

Two time scales difference equation systems

Applications to population dynamics

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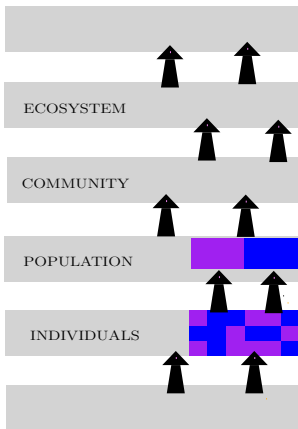
DDays 2014, Badajoz.

Outline

- 1 Context for time scales systems: hierarchy theory
- 2 Two time scales discrete systems
- 3 Approximate aggregation techniques: an example
- 4 Results and ongoing work
- 5 Competing species in patchy environments

Introduction

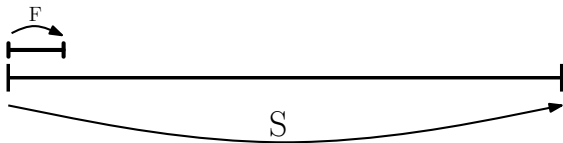
Hierarchy theory and structured populations



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

F: fast process
S: slow process

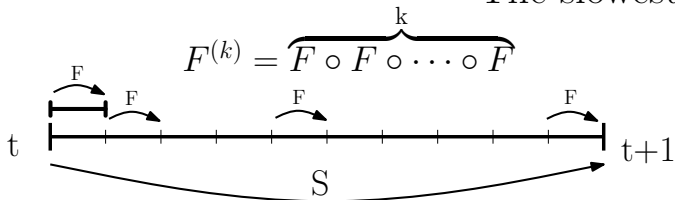
What time unit?



F: fast process
S: slow process

What time unit?

The slowest!

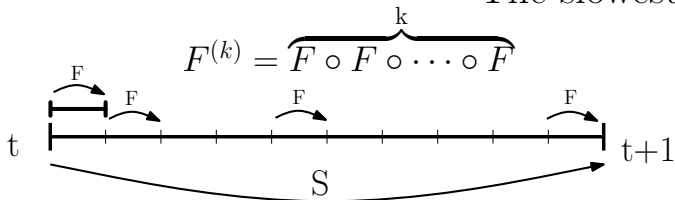


$$X(t+1, k) = S \circ F^{(k)}(X(t, k))$$

F: fast process
S: slow process

What time unit?

The slowest!



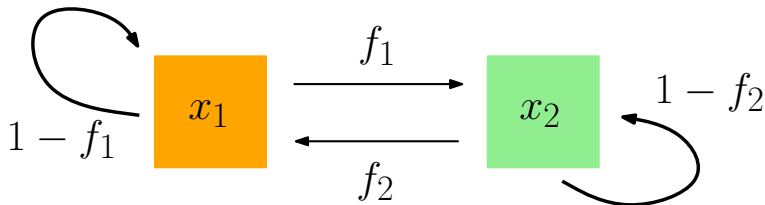
$$X(t+1, k) = S \circ F^{(k)}(X(t, k))$$

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

A simple example

Population inhabiting two patches

Fast process: individuals can change patch



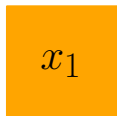
$$F(x_1, x_2) = \begin{pmatrix} 1 - f_1 & f_2 \\ f_1 & 1 - f_2 \end{pmatrix} \begin{pmatrix} x_1 \\ x_2 \end{pmatrix}$$

A simple example

Population inhabiting two patches

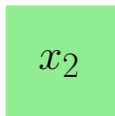
Slow process: local demography

Malthus



$$s_1(x_1) = r_1 x_1$$

Beverton-Holt



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

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

A simple example: fast dynamics equilibrium

Given the two time scales system

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

and given that

$$\lim_{k \rightarrow \infty} \begin{pmatrix} 1-f_1 & f_2 \\ f_1 & 1-f_2 \end{pmatrix}^k = \begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix}, \quad \begin{aligned} \mu_1 &= \frac{f_2}{f_1+f_2} \\ \mu_2 &= \frac{f_1}{f_1+f_2} \end{aligned}$$

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 $(1 \ 1)$ yields the *reduced system*

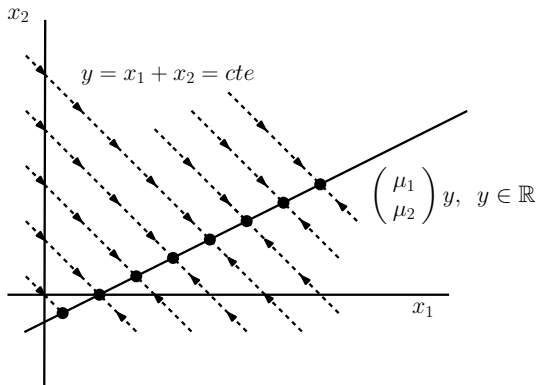
$$(1 \ 1) \begin{pmatrix} x_1(t+1) \\ x_2(t+1) \end{pmatrix} = (1 \ 1) S_0 \left(\begin{pmatrix} \mu_1 \\ \mu_2 \end{pmatrix} (1 \ 1) \begin{pmatrix} x_1(t) \\ x_2(t) \end{pmatrix} \right)$$

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

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

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, $X_k^* \rightarrow X^*$ as $k \rightarrow \infty$.

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:

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

$$\Downarrow$$

$$\boxed{\text{H1}} \quad \lim_{k \rightarrow \infty} F^{(k)}(X) = \bar{F}(X)$$

$$\Downarrow$$

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

$$\Downarrow$$

$$\boxed{\text{H2}} \quad \begin{array}{ccc} \mathbb{R}^n & \xrightarrow{\bar{F} = E \circ G} & \mathbb{R}^n \\ & \searrow G & \nearrow E \\ & & \mathbb{R}^q \end{array}$$

$$\Downarrow$$

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

Results:

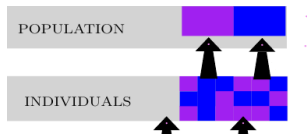
Consider the state variables X (a population)

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

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

Fast dynamics internal to each group allows to reduce

from $A \times q$ eqs system \Rightarrow q eqs system



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

Fast dynamics given by

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

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

Fast dynamics given by

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

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

- M.Marva, E. Sanchez, 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 $H_i, i = 1, 2, 3$ 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. Marva, R. Bravo de la Parra. *A Juvenile-Adult Model with fast density-dependent migrations* . Submitted.
- T. Nguyen Huu, P. Auger, C. Lett, M. Marva. *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. Marva, A. Moussaouf, 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 $\lim_{k \rightarrow \infty} DF^{(k)}(X) = D\bar{F}(X)$

Can be removed using Liapunov functions

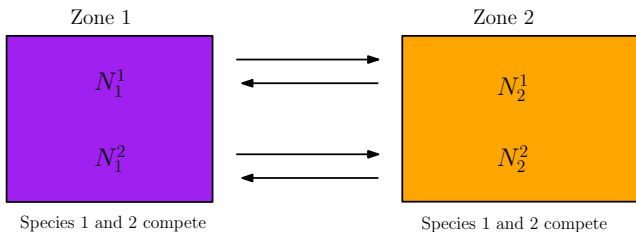
For $F(X) = \mathcal{F}X$, linear primitive with dominant eigenvalue 1

- 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?

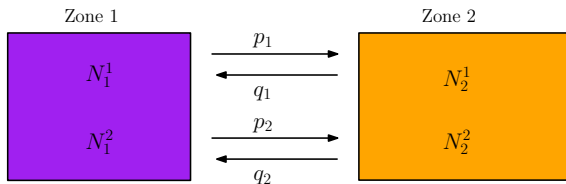
Does fast dispersal yield new dynamic scenarios?

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



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

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

Competing species in patchy environments

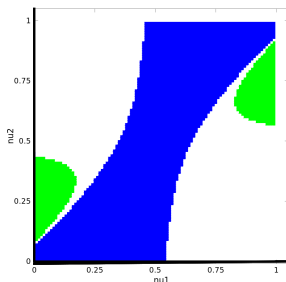
All solutions in $[0, \infty) \times [0, \infty)$ converge to an equilibrium in an eventually monotonic manner

- 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. Marva, 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

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

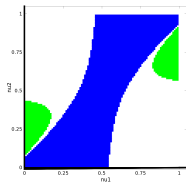


Blue: species 2 extinct | **White:** coexistence | **Green:** species 1 extinct

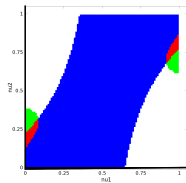
Competing species in homogeneous patchy environments

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

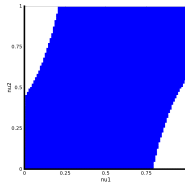
$$b = 1.5, c_{21} = 1.1, c_{12} = 0.9$$



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



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



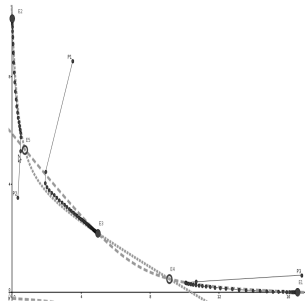
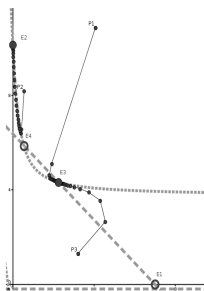
Red	conditional extinction
White	global coexistence
Green	species 1 extinction
Blue	species 2 extinction

Competing species in heterogeneous patchy environments

Spatial heterogeneity + strong asymmetric distribution



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. confusum* is 9 cm/day

The cultures lived in containers of either 9.5×2.5 cm or 10×7 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