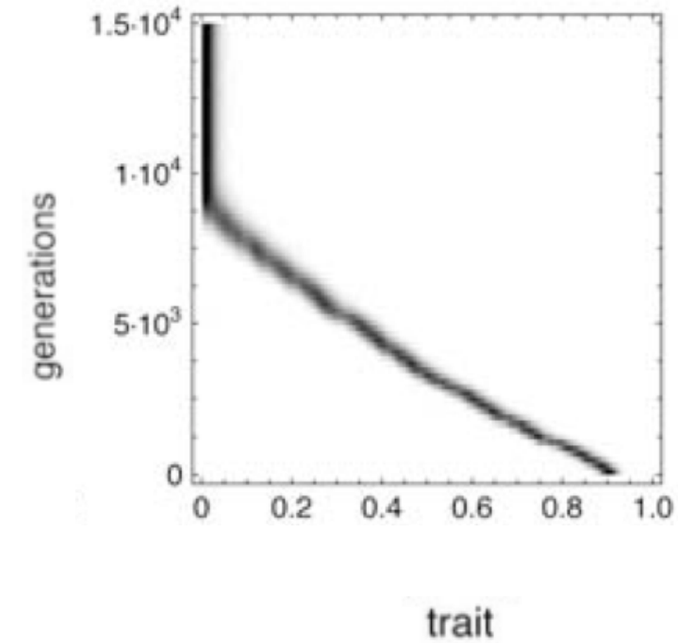
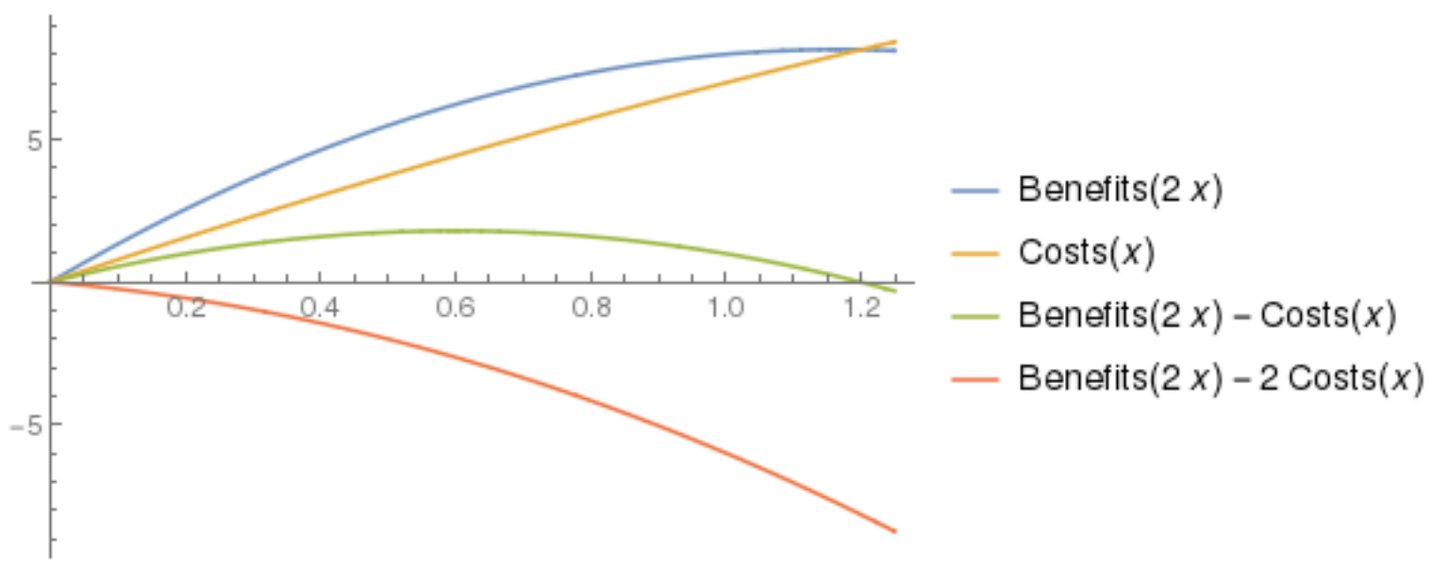


Fig. 1D

```
In[109]:= Plot[{Benefits[2 x], Costs[x], Benefits[2 x] - Costs[x], Benefits[2 x] - 2 * Costs[x]}, {x, 0, 1.25},
  PlotLegends → "Expressions"]
```

Out[109]=

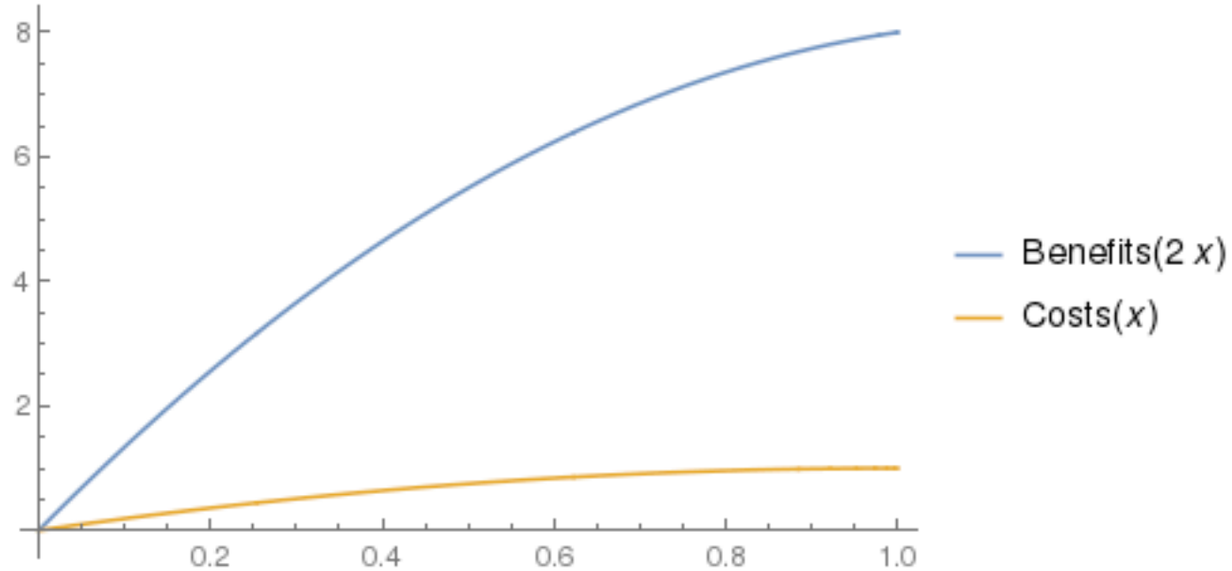


```
In[102]:= b1 = 7; b2 = -1.5; c1 = 2.0; c2 = -1;

In[103]:= Benefits[x_] := b1 * x + b2 * x^2; Costs[x_] := c1 * x + c2 * x^2;

In[104]:= Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[104]=



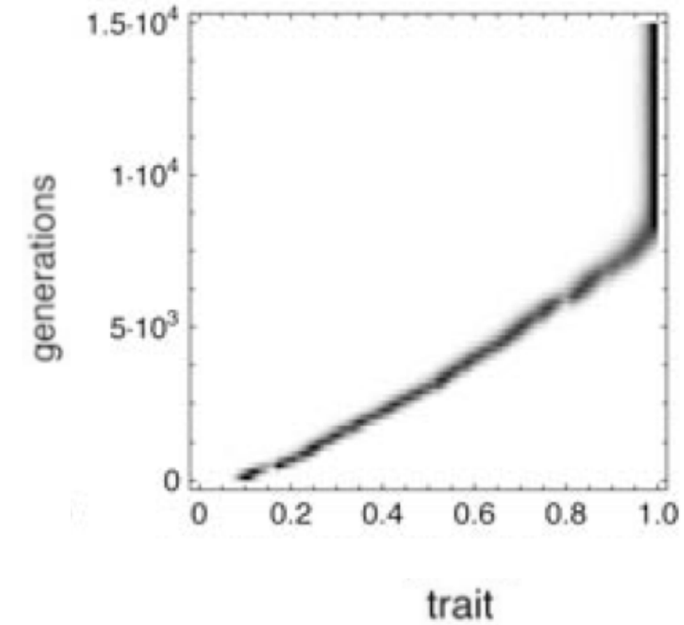


Fig. 1E

```
In[105]:= Plot[{Benefits[2 x], Costs[x], Benefits[2 x] - Costs[x], Benefits[2 x] - 2 * Costs[x]}, {x, 0, 1.25},
  PlotLegends → "Expressions"]
```

Out[105]=

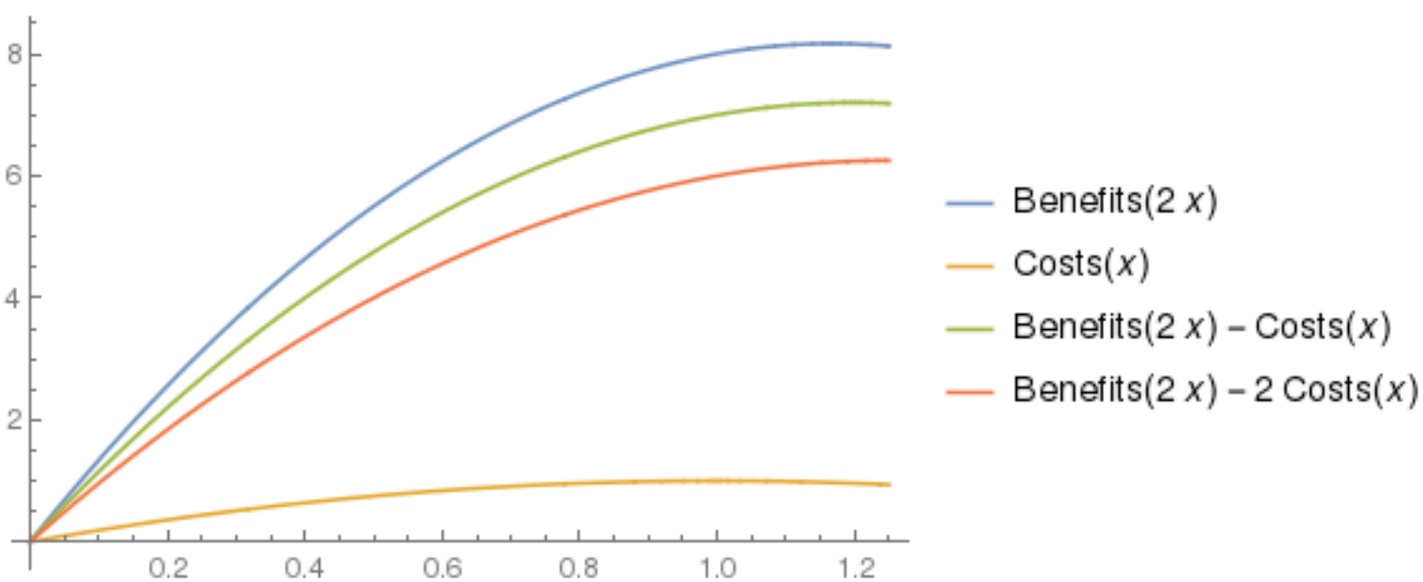


Fig.2

$$\frac{d}{dt}x(t) = \frac{1}{2}\mu\sigma^2 N^* \cdot \underbrace{\frac{\partial}{\partial y} f_x(y)\Big|_{y=x}}_{D(x)}$$

$$\frac{d}{dx}\left(\frac{\partial}{\partial y} f_x(y)\Big|_{y=x}\right)_{x=x^*}$$

$$B''(2x^*) - C''(x^*)$$

< 0

> 0

$$B''(2x^*) - C''(x^*)$$

$$\frac{\partial}{\partial y}\left(\frac{\partial}{\partial y} f_{x^*}(y)\right)\Big|_{y=x}$$

< 0 $\quad$ > 0

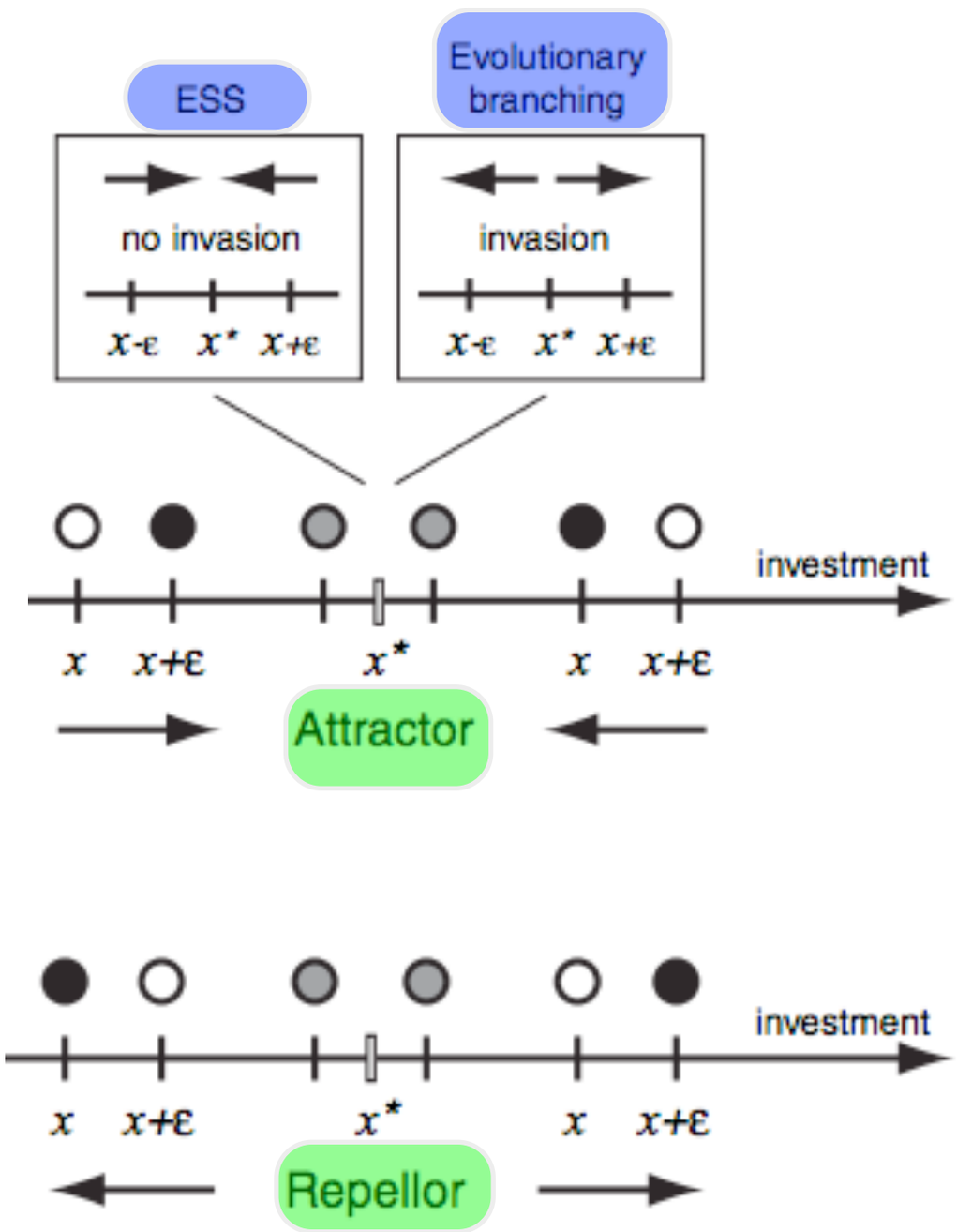
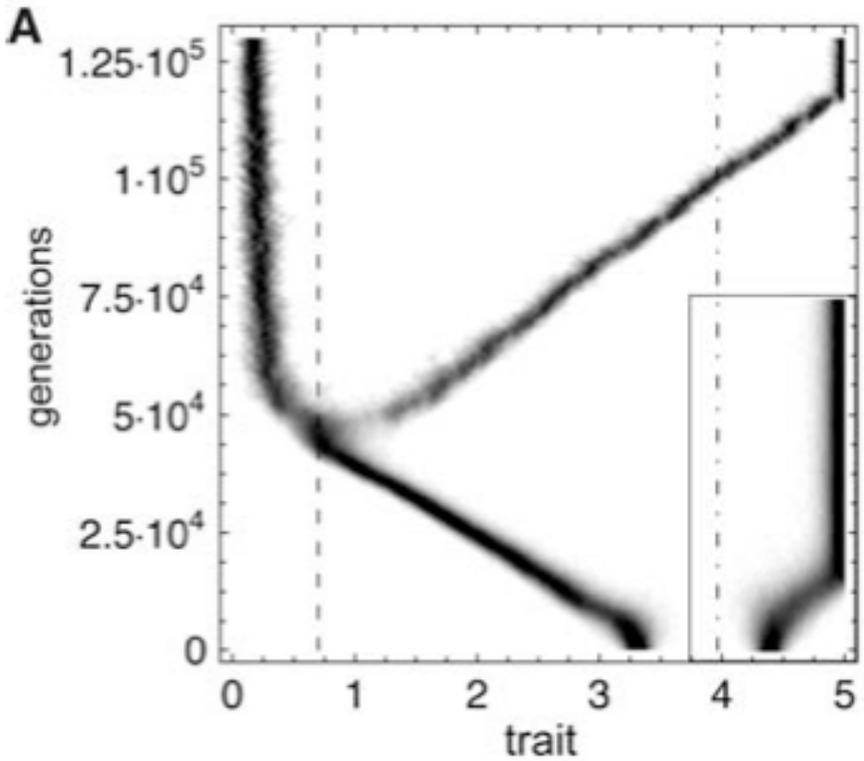


Fig.3 multiple x^*'s

$$B(x) = b\sqrt{x}$$

$$C(x) = \ln(cx + 1)$$




```
In[17]:= b = 1; c = 0.6;
         Benefits[x_] := b * Sqrt[x]; Costs[x_] := Log[c * x + 1];
         Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[19]=

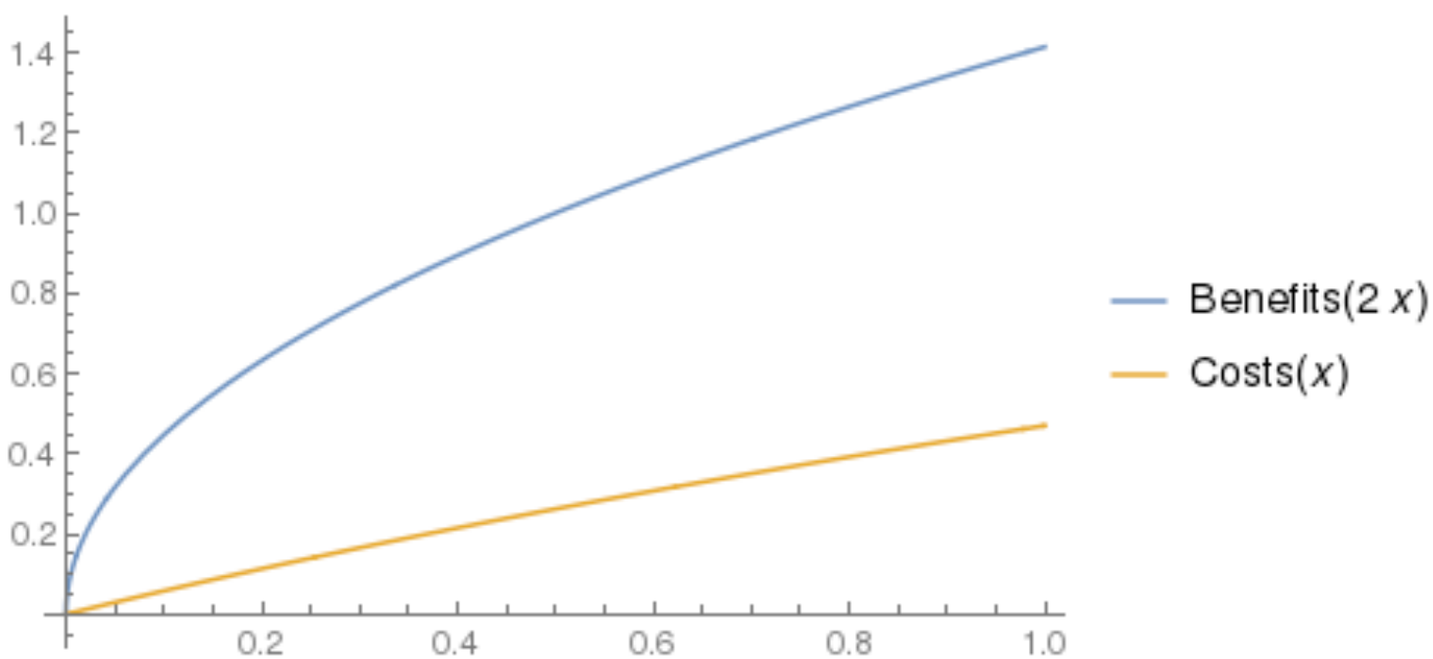
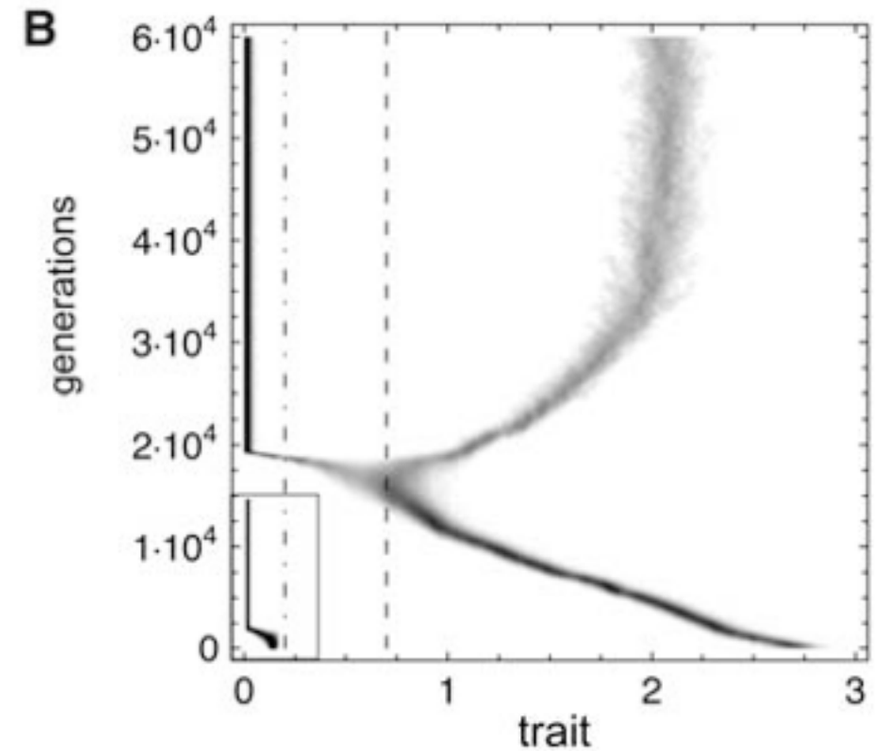


Fig.3 multiple x^*'s



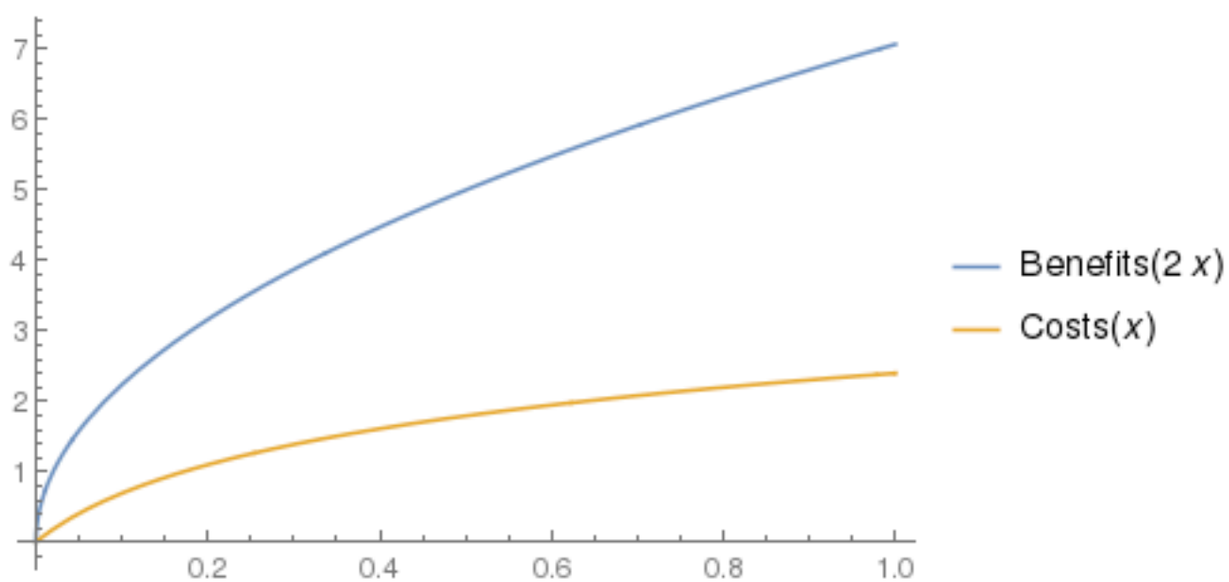
$$B(x) = b \cdot \left[1 - e^{-x}\right]$$

$$C(x) = \ln(cx + 1)$$

```
In[23]:= b = 5; c = 10;
         Benefits[x_] := b * Sqrt[x]; Costs[x_] := Log[c * x + 1];

         Plot[{Benefits[2 x], Costs[x]}, {x, 0, 1}, PlotLegends → "Expressions"]
```

Out[25]=



On the origin of species by sympatric speciation

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Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland

$$\frac{d}{dt}N(x,t) = r \cdot N(x,t) \cdot \left[1 - \frac{N(x,t)}{K(x)}\right]$$

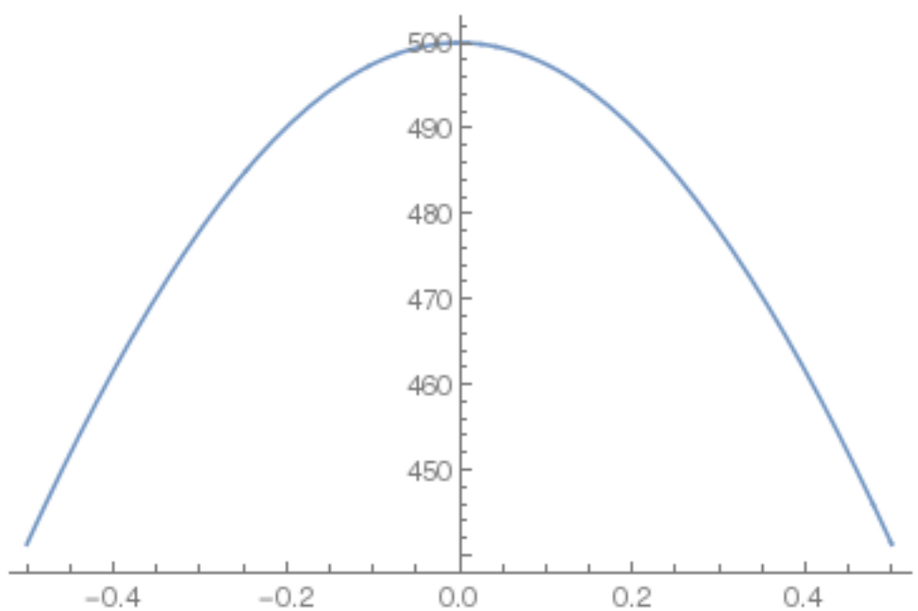
$$C(x-y) \cdot K(x)$$

$$K(x) = K_0 \cdot e^{-\frac{(x-x_0)^2}{2\sigma_K^2}}$$

$$C(x-y) = e^{-\frac{(x-y)^2}{2\sigma_C^2}}$$

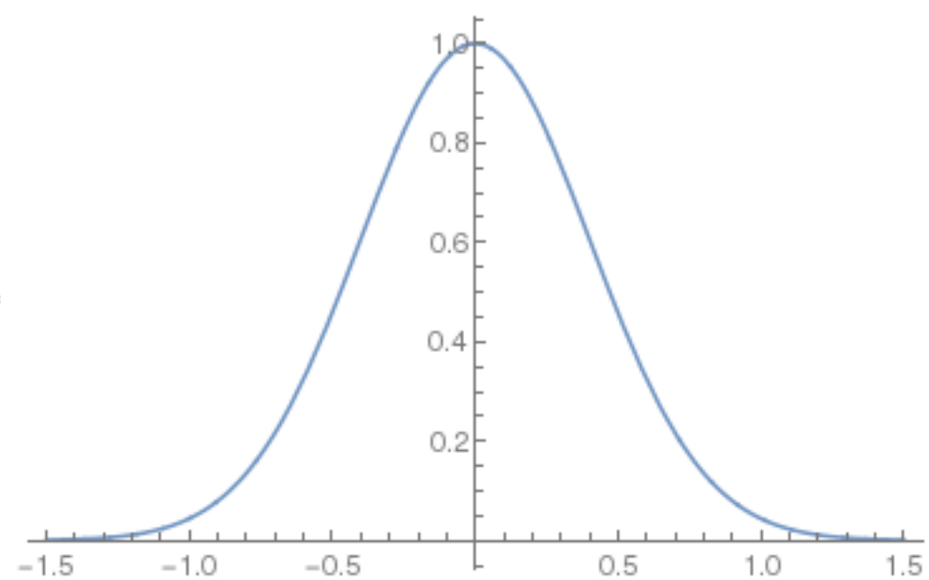
```
In[27]:= K0 = 500; sigmaK = 1;
         K[x_] := K0 * Exp[-(x - 0)^2 / 2 sigmaK^2]
         Plot[K[x], {x, -0.5, 0.5}]
```

Out[29]=




```
In[107]:= sigmaC = 0.4;
          Competition [r_] := Exp[-(r^2 / (2 * sigmaC^2))];
In[110]:= Plot[Competition[x], {x, -1.5, 1.5}]
```

Out[110]=



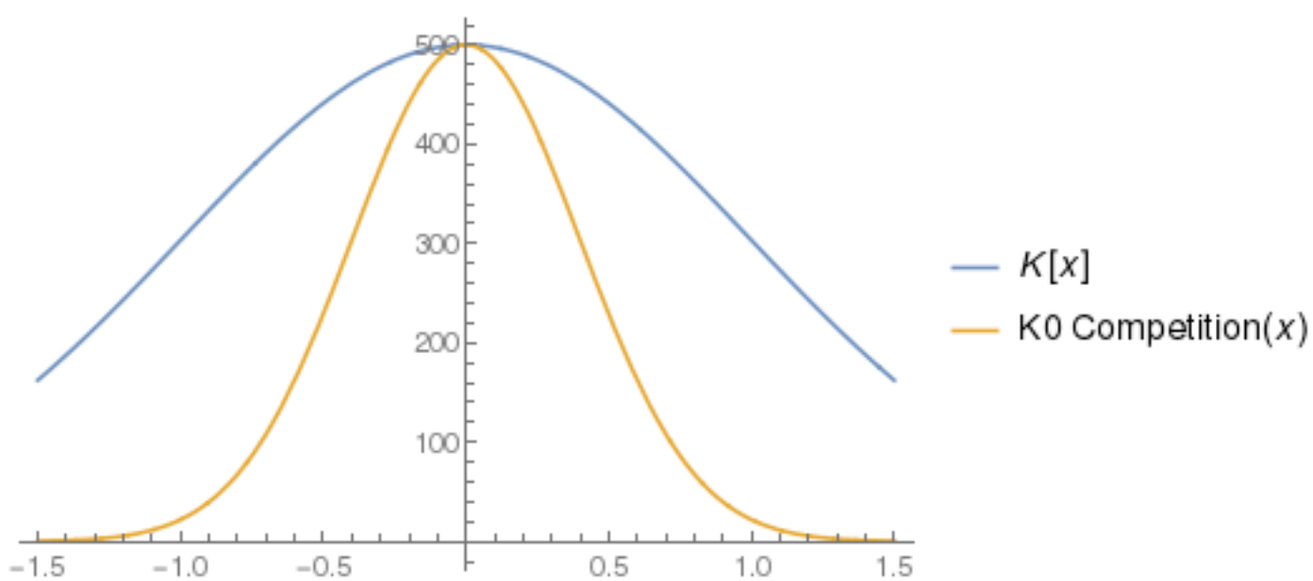
$$\frac{d}{dt}N(x,t) = r \cdot N(x,t) \cdot \left[1 - \frac{N(x,t)}{K(x)}\right]$$

$$K(x) = K_0 \cdot e^{-\frac{(x-x_0)^2}{2\sigma_K^2}}$$

$$C(x-y) = e^{-\frac{(x-y)^2}{2\sigma_C^2}}$$

In[107]:=
```
sigmaC = 0.4;
Competition [r_] := Exp[-(r^2 / (2 * sigmaC^2))];
Plot[{K[x], K0 * Competition[x]}, {x, -1.5, 1.5}, PlotLegends → "Expressions"]
```

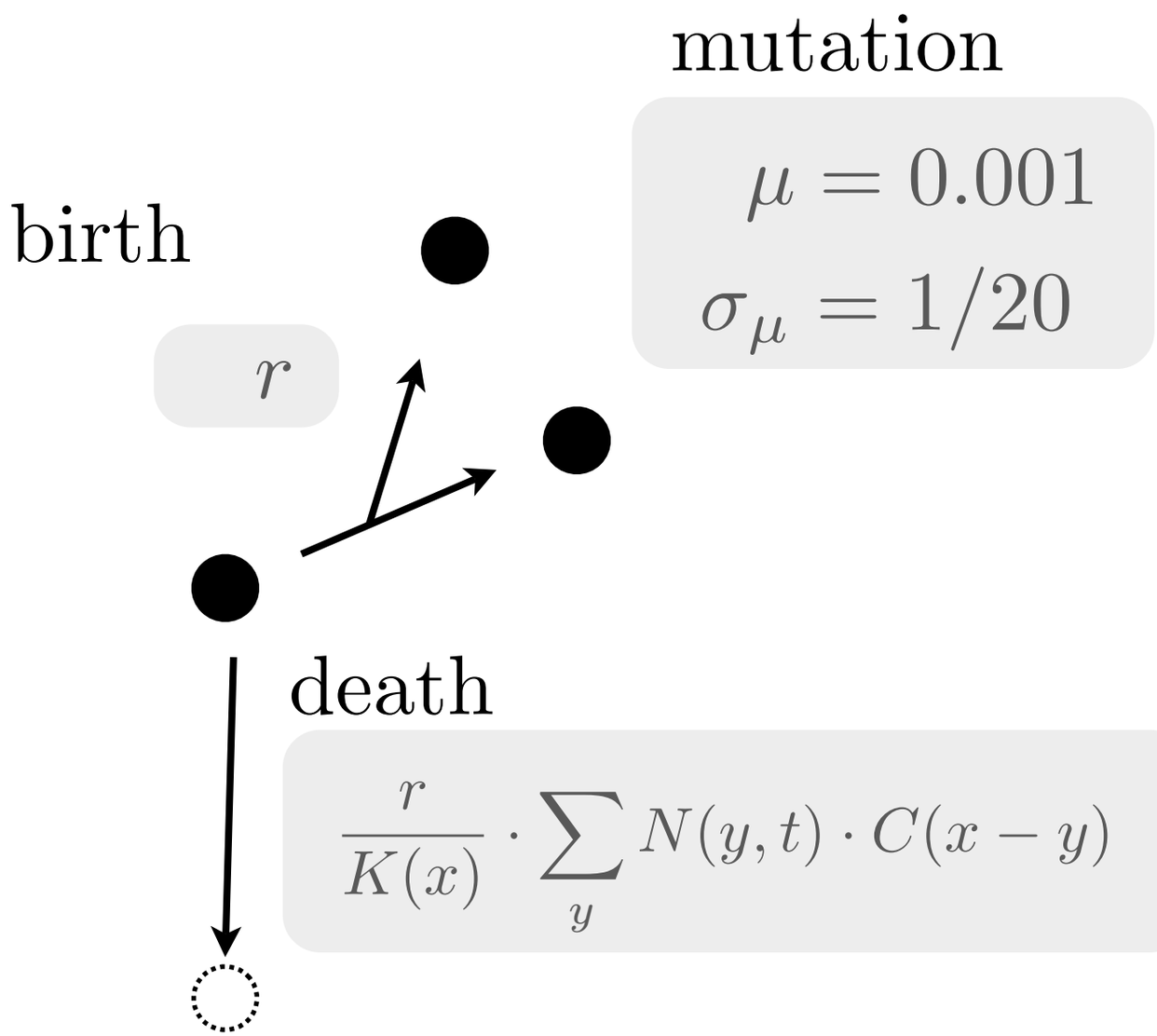
Out[109]=



$$C(x-y) \cdot K(x)$$

discounted density competition

Individual Based Model (IBM)



invasion fitness

$$s(y,x) = r \cdot \left(1 - \frac{C(x-y)K(x)}{K(y)}\right) = s_r(m) \equiv f_x(y)$$

selection gradient

$$D(x) = \left.\frac{\partial}{\partial y} s(y,x)\right|_{y=x}$$

$$\left.\frac{\partial}{\partial y} s(y,x)\right|_{y=x} = r\frac{K'(x)}{K(x)} \quad \begin{cases} > 0 & \text{if } x < x_0 \\ < 0 & \text{if } x > x_0 \end{cases}$$

$x_0 = x^*$ singular strategies ?

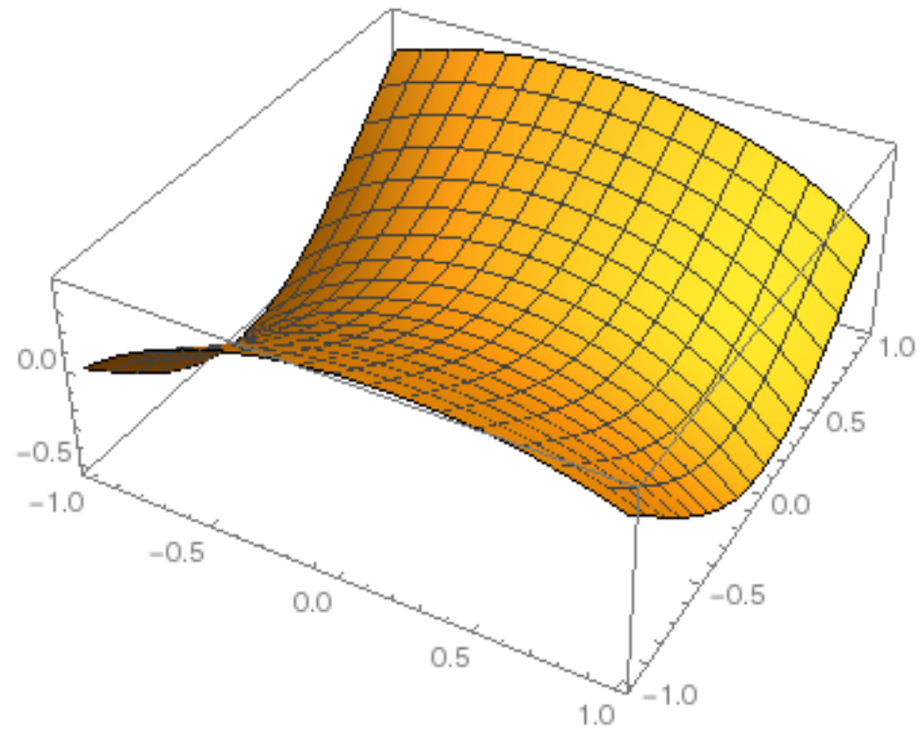
evolutionary attractor

$D(x^*) = 0$

```
In[49]:= r = 1;
         S[y_, x_] := r * (1 - (Competition[x - y] * K[x] / K[y]))

In[67]:= Plot3D[S[y, x], {y, -1, 1}, {x, -1, 1}]
```

Out[67]=



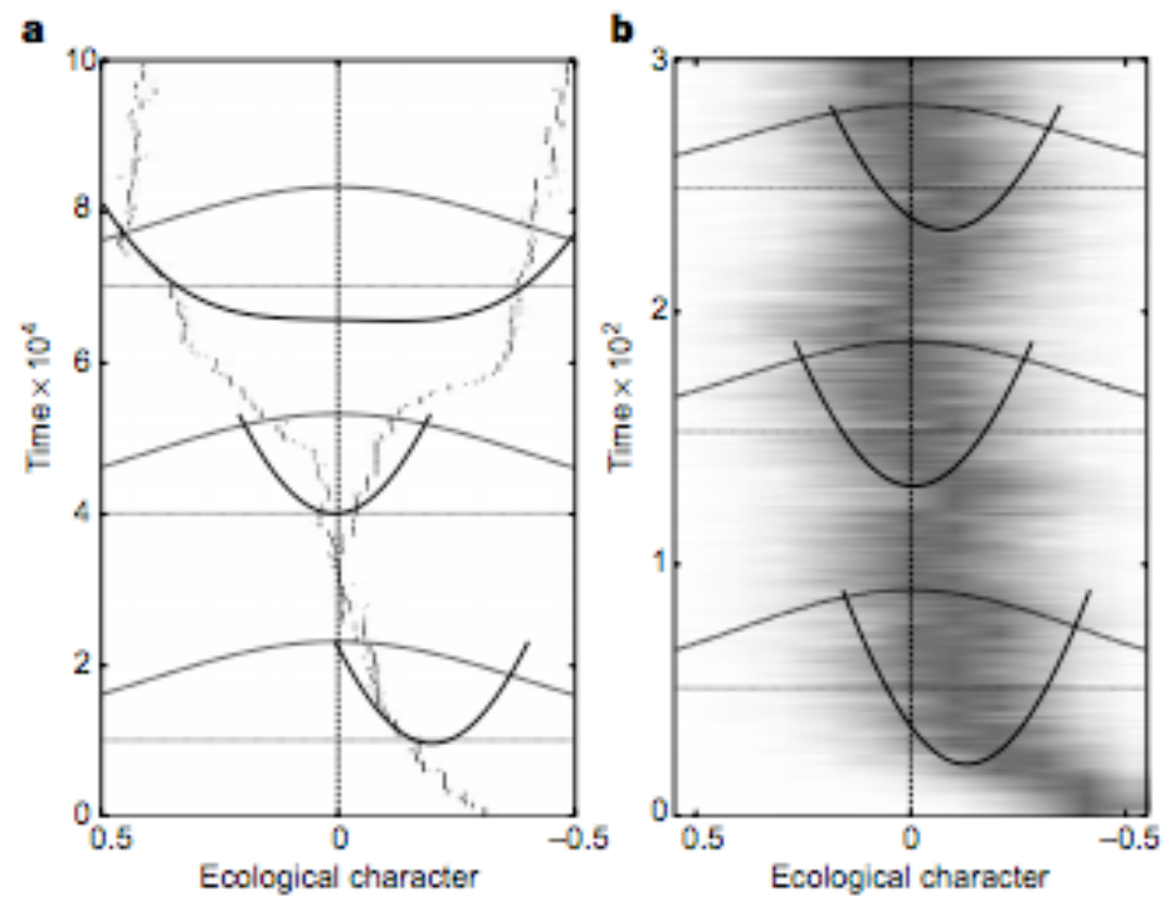
$$s(y,x) = r \cdot \left(1 - \frac{C(x-y)K(x)}{K(y)}\right)$$

If $\sigma_C < \sigma_K$

branching

IBM, asexual

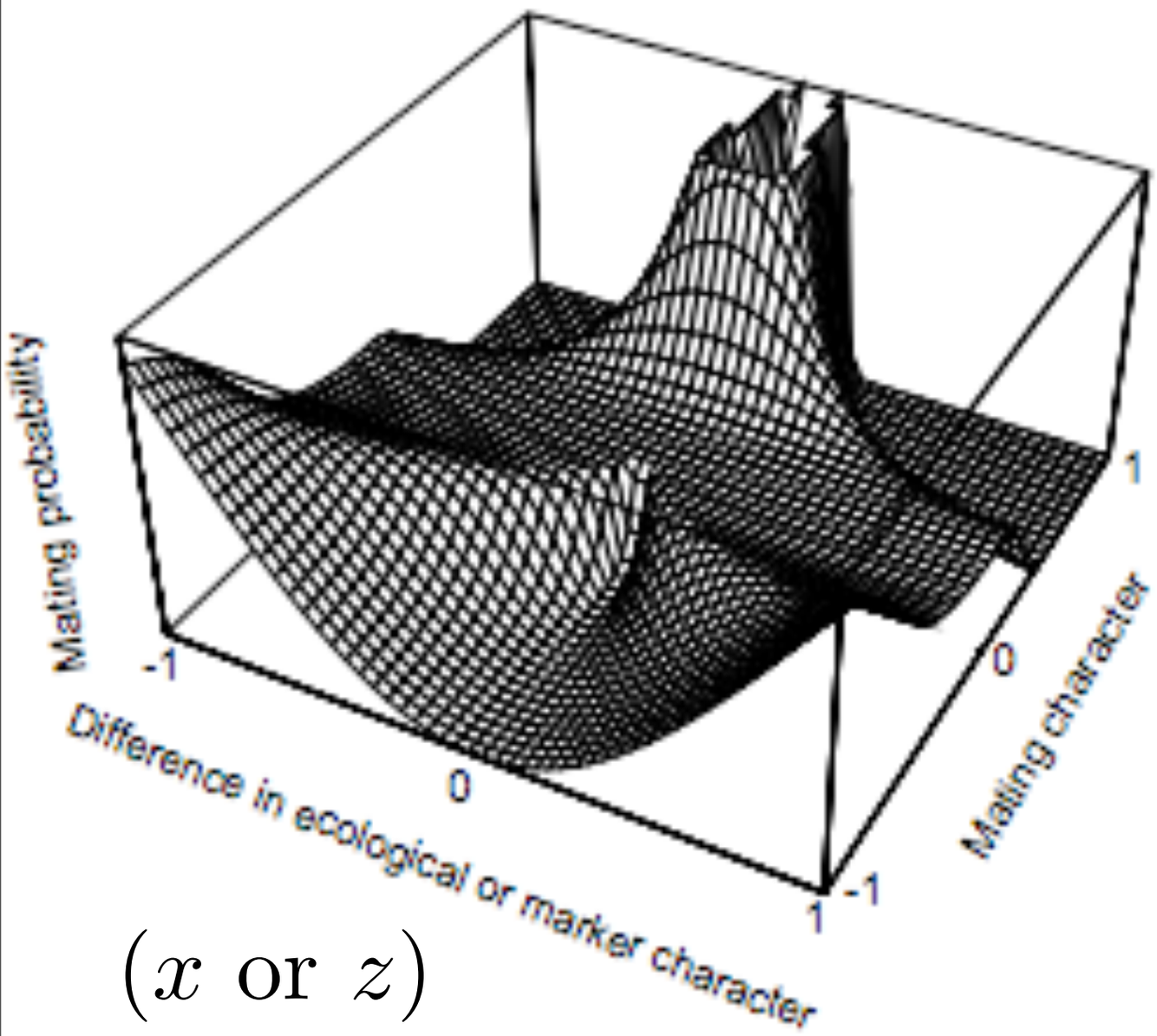
a + multi locus genetics



evolutionary attractor

$[x, m, z] \in [-1, +1]^3$

mating character



$(x \text{ or } z)$

m

$+1 = +$ assortment

$0 = \text{random}$

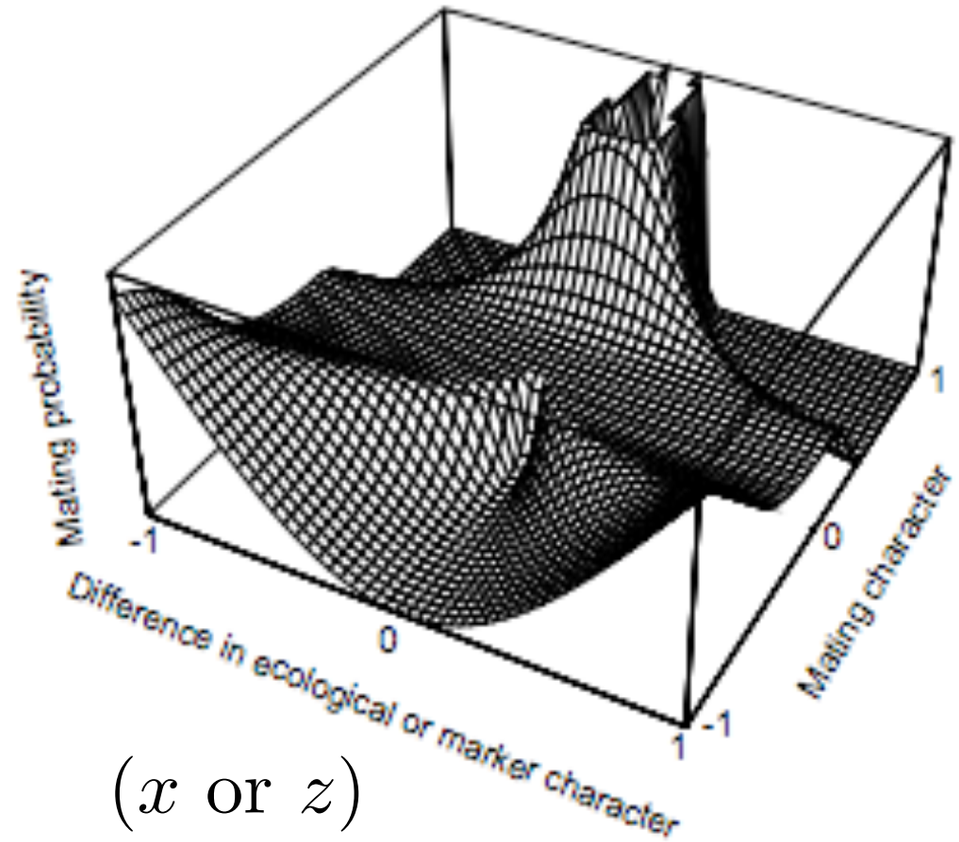
$-1 = -$ assortment

$[G_x, G_m, G_z] \in (Z_2^5 \times Z_2^5)^3$

1 ecological character

++ -- ++ -- ++ $\cdots$ -- ++ -- ++ -- x

$\frac{N_+ - N_-}{10}$



$(x \text{ or } z)$ m

3 marker character

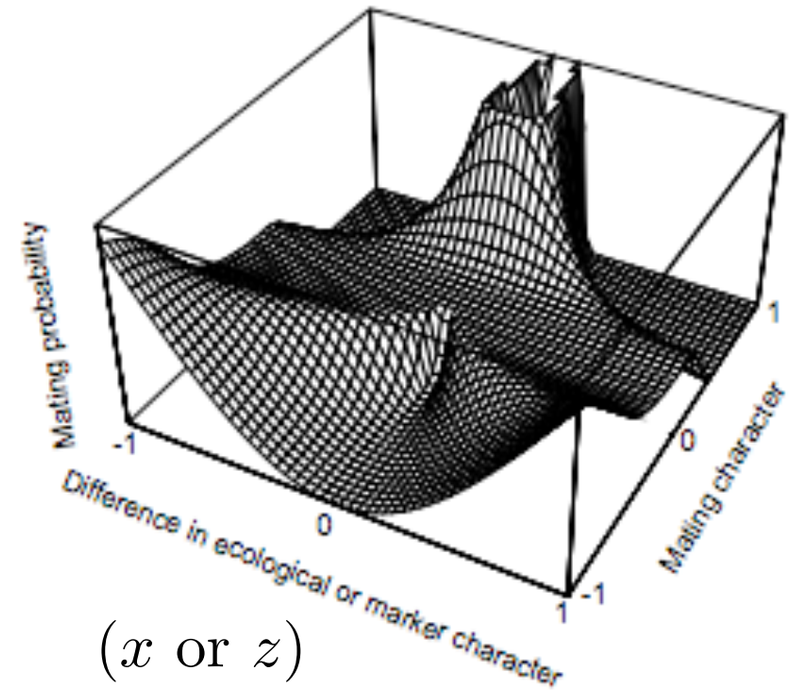
++ -- ++ -- ++ $\cdots$ -- ++ -- ++ -- z

$\frac{N_+ - N_-}{10}$

2 mating character

++ -- ++ -- ++ $\cdots$ -- ++ -- ++ -- m

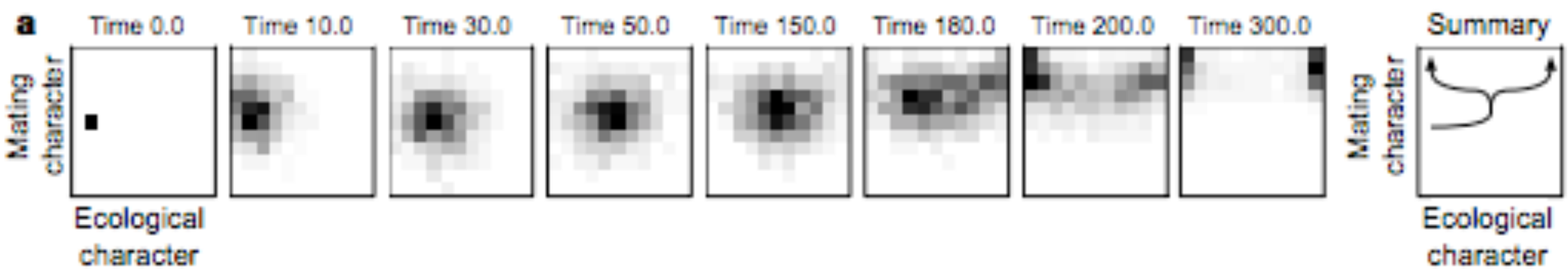
$\frac{N_+ - N_-}{10}$

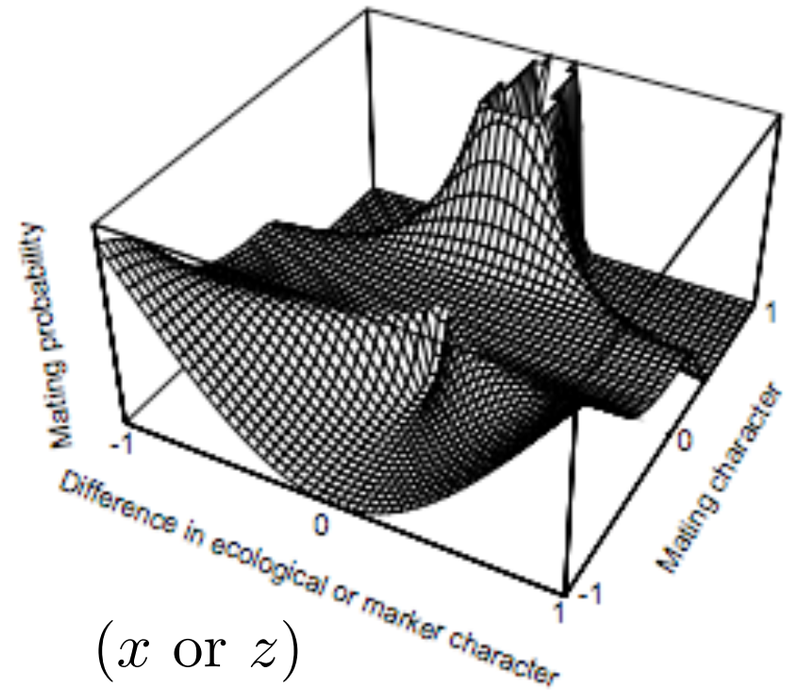


m

$(x \text{ or } z)$

scenario 1: m linked to x ecological character

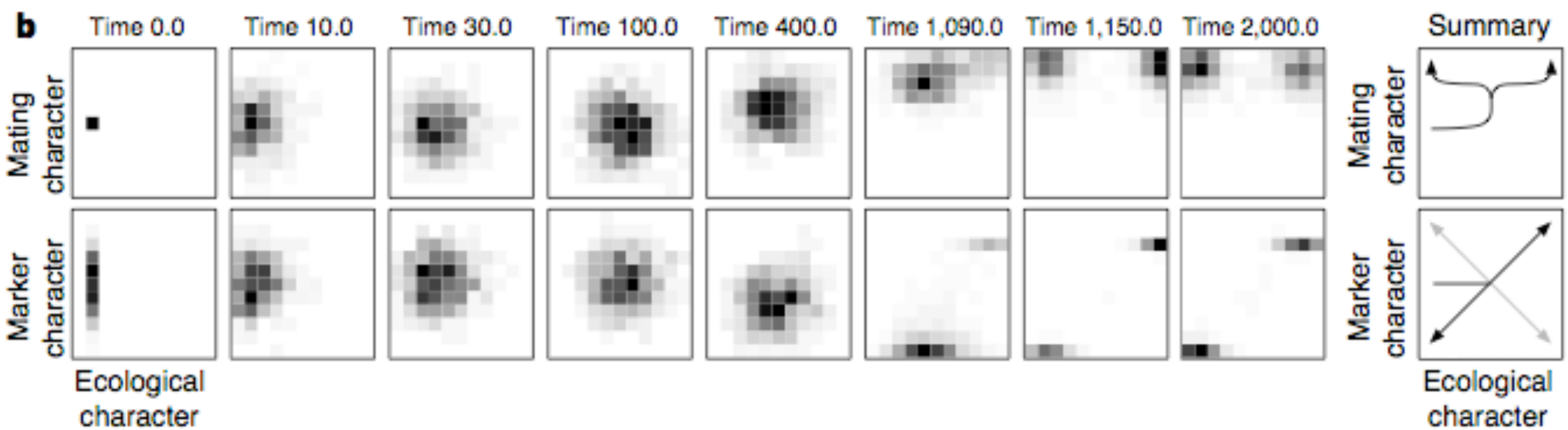




$(x \text{ or } z)$

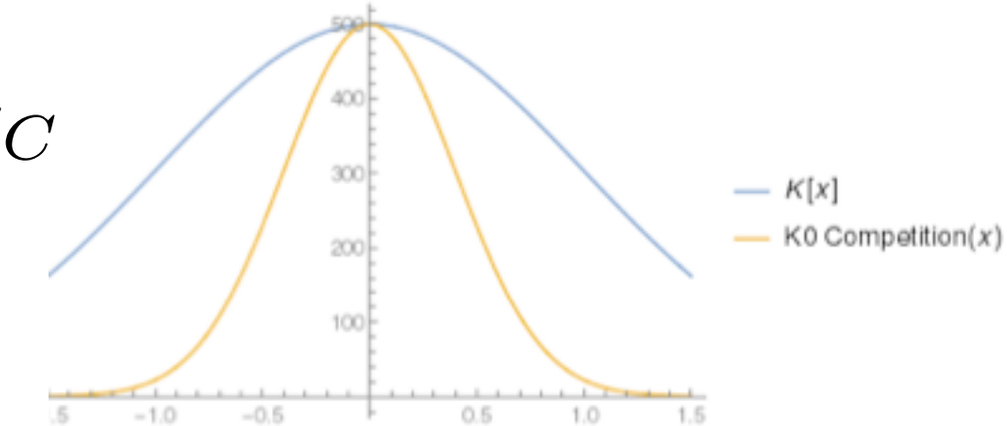
m

scenario 2: m linked to z marker character

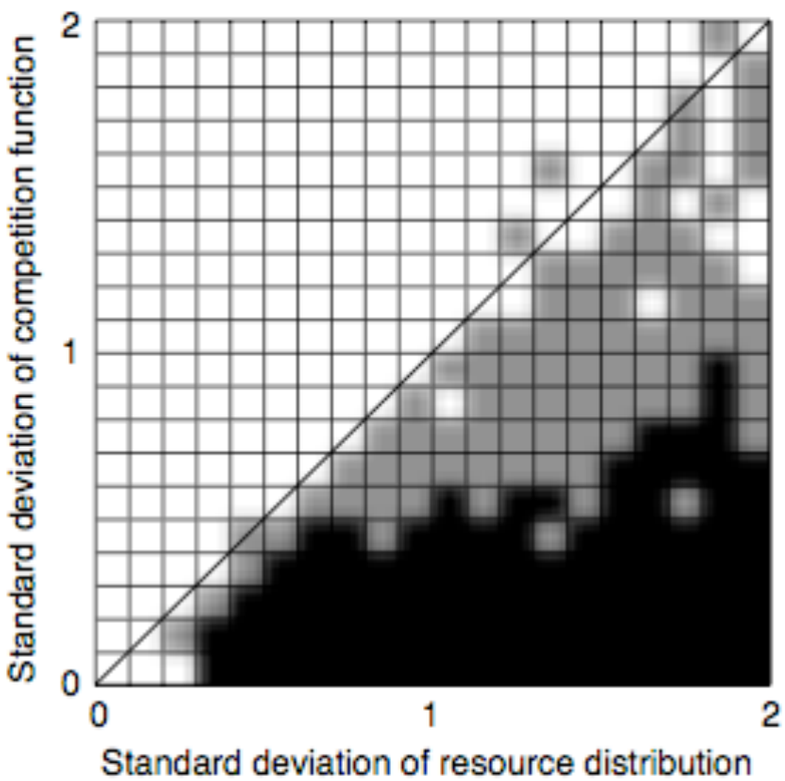


Conditions for branching

$\sigma_K > \sigma_C$



σ_C



σ_K

no branching

ecological character

marker character

fewer loci, branching is more likely