

1 a). SIS model with

$\lambda(N)$ : density-dependent birth rate of susceptible;

$\alpha(x_i)$ : virus-related death rate;

$\beta(x_i)$ : virus-related transmission rate;

$x_i$ : a property of the  $i$ th virus;

$\mu$ : natural death rate.

b). Rewrite as

$$\frac{\dot{n}_i}{n_i} = \beta(x_i) E - \mu - \alpha(x_i) = r(x_i, E), \quad i=1, 2, \dots, k,$$

$$\dot{E} = \lambda(N)E - \mu E - E \sum_j \beta(x_j) I_j.$$

c). Invader dynamic:

$$\frac{\dot{m}}{m} = \beta(y) E - \mu - \alpha(y) = r(y, E).$$

Invasion fitness:

$$S_E(y) = \langle r(y, E) \rangle = \beta(y) \langle E(t) \rangle - \mu - \alpha(y).$$

Essential dimension of  $E$  is one, thus coexistence is impossible.

d). Selective neutrality:

$$S_E(x) = 0 \Rightarrow \langle E(t) \rangle = \frac{\mu + \alpha(x)}{\beta(x)}.$$

Invasion fitness becomes

$$S_x(y) = \beta(y) \frac{\mu + \alpha(x)}{\beta(x)} - \mu - \alpha(y).$$

e).  $S_x(y) > 0 \Leftrightarrow \frac{\mu + \alpha(x)}{\beta(x)} > \frac{\mu + \alpha(y)}{\beta(y)}$ , that is to say,

there is an optimal principle which minimizes  $\frac{\mu + \alpha}{\beta}$ .

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a). SIS model with

 $\mu(N)$ : density-dependent natural death rate; $\lambda N$ : density-dependent recruitment rate of susceptible.

b). Rewrite as

$$\frac{\dot{n}_i}{n_i} = \beta(x_i) E_1 - E_2 - \alpha(x_i) := r(x_i, E), \quad i=1, 2, \dots, k,$$

$$E = (E_1, E_2),$$

$$\dot{E}_1 = \lambda(E_1 + \sum_i n_i) - E_2 \cdot E_1 - E_1 \cdot \sum_j \beta(x_j) \cdot n_j,$$

$$\dot{E}_2 = \mu(E_1 + \sum_j n_j).$$

c). Invader dynamic:

$$\frac{\dot{m}}{m} = \beta(y) \cdot E_1 - E_2 - \alpha(y) = r(y, E).$$

Invasion fitness:

$$S_E(y) = \beta(y) \langle E_1(t) \rangle - \langle E_2(t) \rangle - \alpha(y).$$

Essential dimension of  $E$  is two, thus at most two different resident types can coexist.

d). Selective neutrality:

$$S_E(x_1) = S_E(x_2) = 0 \Rightarrow \langle E_1 \rangle = \frac{\alpha(x_1) - \alpha(x_2)}{\beta(x_1) - \beta(x_2)}, \quad \langle E_2 \rangle = \frac{\alpha(x_1) - \alpha(x_2)}{\beta(x_1) - \beta(x_2)} - \alpha(x_1)$$

Invasion fitness becomes

$$S_{x_1, x_2}(y) = (\beta(y) - \beta(x_1)) \frac{\alpha(x_1) - \alpha(x_2)}{\beta(x_1) - \beta(x_2)} - (\alpha(y) - \alpha(x_1)).$$

$$e). S_{x_1, x_2}(y) > 0 \Leftrightarrow \frac{\alpha(x_1) - \alpha(x_2)}{\beta(x_1) - \beta(x_2)} > \frac{\alpha(y) - \alpha(x_1)}{\beta(y) - \beta(x_1)}.$$

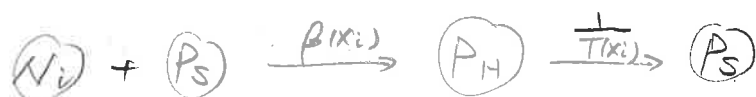
Here we cannot find a function  $\varphi: X \rightarrow \mathbb{R}$  such that  $\varphi(y) \geq \varphi(x)$ . Thus there isn't an optimisation principle.

3 a). Prey - Predator model (or resource - consumer) with

$\alpha(x_i) (1 - \frac{\sum_j N_j}{K})$  : logistic growth rate;

$\beta(x_i)$  : encounter rate of prey  $(x_i)$  and predator;

$T(x_i)$  : handling time for prey  $(x_i)$ ;



prey  $(x_i)$       searching predator

handling predator

Through some steps calculations, then at equilibrium,

$$\left\{ \begin{aligned} P_S &= \frac{1}{1 + \sum_j T(x_j) \beta(x_j) N_j} \cdot P \\ P_H &= P - P_S \end{aligned} \right.$$

Thus, in the dynamic of  $N_i$ , this gives a predator

term  $\beta(x_i) N_i P_S = \frac{\beta(x_i) N_i}{1 + \sum_j T(x_j) \beta(x_j) N_j} \cdot P$ .

b). Rewrite as

$$\frac{\dot{n}_i}{n_i} = \alpha(x_i) E_1 - \beta(x_i) E_2, \quad i=1, 2, \dots, k,$$

$$E = (E_1, E_2)$$

$$E_1 = 1 - \frac{\sum_j N_j}{K}$$

$$E_2 = \frac{P}{1 + \sum_j T(x_j) \beta(x_j) n_j}$$

c). Invader dynamic:

$$\frac{\dot{m}}{m} = \alpha(y) E_1 - \beta(y) E_2$$

Invasion fitness:

$$S_E(y) = \alpha(y) \langle E_1(t) \rangle - \beta(y) \langle E_2(t) \rangle$$

$$\Rightarrow \text{Sign} [S_E(y)] = \text{Sign} \left[ \alpha(y) \frac{\langle E_1(t) \rangle}{\langle E_2(t) \rangle} - \beta(y) \right]$$

Thus we can define the fitness proxy as

$$\tilde{S}_E(y) = \alpha(y) \frac{\langle E_1(t) \rangle}{\langle E_2(t) \rangle} - \beta(y).$$

Here the environment acts one-dimensionally.

d). Selective neutrality:

$$\tilde{S}_E(x) = 0 \Rightarrow \frac{\langle E_1(t) \rangle}{\langle E_2(t) \rangle} = \frac{\beta(x)}{\alpha(x)}.$$

The invasion fitness proxy becomes

$$\tilde{S}_X(y) = \alpha(y) \frac{\beta(x)}{\alpha(x)} - \beta(y).$$

e).  $\tilde{S}_X(y) > 0 \Leftrightarrow \frac{\beta(x)}{\alpha(x)} > \frac{\beta(y)}{\alpha(y)}$

ie. there is an optimal principle which minimises  $\frac{\beta}{\alpha}$ .

f). In above calculation, we don't need the dynamic of P.

⇒ Different way to rewrite the dynamics in the form

b).  $\frac{\dot{n}_i}{n_i} = \alpha(x_i) \left(1 - \frac{E_1}{K}\right) - \beta(x_i) E_2, \quad i = 1, 2, \dots, k$

\*  $E = (E_1, E_2),$

$E_1 = \sum_j n_j,$

$E_2 = \frac{\rho}{1 + \sum_j T(x_j) \beta(x_j) n_j}.$

Note that we cannot absorb  $K$  into  $E_1$  if  $K$  is a function of strategy.

c). Invader dynamic:

$$\frac{\dot{m}}{m} = \alpha(y) \left(1 - \frac{E_1}{K}\right) - \beta(y) E_2$$

Invasion fitness:

$$S_E(y) = \alpha(y) \left(1 - \frac{\langle E_1 \rangle}{K}\right) - \beta(y) \langle E_2 \rangle.$$

Here the environment acts two-dimensionally. From the principle of selective neutrality

$$S_E(x_1) = S_E(x_2) = 0 \Rightarrow \langle E_2 \rangle = \frac{\alpha(x_1)}{\beta(x_1)} \left(1 - \frac{\langle E_1 \rangle}{K}\right) \\ = \frac{\alpha(x_2)}{\beta(x_2)} \left(1 - \frac{\langle E_1 \rangle}{K}\right)$$

Case I: As  $\langle E_2 \rangle \neq 0$  and  $\langle E_1 \rangle \neq K$ , it leads to  $\frac{\alpha(x_1)}{\beta(x_1)} = \frac{\alpha(x_2)}{\beta(x_2)}$  for any two different resident types. In general, the proportion of p.c. birth rate  $\alpha(x)$  and encounter rate  $\beta(x)$  are strategy-dependent.

Case II: As  $\langle E_2 \rangle = 0$ , then  $\langle E_1 \rangle = K$ . It means that predator eventually extincts and prey population stays at carry capacity  $K$ . At this moment, the environment acts one-dimensionally.

To sum up, the effective environment is only one for general situations.

d)' From the principle of selective neutrality,

$$S_E(x) = 0 \Rightarrow \langle E_2 \rangle = \frac{\alpha(x)}{\beta(x)} \left(1 - \frac{\langle E_1 \rangle}{K}\right) > 0 \\ \Rightarrow \langle E_1 \rangle < K$$

Invasion fitness becomes

$$S_x(y) = \alpha(y) \left(1 - \frac{\langle E_1 \rangle}{K}\right) - \beta(y) \frac{\alpha(x)}{\beta(x)} \left(1 - \frac{\langle E_1 \rangle}{K}\right) \\ = \left(\alpha(y) - \beta(y) \frac{\alpha(x)}{\beta(x)}\right) \left(1 - \frac{\langle E_1 \rangle}{K}\right)$$

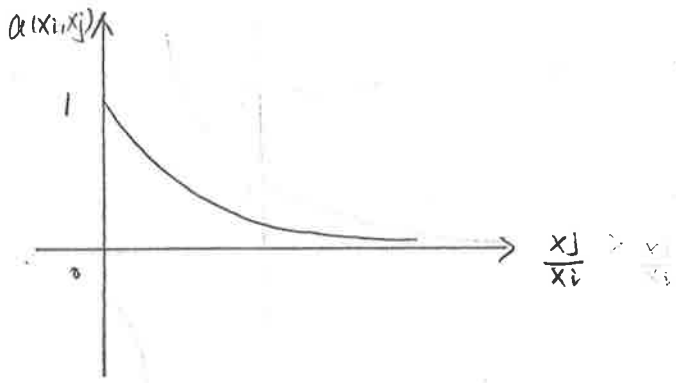
$$e)' \quad S_x(y) > 0 \Leftrightarrow \frac{\alpha(y)}{\beta(y)} > \frac{\alpha(x)}{\beta(x)}$$

There is an optimal principle which maximizes  $\frac{\alpha}{\beta}$ .

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a). Lotka-Volterra competition model with competition kernel.

$$\alpha(x_i, x_j) = \gamma x_i \frac{1}{x_i + x_j} = \gamma \cdot \frac{1}{1 + \frac{x_j}{x_i}}$$



$\forall x_i, x_j \in X \subset \mathbb{R}_+^1$   
for  $i, j = 1, \dots, k$ .

b). There aren't more conditions and definitions about the strategy space  $X$  such that the term

$$\gamma x_i \sum_j \frac{1}{x_i + x_j} \cdot n_j$$

can be splitted as

$$= \gamma x_i \cdot (f(x_i) \cdot g(x_1, \dots, x_k, n_1, \dots, n_k)).$$

Thus, if we set  $E = \sum_j \frac{1}{x_i + x_j} n_j$ , then the dynamic of  $n_i$  can be rewritten as

$$\frac{\dot{n}_i}{n_i} = \alpha(x_i) - f(x_i) - \gamma x_i \cdot E(x_i, t).$$

Further, in the invader dynamic,

$$\frac{\dot{m}}{m} = \alpha(y) - f(y) - \gamma y \cdot E(y, t).$$

However, we now cannot define the invasion fitness since the  $E$  is a function of invader strategy.

From the loop of environmental feedback and the basic assumption of adaptive dynamic, invaders are rare such that they cannot affect environment.

In short,  $E$  should be  $y$ -independent.

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Therefore, we cannot continuously to ask the questions c), d) and e).