# Two time scales difference equation systems

## Applications to population dynamics

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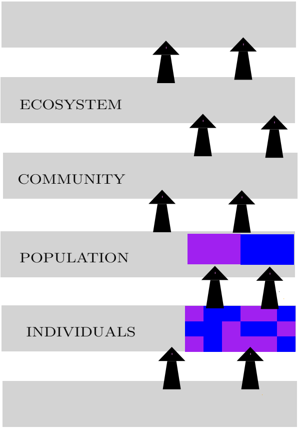
# Outline

# Introduction

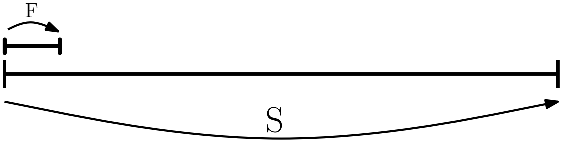
## Hierarchy theory and structured populations




- Hierarchic organization levels
- Internal strong interactions
- Structured populations
- Time scales and up-scaling

F: fast process
S: slow process

What time unit?

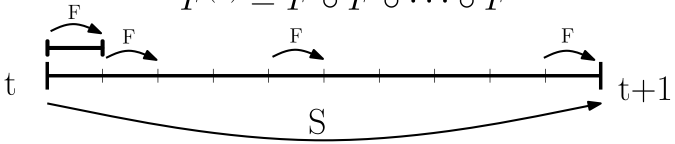


F: fast process
S: slow process

What time unit?

The slowest!

$$F^{(k)} = \overbrace{F \circ F \circ \cdots \circ F}^{k}$$

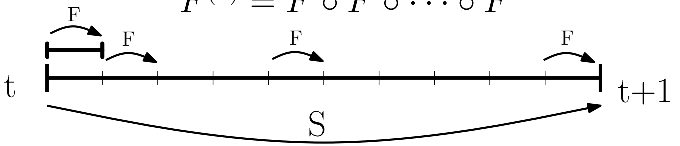



$$X(t+1,k) = S \circ F^{(k)}(X(t,k))$$

F: fast process
S: slow process

What time unit?
The slowest!

$$F^{(k)} = \overbrace{F \circ F \circ \cdots \circ F}^{\text{k}}$$



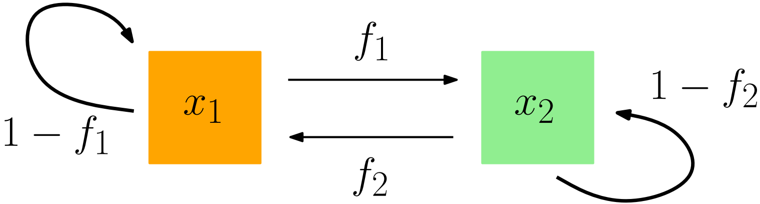

$$X(t+1,k) = S \circ F^{(k)}(X(t,k))$$

$$X(\tau+1) = F(X(\tau)) + \epsilon S(X(\tau,k))$$

# A simple example

## Population inhabiting two patches

Fast process: individuals can change patch




$$F(x_1, x_2) = \begin{pmatrix} 1 - f_1 & f_2 \\ f_1 & 1 - f_2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$$

# A simple example

## Population inhabiting two patches

Slow process: local demography

Malthus

$x_1$

$s_1(x_1) = r_1 x_1$

Beverton-Holt

$x_2$

$s_2(x_2) = \frac{r_2}{1+x_2/M} x_2$

$$S(x_1, x_2) = \left(r_1 x_1, \ \frac{r_2}{1+x_2/M} x_2\right)^T$$

# A simple example: fast dynamics equilibrium

Given the two time scales system

$$X(t+1,k) = S\left(F^k \cdot X(t,k)\right)$$

and given that

$$\lim_{k\to\infty} \begin{pmatrix} 1-f_1 & f_2 \\ f_1 & 1-f_2 \end{pmatrix}^k = \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix},$$

$$\mu_1 = \frac{f_2}{f_1+f_2}$$

$$\mu_2 = \frac{f_1}{f_1+f_2}$$

we get the *auxiliary system*

$$\begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = S \circ \left( \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \right)$$

# A simple example: decomposition and the global variable

Multiplying by the left by $(1 \quad 1)$ yields the *reduced system*

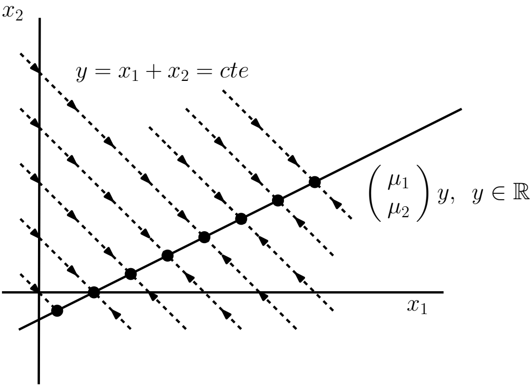
$$\begin{pmatrix} 1 & 1 \end{pmatrix} \begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = \begin{pmatrix} 1 & 1 \end{pmatrix} S \circ \left( \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix} \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \right)$$

written in terms of the *global (slow) variable* $\boxed{y = x_1 + x_2}$

$$y(t+1) = \left( r_1\mu_1 + \frac{r_2\mu_2}{1 + \mu_2 y(t)/M} \right) y(t)$$

## For the fast process, there exist

- Slow variables: invariant quantities by the fast dynamics.
- A center manifold, global attractor, parametrized by the slow variable.



# Results: $X(t+1,k) = S \circ F^{(k)}(X(t+1,k))$

Given $y^*$ a fixed of system $y(t+1) = \left( r_1\mu_1 + \frac{r_2\mu_2}{1+\mu_2 y(t)/M} \right) y(t)$

$X^* = \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} y^*$ is a fixed point of the auxiliary system.

For $k$ large enough, $X_k^* \to X^*$ as $k \to \infty$.

$y^*$ hyperbolic $\Rightarrow X^*, X_k^*$ hyperbolic, same stability as $y^*$.

The basins of attraction of $X_k^*$ can be analyzed by that of $y^*$.

Everything holds for periodic orbits.

- L. Sanz, R. Bravo de la Parra, E. Sánchez. *Two time scales non-linear discrete models approximate reduction*. Journal of Difference Equations and Applications, 14 (2008), No. 6, 607–627.

# Results:

$$X(t+1,k) = S \circ F^{(k)}(X(t+1,k))$$

$$\Downarrow$$

H1 $$\lim_{k\to\infty} F^{(k)}(X) = \bar{F}(X)$$

$$\Downarrow$$

$$X(t+1) = S \circ \bar{F}(X(t+1))$$

$$\Downarrow$$

H2 $$\mathbb{R}^n \xrightarrow{\bar{F} = E \circ G} \mathbb{R}^n, \qquad \mathbb{R}^n \xrightarrow{G} \mathbb{R}^q \xrightarrow{E} \mathbb{R}^n$$

$$\Downarrow$$

$$Y(t+1) = G \circ S \circ E(Y(t)) \Leftrightarrow$$ H3 $$\lim_{k\to\infty} DF^{(k)}(X) = D\bar{F}(X)$$

# Results:

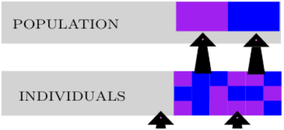
Consider the state variables $X$ (a population)

- divided into $q$ groups (age, size, ...)
- each group divided in $A$ subgroups (individ spread in $A$ zones)

$$X \to (\overbrace{X_1}^{\text{class 1}}, \cdots, \overbrace{X_q}^{\text{class q}}) \to (\overbrace{x_{11}, \cdots, x_{1A}}^{\text{spatial distr class 1}}, \cdots, \overbrace{x_{q1}, \cdots, x_{qA}}^{\text{spatial distr class q}})$$

Fast dynamics internal to each group allows to reduce

$$\boxed{\text{from } A \times q \quad \text{eqs system} \ \Rightarrow \ q \quad \text{eqs system}}$$



# Results: given $F$, does exist $\bar{F}$ such that $Hi$, $i = 1, 2, 3$ hold?

Fast dynamics given by

$$F(X) = \text{diag}(\mathcal{F}_1, \cdots, \mathcal{F}_q)X,$$

where $\mathcal{F}_i$ primitive matrix with simple dominant eigenvalue 1.

Fast dynamics given by

$$F(X) = \text{diag}(\mathcal{F}_1(Y), \cdots, \mathcal{F}_q(Y))X, \qquad Y \text{ global variables},$$

where $\mathcal{F}_i(Y)$ primitive matrix with simple dominant eigenvalue 1.

- M.Marvá, E. Sánchez, R. Bravo de la Parra, L. Sanz. *Reduction of slow-fast discrete models coupling migration and demography*. Journal of theoretical biology. Volume 258. 2009. 371–379.

# Results: given $F$, does exist $\bar{F}$ such that $Hi$, $i = 1, 2, 3$ hold?

Matrices $\mathcal{F}_i$ stochastic

$$F(X) = \begin{pmatrix} \mathcal{F}_1 & 0 \\ 0 & \mathcal{F}_2(X_1) \end{pmatrix} \begin{pmatrix} X_1 \\ X_2 \end{pmatrix} = (\mathcal{F}_1 X_1, \mathcal{F}_2(X_1) X_2),$$

$$\Downarrow$$

$$F^{(k)}(X) = \left( \mathcal{F}_1^k X_1, \prod_{j=0}^{k-1} \mathcal{F}_2(\mathcal{F}_1^{k-j} X_1) X_2 \right)$$

- M. Marvá, R. Bravo de la Parra. *A Juvenile-Adult Model with fast density-dependent migrations* . Submitted.
- T. Nguyen Huu, P. Auger, C. Lett, M. Marvá. *Emergence of global behaviour in a host-parasitoid model with density-dependent dispersal in a chain of patches*. Ecological complexity. Volume 5(2) 9–21, 2008.

Full nonlinear fast dynamics $F$ stands for the discrete hawk-dove game.

- M. Marvá, A.Moussaouí, R. Bravo de la Parra, P. Auger. *A density dependent model describing age-structured population dynamics using hawk-dove tactics* . Journal of difference equations and applications. 19(6):1022-1034, 2013.

# New results

**Condition $\lim_{k\to\infty} DF^{(k)}(X) = D\bar{F}(X)$**

Can be removed using Liapunov functions

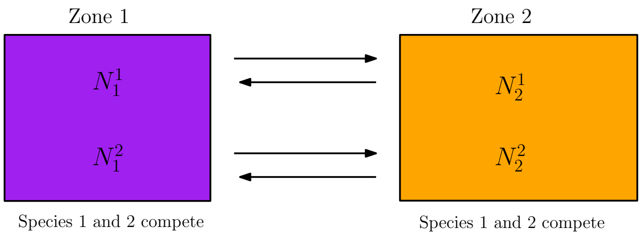
For $F(X) = \mathcal{F}X$, linear primitive with dominant eigenvalue 1

- The decomposition is straightforward.
- Same results for **compact attractors** instead of equilibrium points.

For a general $F(X)$,

- Same results as for **equilibrium points** (not uniqueness).
- For any compact attractor: in progress!
- Decomposition!!

# Competing species in patchy environments




**Dispersal-competition tradeoff?**

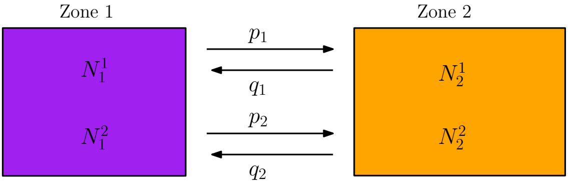
**Does fast dispersal yield new dynamic scenarios?**

The Leslie-Gower competition model (discrete) allows

* Species coexistence.
* One species extinction (unconditionally).
* One species extinction (depending on initial values).

- D. Nguyen Ngoc, R. Bravo de la Parra, M.A. Zavala, P. Auger. Competition and species coexistence in a metapopulation model: Can fast asymmetric migration reverse the outcome of competition in a homogeneous environment? J. Theor. Biol. 266, 256–263, 2010

# Competing species in patchy environments




$$s_1(x,y) = \begin{pmatrix} \frac{b_1^1 N_1^1}{1+c_{11}^1 N_1^1 + c_{12}^1 N_2^1} \\ \frac{b_1^2 N_1^2}{1+c_{11}^2 N_1^2 + c_{12}^2 N_2^2} \end{pmatrix} \qquad s_2(x,y) = \begin{pmatrix} \frac{b_2^1 N_2^1}{1 + c_{21}^1 N_1^1 + c_{22}^1 N_2^1} \\ \frac{b_2^2 N_2^2}{1 + c_{21}^2 N_1^2 + c_{22}^2 N_2^2} \end{pmatrix}$$

$$\begin{cases} n_1(t+1) = \left( \frac{b_1^1 \mu_1}{1+c_{11}^1 \mu_1 n_1(t) + c_{12}^1 \mu_2 n_2(t)} + \frac{b_1^2 (1-\mu_1)}{1+c_{11}^2 (1-\mu_1) n_1(t) + c_{12}^2 (1-\mu_2) n_2(t)} \right) n_1(t) \\ n_2(t+1) = \left( \frac{b_2^1 \mu_2}{1+c_{21}^1 \mu_1 n_1(t) + c_{22}^1 \mu_2 n_2(t)} + \frac{b_2^2 (1-\mu_2)}{1+c_{21}^2 (1-\mu_1) n_1(t) + c_{22}^2 (1-\mu_2) n_2(t)} \right) n_2(t) \end{cases}$$

# Competing species in patchy environments

**All solutions in $[0,\infty)\times[0,\infty)$ converge to an equilibrium in an eventually monotonic manner**

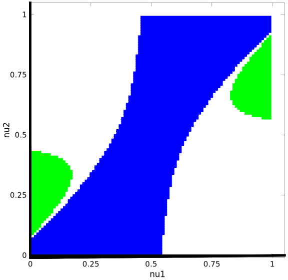
- Explicit stability conditions for $(0,0)$.
- Explicit expressions for fixed points $(n_1^*,0)$, $(0,n_2^*)$.
- Explicit stability conditions for $(n_1^*,0)$, $(0,n_2^*)$.


- M. Marvá, R. Bravo de la Parra. *Coexistence and superior competitor exclusion in Leslie-Gower competition model with dispersal*. Accepted in Ecological Modeling.

# Competing species in **homogeneous** patchy environments

- At most one interior equilibrium state.
- Outcomes as in the Leslie-Gower model, but
- There are dispersal-competition tradeoffs

$$b = 1.5, \mathbf{c_{21} = 1.1}, \mathbf{c_{12} = 0.9}$$

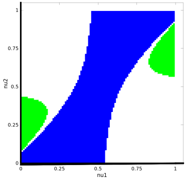



**Blue**: species 2 extinct | **White**: coexistence | **Green**: species 1 extinct

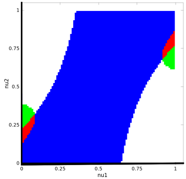
# Competing species in **homogeneous** patchy environments

- In absence of dispersal: species 1 outcompetes species 2.

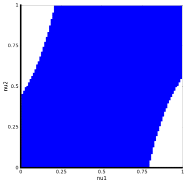
$b = 1.5$, $\mathbf{c_{21} = 1.1}$, $\mathbf{c_{12} = 0.9}$




$b = 1.5$, $\mathbf{c_{21} = 1.5}$, $\mathbf{c_{12} = 0.85}$




$b = 1.5$, $\mathbf{c_{21} = 3}$, $\mathbf{c_{12} = 0.7}$



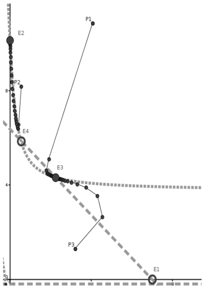

| | |
|---|---|
| **Red** | conditional extinction |
| **White** | global coexistence |
| **Green** | species 1 extinction |
| **Blue** | species 2 extinction |

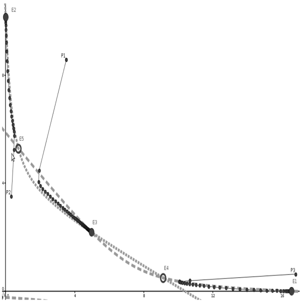
# Competing species in **heterogeneous** patchy environments

Spatial heterogeneity + strong asymmetric distribution

$\Downarrow$

at most three coexistence equilibria



# Competing species in **heterogeneous** patchy environments

Park *et al.* performed lab experiments with flour beetle to test the competitive exclusion principle

## Experimental outcomes observed by Park *et al.*:

* They kept in mind Leslie-Gower model.
* All the classical ones: coexistence, (un)conditional exclusion.
* But also found coexistence/species exclusion depending on initial population sizes


- T. Park. Experimental studies of interspecies competition. I. Competition between populations of the flour beetles Tribolium confusum Duval and Tribolium castaneum Herbst, Ecol. Monogr., 18, 265–308, 1948.
- T. Park. Experimental studies of interspecies competition. III. Relation of initial species proportion to the competitive outcome in populations of Tribolium, Physiol. Zool., 30, 22–40, 1957.
- T. Park, P. H. Leslie and D. B. Mertz. Genetic strains and competition in populations of Tribolium, Physiol. Zool., 37, 97–162, 1964.

# Competing species in **heterogeneous** patchy environments

Subsequent studies reported that

## Relatively high mobility

The average mobility of T. confunsum is 9 cm/day
The cultures lived in containers of either $9.5 \times 2.5$ cm or $10 \times 7$ cm

## Medium became heterogeneous

Tribolium modifies the medium:

- depletion of the nutritive value of the medium
- accumulation of the quinones

Medium preference:

* T. castaneum was repelled by conditioned flour
* T. confusum was strongly attracted by conditioned flour


- A.W. Ghent, Studies of Behavior of the Tribolium Flour Beetles. II. Distributions in Depth of T. Castaneum and T. Confusum in Fractionable Shell Vials Flours. Ecol, 47(3) pp. 355–367. (1966)
- D.J. McDonald, Mobility in Tribolium Confusum. Ecol, 49(4), pp. 770–771. (1968).

# Questions