Discrete population models and dispersal: Part I

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Motivation

(2019) Habitat **fragmentation** has become one of the main drivers of species **extinction and biodiversity loss.**

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Effects of dispersal on population fitness

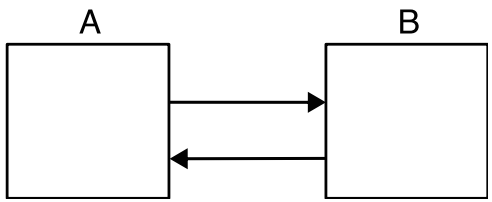
How does increased connectivity affect...?

- **Persistence**
- **Synchrony**
- **Stability**
- ⋮

Recently, there is increasing interest in the effect on

- **Total biomass**

We study the simplest network of two patches that behave as **sources** when isolated.



Experimental results

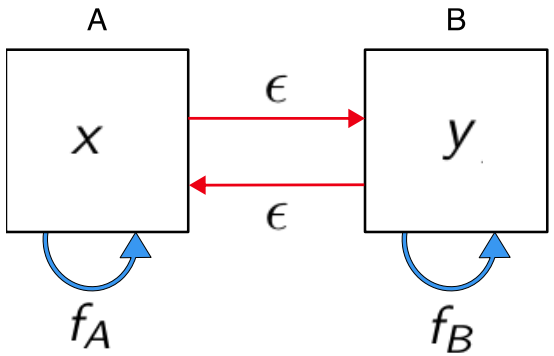
1. (Ives et al., 2004) Increasing dispersal **always increases** total biomass for yeast-like fungus.
2. (Aström and Pärt,2013) Increasing dispersal **always decreases** total biomass for oribatid mites.
3. (Dey et al., 2014) Dispersal has **no significant effect** on the total biomass regardless of the dispersal intensity for fruit flies.
4. (Vortkamp et al., 2022) Low dispersal **increases** total biomass but high dispersal **decreases** it for *Escherichia coli*.

Symmetric dispersal

Models for symmetric dispersal

Continuous time

Freedman and Waltman (1977):



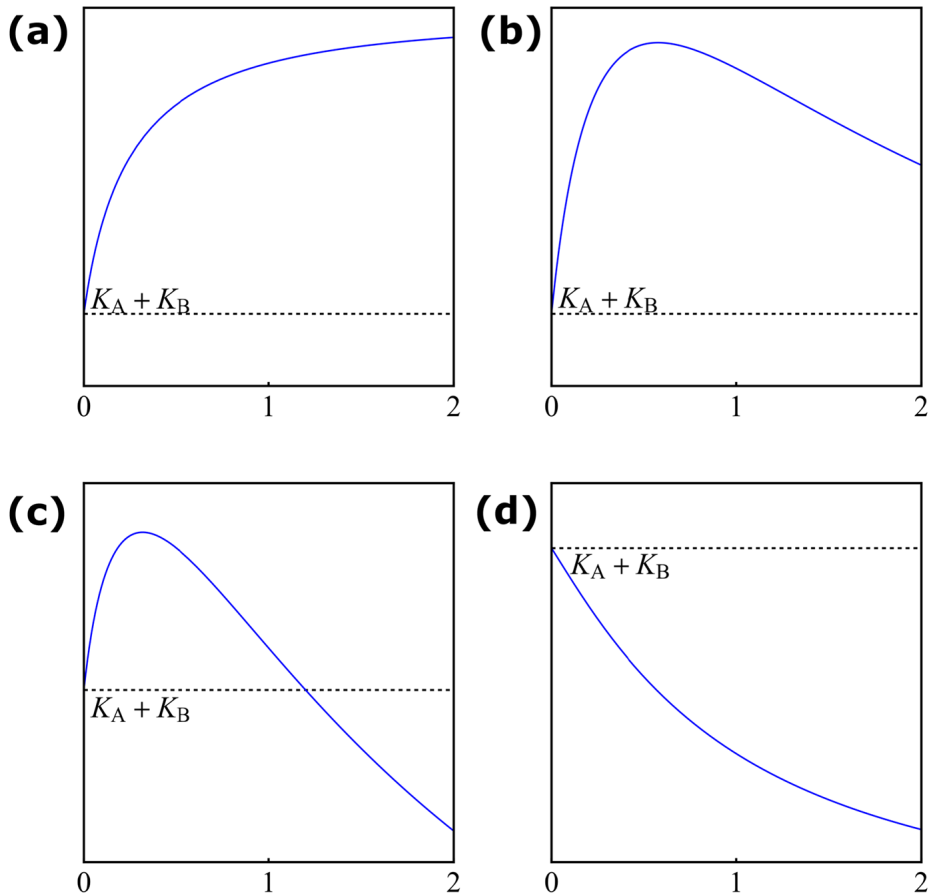
$$\begin{cases} \frac{dx}{dt} = f_A(x) - \epsilon(x - y), \\ \frac{dy}{dt} = f_B(y) - \epsilon(y - x), \end{cases} \tag{1}$$

Maps f_A and f_B are the **logistic maps**

$$f_i(x) = r_i x \left(1 - \frac{x}{K_i}\right),$$

and the dispersal rate is $\epsilon \in [0, \infty)$.

Gao D, Lou Y (2022) Total biomass of a single population in two-patch environments. Theor Popul Biol 146:1–14.



Models for symmetric dispersal

Discrete time

Reproduction/Dispersal (Gadgil, 1971):

$$\begin{cases} x_{t+1} = (1-m)f_A(x_t) + mf_B(y_t), \\ y_{t+1} = mf_A(x_t) + (1-m)f_B(y_t), \end{cases} \tag{2}$$

Dispersal/Reproduction

$$\begin{cases} x_{t+1} = f_A((1-m)x_t + my_t), \\ y_{t+1} = f_B(mx_t + (1-m)y_t), \end{cases} \tag{3}$$

Maps f_A and f_B are the **Beverton-holt maps**

$$f_i(x) = \frac{r_i x}{1 + \zeta_i x},$$

where $r_i > 1$ (sources), $\zeta_i = (r_i - 1)/K_i$ is the strength of intraspecific competition, and $m \in [0, 1]$ is the dispersal rate.

To our knowledge, **only 2 previous** works have addressed the considered questions in discrete time.

1. Gadgil (1971) studied model (2) with quadratic local dynamics and proved increasing dispersal **always decreases** total biomass.

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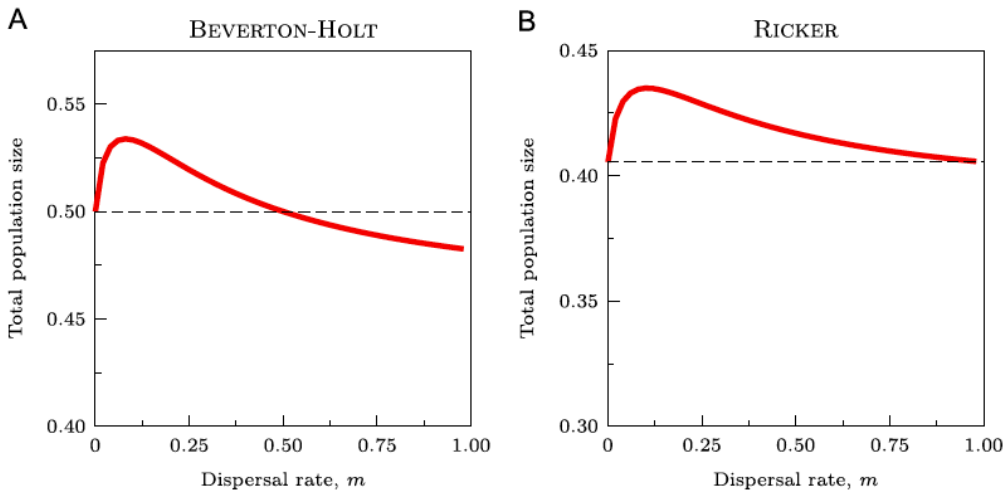
1. Gadgil (1971) studied model (2) with quadratic local dynamics and proved increasing dispersal **always decreases** total biomass.
2. Franco and Ruiz-Herrera (2015) studied model (2) with Beverton-Holt and Ricker local dynamics. They showed...
   - **Theoretically:** for $m \to 0^+$, increasing dispersal **always increases** total biomass.
   - **Numerically:** unique response scenario **(hump-shaped)**.



Why these contradictory results?

Gao & Lou (2022) results vere obtained for **heterogeneous patches.**

This was **NOT true for the previous works:**

- Gadgil (1971) assumed a **common growth rate** in the two patches, $r_A = r_B$.
- Franco & Ruiz-Herrera (2015) implicitly assumed a **common strength of intraspecific competition** in the two patches since they used B-H maps in the form

$$f_i(x) = \frac{r_i x}{1 + x},$$

which implies $\zeta_A = \zeta_B = 1$.

Extending the results in discrete time

The order of events doesn't matter

Reproduction/Dispersal:

$$\begin{cases} x_{t+1} = (1-m)f_A(x_t) + mf_B(y_t), \\ y_{t+1} = mf_A(x_t) + (1-m)f_B(y_t), \end{cases} \tag{2}$$

Dispersal/Reproduction

$$\begin{cases} x_{t+1} = f_A((1-m)x_t + my_t), \\ y_{t+1} = f_B(mx_t + (1-m)y_t), \end{cases} \tag{3}$$

Proposition 1

For B-H local dynamics, systems (2) *and* (3) *are topologically equivalent.*

Extending the results in discrete time

Stability

Lemma 1

Assume $K_A = K_B$. Then, connecting the two patches with any dispersal rate $m \in (0, 1]$ has no effect on the asymptotic total biomass.

In what follows, we **assume $K_A \neq K_B$**.

Proposition 2 (Application of Kirkland, S., Li, C.K., & Schreiber, S.J. **SIAM J. Appl. Math.** 2006)

Assume $K_A \neq K_B$. For each $m \in [0, 1]$, system (2) has a fixed point $(x(m), y(m)) \in \mathbb{R}^2_{++}$ such that

$$\lim_{t \to +\infty} (x_t, y_t) = (x(m), y(m))$$

for any initial condition $(x_0, y_0) \in \mathbb{R}^2_+ \setminus \{(0, 0)\}$.

Extending the results in discrete time

(Asymptotic) total biomass

By Lemma 3, for each dispersal rate $m \in [0,1]$, we can define the (asymptotic) **total biomass** as $x(m) + y(m)$.

To study the effect of dispersal on the total biomass, we consider $H\colon [0,1] \to \mathbb{R}$ with

$$H(m) := x(m) + y(m) - (K_A + K_B).$$

$$\begin{cases} H(m) > 0 \to & \text{connecting patches is } \textit{beneficial,} \\ H(m) < 0 \to & \text{connecting patches is } \textit{detrimental.} \end{cases}$$

The possible response scenarios depend on two aspects:

1. Shift points ($H(m) = 0$ for $m \in (0,1)$).
2. Monotonicity of H.

Extending the results in discrete time

Shift points (zeros of H in $(0,1)$)

Define

$$\tilde{m} := \frac{K_A K_B (r_A - 1)(r_B - 1)(r_A - r_B)}{(K_A(r_B - 1) + K_B(r_A - 1))(K_A r_A (r_B - 1) - K_B r_B (r_A - 1))}.$$

Proposition 3

Assume $K_A \neq K_B$. If $r_A = r_B$, $K_A r_A (r_B - 1) = K_B r_B (r_A - 1)$, or $\tilde{m} \notin (0,1]$, then H has **no zeros** *in $(0,1)$. Otherwise, H has* **one zero** *in $(0,1)$, $m = \tilde{m}$.*

At most one shift point!!

beneficial→detrimental or detrimental→beneficial

Extending the results in discrete time

Derivative of H at $m = 0^+$

Proposition 4

Assume $K_A \neq K_B$. Then,

$$H'(0^+) = \frac{(r_A - r_B)(K_A - K_B)}{(r_A - 1)(r_B - 1)} \qquad \textbf{(either } \geq \textbf{0 or } \leq \textbf{0).}$$

Remark: Franco & Ruiz-Herrera (2015) considered $\zeta_i = 1$, i.e., $K_i = r_i - 1$, and in that case

$$H'(0^+) = \frac{(r_A - r_B)^2}{(r_A - 1)(r_B - 1)} \geq \textbf{0.}$$

Extending the results in discrete time

Monotonicity of H

Consider

$$a := (r_B - 1)(K_A\sqrt{r_A}(r_B - 1) + K_B\sqrt{r_B}(r_A - 1)),$$
$$b := K_B(r_B - 1)(2K_A\sqrt{r_A} - (K_A - K_B + (K_A + K_B)r_A)\sqrt{r_B}),$$
$$c := -K_A K_B^2(\sqrt{r_A} - \sqrt{r_B})(\sqrt{r_A r_B} - 1).$$

Lemma 2

Equation $ay^2 + by + c = 0$ has two simple real roots.

Define y^* as the largest root of $ay^2 + by + c = 0$ and

$$x^* := \frac{K_A(K_B(\sqrt{r_A} - \sqrt{r_B}) + \sqrt{r_A}(r_B - 1)y^*)}{K_B\sqrt{r_B}(r_A - 1)}.$$

Extending the results in discrete time

H is either **monotonic** or **hump-shaped...**

Proposition 5

Assume $K_A \neq K_B$. Then, $f_A(x^*) \neq f_B(y^*)$, and if we define

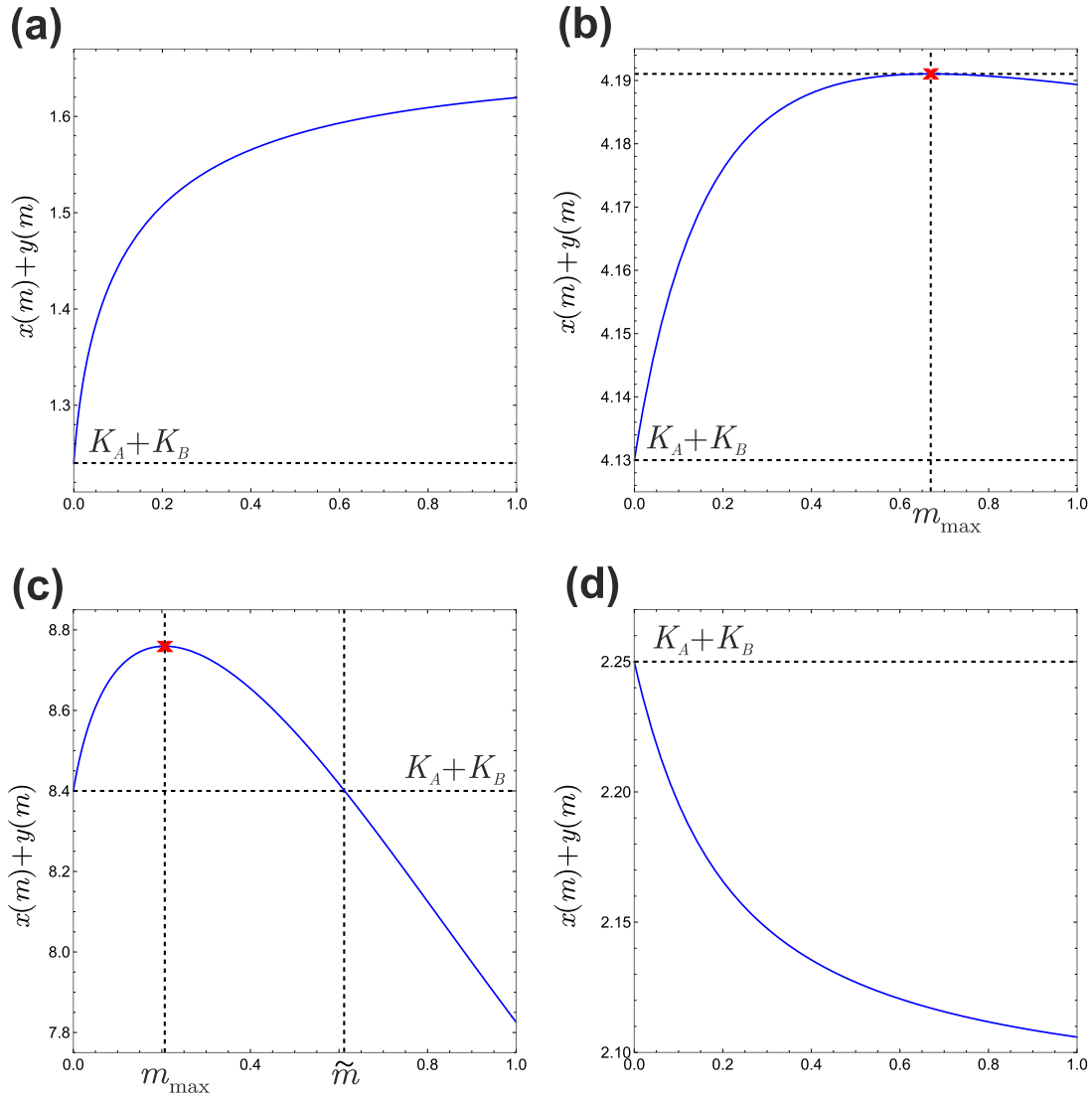
$$m_{\max} := \frac{y^* - f_B(y^*)}{f_A(x^*) - f_B(y^*)},$$

then the following holds:

1. *If $m_{\max} \notin (0,1)$, then H is strictly monotonic in $[0,1]$.*
2. *If $m_{\max} \in (0,1)$, then H is strictly increasing in $[0, m_{\max})$ and strictly decreasing in $(m_{\max}, 1]$.*

Extending the results in discrete time

Response scenarios



Extending the results in discrete time

Theorem 1

Assume $K_A \neq K_B$.

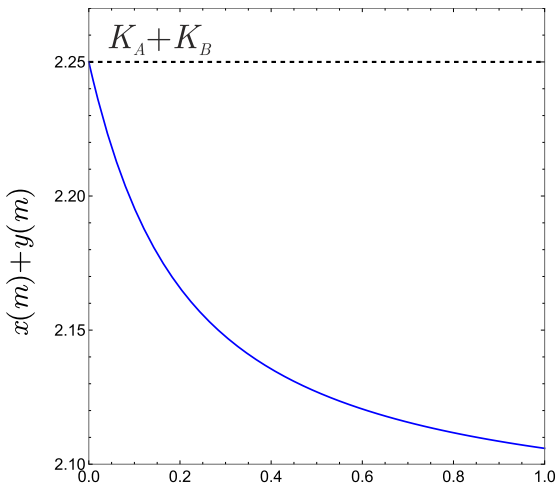
1. *If* $\frac{\sqrt{r_A}(r_B-1)}{\sqrt{r_B}(r_A-1)} \leq \frac{K_B}{K_A} < 1$, *then* H *is positive in* $(0,1)$. *Moreover,*
   - (i) *If* $m_{\max} \notin (0,1)$, *then* H *is strictly increasing in* $[0,1]$ *(monotonically beneficial).*
   - (ii) *If* $m_{\max} \in (0,1)$, *then* H *is strictly increasing in* $[0, m_{\max})$ *and strictly decreasing in* $(m_{\max}, 1]$ *(unimodally beneficial).*
2. *If* $\frac{K_B}{K_A} < \frac{\sqrt{r_A}(r_B-1)}{\sqrt{r_B}(r_A-1)}$, *then* $0 < m_{\max} < \tilde{m} < 1$. *Moreover,* H *is positive and strictly increasing in* $(0, m_{\max})$, *positive and strictly decreasing in* $(m_{\max}, \tilde{m})$, *and negative and strictly decreasing in* $(\tilde{m}, 1]$ *(beneficial turning detrimental).*
3. *If* $\frac{K_B}{K_A} > 1$, *then* H *is negative and strictly decreasing in* $[0,1]$ *(monotonically detrimental).*

Asymmetric dispersal

Studying the effect of dispersal asymmetry

Motivation

- Asymmetric dispersal naturally appears in many populations (e.g., wind carrying seeds in a particular direction).
- Assume that the response to symmetric dispersal is

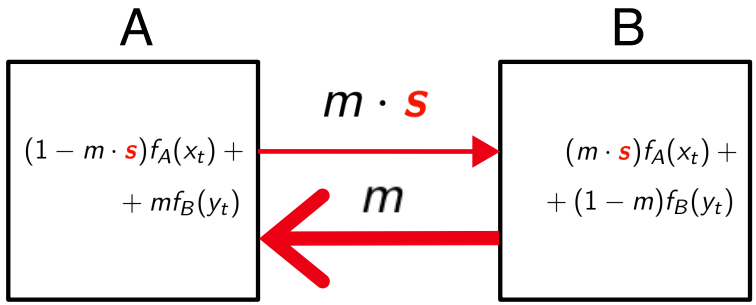


Modifying this scenario implies modifying r_i or K_i since symmetric dispersal has a fixed response for r_i and K_i given. This is **unfeasible** in most cases.

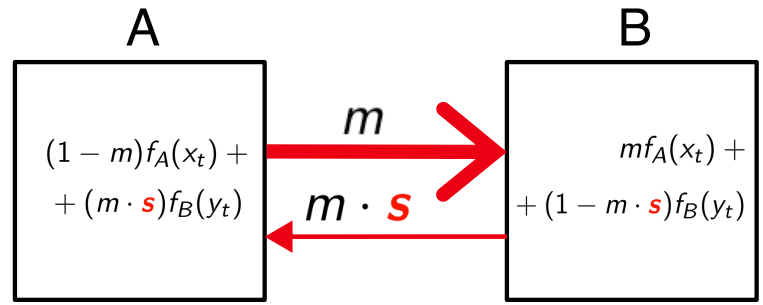
Can induced asymmetry modify the scenario?

Models for asymmetric dispersal

Assume a **symmetry level** $s \in [0,1]$ ($s = 1$ symmetry, $s = 0$ total asymmetry).



$$\begin{cases} x_{t+1} = (1 - m \cdot s)f_A(x_t) + mf_B(y_t), \\ y_{t+1} = (m \cdot s)f_A(x_t) + (1 - m)f_B(y_t), \end{cases} \quad (4)$$



$$\begin{cases} x_{t+1} = (1 - m)f_A(x_t) + (m \cdot s)f_B(y_t), \\ y_{t+1} = mf_A(x_t) + (1 - m \cdot s)f_B(y_t), \end{cases} \quad (5)$$

Focus on model (4) and define

$$s_1 := \frac{K_B(r_A - 1)(K_A r_A(r_B - 1) + K_B r_B(r_A - 1))}{K_A r_A(r_B - 1)(K_A(r_B - 1) + K_B(r_A - 1))},$$

$$s_2 := \frac{y^*}{f_A(x^*)}, \quad \text{and} \quad s_3 := \frac{K_B}{K_A}.$$

Asymmetry does not yield new response scenarios

Theorem 2

The following is true for **model (4) (restrict mobility from A to B):**

1. *If* $r_A > r_B$, *then* $s_3 < s_2 < s_1$ *and the following holds:*
   1. *If* $s < s_3$, *then* H *is negative and strictly decreasing in* $(0, 1]$ *(monotonically detrimental).*
   2. *If* $s_3 < s \leq s_2$, *then* H *is positive and strictly increasing in* $(0, 1]$ *(monotonically beneficial).*
   3. *If* $s_2 < s \leq s_1$, *then* $u^* \in (0, 1)$. *Moreover,* H *is positive and strictly increasing in* $(0, u^*]$, *and positive and strictly decreasing in* $[u^*, 1)$ *(unimodally beneficial).*
   4. *If* $s > s_1$, *then* $0 < u^* < m^* < 1$. *Moreover,* H *is positive and strictly increasing in* $(0, u^*]$, *positive and strictly decreasing in* $[u^*, m^*)$, *and negative and strictly decreasing in* $(m^*, 1]$ *(beneficial turning detrimental).*

Asymmetry does not yield new response scenarios

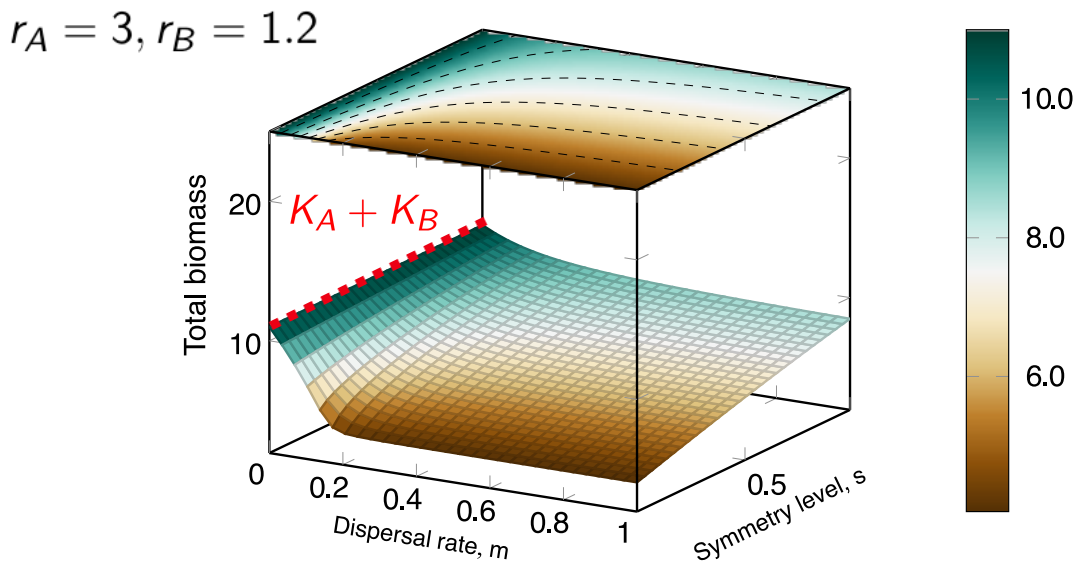
Theorem 2

2. *If* $r_A < r_B$, *then* $s_1 < s_2 < s_3$ *and the following holds:*
   1. *If* $s < s_1$, *then* $0 < u^* < m^* < 1$. *Moreover,* H *is positive and strictly increasing in* $(0, u^*]$, *positive and strictly decreasing in* $[u^*, m^*)$, *and negative and strictly decreasing in* $(m^*, 1]$ *(beneficial turning detrimental).*
   2. *If* $s_1 \leq s < s_2$, *then* $u^* \in (0, 1)$. *Moreover,* H *is positive and strictly increasing in* $(0, u^*]$, *and positive and strictly decreasing in* $[u^*, 1)$ *(unimodally beneficial).*
   3. *If* $s_2 \leq s < s_3$, *then* H *is positive and strictly increasing in* $(0, 1]$ *(monotonically beneficial).*
   4. *If* $s > s_3$, *then* H *is negative and strictly decreasing in* $(0, 1]$ *(monotonically detrimental).*
3. *If* $r_A = r_B$, *then* H *is negative and strictly decreasing in* $(0, 1]$. *(monotonically detrimental).*

Changing the scenario: One way or another...

From Theorem 2, **for model** (4) we observe the following:

- $\boxed{r_A = r_B}$. The only possible scenario is monotonically detrimental for all values of $s \in [0, 1]$.
- $\boxed{r_A \neq r_B}$ Varying asymmetry when restricting mobility from A to B *may* yield different scenarios, but **NOT always:**



Changing the scenario: One way or another...

We can also restrict mobility from B to A!!

$$\begin{cases} x_{t+1} = (1 - m \cdot \boldsymbol{s}) f_A(x_t) + m f_B(y_t), \\ y_{t+1} = (m \cdot \boldsymbol{s}) f_A(x_t) + (1 - m) f_B(y_t), \end{cases} \tag{4}$$

$$\begin{cases} x_{t+1} = (1 - m) f_A(x_t) + (m \cdot \boldsymbol{s}) f_B(y_t), \\ y_{t+1} = m f_A(x_t) + (1 - m \cdot \boldsymbol{s}) f_B(y_t), \end{cases} \tag{5}$$

Proposition 6

Assume $r_A \neq r_B$. *Then,* **the four response scenarios listed in Theorem** (2) **can be obtained by restricting mobility from A to B or from B to A.** *That is, for each of the four scenarios there exists a value* $s \in (0, 1]$ *such that either model* (4) *or model* (5) *shows the scenario.*

Part II by Daniel Franco

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