Discrete population models and dispersal: Part II

Daniel Franco



Universidad Nacional de Educación a Distancia, Madrid (España)

PODE-25, Cartagena, May 2025

▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶
 ▲□▶

Sequels were never good.

◆□▶ ◆御▶ ◆臣▶ ◆臣▶ 三臣 - のへで

Highlights Part I:

- The response of total population to increasing dispersal is monotonic or unimodal.
- That is general: unaffected by asymmetry or considering continuous time.

◆□▶ ◆□▶ ◆□▶ ◆□▶ ●□ ● ●

What does make a sequel good?

◆□▶ ◆御▶ ◆臣▶ ◆臣▶ 三臣 - のへで

A twist!

◆□▶ ◆□▶ ◆臣▶ ◆臣▶ 臣 のへで

Highlight Part II:

There are models with more than four different responses of total population to increasing dispersal.

◆□▶ ◆御▶ ◆臣▶ ◆臣▶ 三臣 - のへで

J. Segura (EADA Business School, Spain)
M. Marvá (U. Alcalá, Spain) -> (U. Alicante, Spain)
J. Perán (UNED, Spain)

J. Theoret. Biol. 2024 and J. Math. Biol. (submitted)



Coupled dynamical systems



Dispersal model

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

<ロ> (四) (四) (三) (三) (三)

æ

with $t \in \mathbb{N}$,

- x, y the population sizes in A and B,
- $m \in [0, 0.5]$ the dispersal rate.

Does local dynamics affect number of responses?



Beverton-Holt maps (monotone, simple dynamics / contest)

$$f_i(x) := \frac{r_i x}{1 + x/M_i}$$

Ricker maps (unimodal, rich dynamics / scramble)

$$f_i(x) := r_i x e^{-x/M_i}$$

Quadratic maps (unimodal, rich dynamics / scramble)

$$f_i(x) := r_i x (1 - x/M_i)$$

with $r_i > 0$ and $M_i > 0$ for $i \in \{A, B\}$.

▲ロト ▲園ト ▲画ト ▲画ト 三回 - のへの

Is H well defined?

Dispersal is beneficial/detrimental depending on the sign of function

 $\mathbf{H}(\mathbf{m}) := \mathbf{x}(\mathbf{m}) + \mathbf{y}(\mathbf{m}) - (\mathbf{K}_{\mathbf{A}} + \mathbf{K}_{\mathbf{B}}),$

with K_A and K_B the attractors of f_A and f_B when isolated.



1 Ricker: $r_i \in (1, e^2)$ and $m \in [0, 0.5]$

Bajo and Ruiz-Herrera. Math. Biosciences (2017).

Positive equilibrium is a strong attractor in the sense of Liz and Ruiz-Herrera, J. Diff. Equations (2013). (Jiménez-López provided them the proof of a key result).

▲ロト ▲団ト ▲ヨト ▲ヨト 三ヨー わらぐ



Lemma

Assume $K_A \neq K_B$. The zeros of *H* are

$$\left\{ rac{x-f_{\mathcal{A}}(x)}{\mathcal{K}_{\mathcal{A}}+\mathcal{K}_{\mathcal{B}}-2f_{\mathcal{A}}(x)} \middle| \psi(x)=0
ight\} \cap [0,0.5],$$

where $\psi \colon [\mathbf{0}, \mathbf{K}_{\mathbf{A}} + \mathbf{K}_{\mathbf{B}}] \to \mathbb{R}$ is given by

$$\psi(\mathbf{x}) := f_{\mathcal{A}}(\mathbf{x}) + f_{\mathcal{B}}(K_{\mathcal{A}} + K_{\mathcal{B}} - \mathbf{x}) - K_{\mathcal{A}} - K_{\mathcal{B}}.$$

Proposition (Ricker)

Assume $0 < r_A, r_B \le e^2$ and $K_A \ne K_B$. Then, ψ (equivalently, *H*) has at most four zeros.

▲ロト ▲団ト ▲ヨト ▲ヨト 三ヨー わらぐ



æ

◆□▶ ◆圖▶ ◆厘▶ ◆厘≯

Relevance. No characterization as in B-H.

Proposition.

Assume H is well defined in [0, 0.5]. Then, the response scenario Detrimental/Beneficial/Detrimental/Beneficial is not possible.

<u>Proof.</u> Assume that *H* has four zeros in the interval [0, 0.5). To rule out the scenario in the statement, we prove H(0.5) < 0. For given $m \in [0, 0.5)$, (x(m), y(m)) belongs to the set

$$C = \{(x, y) \in \mathbb{R}^2_+ \mid f_A(x) - x + f_B(y) - y = 0\}.$$

<ロト <四ト <注入 <注下 <注下 <

C is a simple curve of class one joining the points (K_A , 0) and (0, K_B), and passing through (K_A , K_B).





C is a simple curve of class one joining the points (K_A , 0) and (0, K_B), and passing through (K_A , K_B).



Consider the segment of C parametrized by the dispersal rate

$$C_H = \{(x(m), y(m)) \mid m \in [0, 0.5)\}.$$

イロト イヨト イヨト イヨト

Consider

$$L = \left\{ (x, y) \in \mathbb{R}^2 \, | \, x + y = K_A + K_B \right\}.$$

By hypothesis,

$$L \cap (C \setminus C_H) = \emptyset.$$

Since $x + y < K_A + K_B$ for both $(K_A, 0) \notin C_H$ and $(0, K_B) \notin C_H$, then the inequality holds for all points in $C \setminus C_H$. Given that $(x(0.5), y(0.5)) \in C \setminus C_H$, we have

$$x(0.5) + y(0.5) < K_A + K_B \Longrightarrow H(0.5) < 0$$

Why the differences between B-H and Ricker?

▲ロト ▲団ト ▲ヨト ▲ヨト 三ヨー わらぐ

Scramble/Contest? Unimodal/Monotone?

Why the differences between B-H and Ricker?

▲ロト ▲団ト ▲ヨト ▲ヨト 三ヨー わらぐ

Scramble/Contest? Unimodal/Monotone?

No

Quadratic Similar results to B-H



500

臣

BH and the quadratic map are concave downward in their whole domains, but Ricker has an inflection point.

Shift points are obtained by transforming the zeros of

$$\psi(\mathbf{x}) = f_{A}(\mathbf{x}) + f_{B}(K_{A} + K_{B} - \mathbf{x}) - (K_{A} + K_{B})$$

by the map $x \mapsto m = \frac{x - f_A(x)}{K_A + K_B - 2f_A(x)}$.

If $f_A'' < 0$ and $f_B'' < 0$, then $\psi'' < 0$ and ψ can have at most two zeros.

▲ロト ▲団ト ▲ヨト ▲ヨト 三ヨー わらぐ

Coupling *n* maps

$$x_i(t+1) = \sum_{j=1}^n d_{ij}f_j(x_j(t)), \quad i \in \{1, \dots, n\},$$

 $0 \le d_{ji} \le 1$ give the fraction that moves from *i* to *j*. We assume no cost to dispersal, i.e., $\sum_{i=1}^{n} d_{ij} = 1$ for all $j \in \{1, ..., n\}$.

With matrix notation

$$X(t+1) = DF(X(t))^T,$$

 $D = (d_{ij}), X(t) = (x_1(t), \ldots, x_n(t)), F(X(t)) = (f_1(x_1(t)), \ldots, f_n(x_n(t))).$

《曰》 《聞》 《臣》 《臣》 三臣 …

Do the response scenarios depend on the number of patches within the metapopulation?

◆□▶ ◆御▶ ◆臣▶ ◆臣▶ 三臣 - のへで

Revisiting previous results about the effect of increasing connectivity.



Assumption

The probability of using a path *i* depends on the number n_i of colonization routes leaving it: each path has the same probability of being used.

$$D = \begin{pmatrix} 1 - m & \frac{m}{2} & \frac{m}{2} \\ \frac{m}{2} & 1 - m & \frac{m}{2} \\ \frac{m}{2} & \frac{m}{2} & 1 - m \end{pmatrix}$$

イロト イヨト イヨト イヨト

æ

New scenarios!

A 3-patch ring topology under the previous assumption and with B-H local dynamics presents the same responses of the 2-patch Ricker case.



◆ロト ◆母ト ◆臣ト ◆臣ト 三臣 → ���?

Effect of increasing connectivity

Change a chain to a ring



Ruiz-Herrera, A. Metapopulation dynamics and total biomass: Understanding the effects of diffusion in complex networks, Theor. Popul. Biol. (2018).

▲□▶ ▲圖▶ ▲厘▶ ▲厘▶

æ



 $\delta'(0) = H'_c(0) - H'_r(0) > 0$

R-H affirms that connecting source patches that were initially disconnected is always beneficial. However, this becomes false when more biologically realistic maps allowing for different intraspecific competition strengths in the subpopulations are considered.



<ロト <部ト <きト <きト = 3



Assumption B

Dispersal depends on the probability to remain in a patch with independence of the number of connections of it with other patches.

$$D_{c} = \begin{pmatrix} 1 - m & 0 & \frac{m}{2} \\ 0 & 1 - m & \frac{m}{2} \\ m & m & 1 - m \end{pmatrix} \qquad D_{r} = \begin{pmatrix} 1 - m & \frac{m}{2} & \frac{m}{2} \\ \frac{m}{2} & 1 - m & \frac{m}{2} \\ \frac{m}{2} & \frac{m}{2} & 1 - m \end{pmatrix}$$

イロト イヨト イヨト イヨト

- 2

Under Assumption B

Connecting source patches that were initially disconnected, even with the same intraspecific competition strengths in the subpopulations!, can be beneficial or detrimental.



イロト イヨト イヨト イヨト

Thank you!

DULED



A final twist

Some species have breeding areas where move for reproduction. Consider a population using three patches: one is the breeding site and the other two (labelled 1 and 2) are feeding sites. Model the following basic processes:

- Adults produce Juveniles, denoted *J*, in the breeding site;
- Juveniles become Adults and move to patch 1 or 2, denoted A₁ and A₂;
- Adults in patch 1 or 2 remain in that patch or move to the other.



$$\left. \begin{array}{l} J(t+1) = f(A_1(t) + A_2(t)), \\ A_1(t+1) = (1-s)J(t) + (1-r)\lambda A_1(t) + r\mu A_2(t), \\ A_2(t+1) = sJ(t) + r\lambda A_1(t) + (1-r)\mu A_2(t), \end{array} \right\}$$
(1)

where $r, s, \lambda, \mu \in [0, 1]$ are constants and $f : \mathbb{R}_+ \to \mathbb{R}_+$. **Remark:** System (1) extends the Allen-Clark model ($\lambda = \mu$)

$$z(t+1) = \alpha z(t) + \beta f(z(t-1)).$$

Symbol	Interpretation (each per time-step)
f	recruitment function of new Juveniles
r _i	proportion of Adults who move from site <i>i</i> to $3 - i$
S	proportion of Juveniles who move to patch 2
λ	survival probability of Adults in site 1
μ	survival probability of Adults in site 2