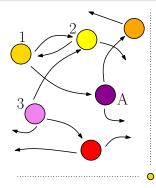
Approximate aggregation methods and spatially distributed structured population discrete models An application to a spatially competition model

### Marcos Marvá, Rafael Bravo de la Parra

Departamento de Física y Matemáticas, Universidad de Alcalá Alcalá de Henares (Madrid), Spain

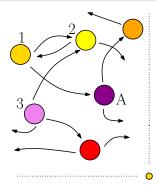
October 2013



Population divided in c classes  $\vec{N} = (\vec{N_1}, ..., \vec{N_c})$ 

Spatial distribution of individuals of class j $\vec{N_j} = (N_{j1},...,N_{jA})$ 

 $p_{rs}^{j}$  fraction of individuals of class  ${\bf j}$  patch  ${\bf s}$   $\rightarrow$  patch  ${\bf r}$ 



Population divided in c classes  $\vec{N} = (\vec{N_1}, ..., \vec{N_c})$ 

Spatial distribution of individuals of class j  $\vec{N_j} = (N_{j1},...,N_{jA})$ 

 $p_{rs}^{j}$  fraction of individuals of class j patch s  $\rightarrow$  patch r

Matrix  $\mathcal{F}_j = (p_{rs}^j)$  is stochastic; movements are given by  $\vec{N}(t+1) = diag \left(\mathcal{F}_1, \cdots, \mathcal{F}_c\right) \vec{N}(t) = \mathcal{F}\vec{N}(t)$ 

Local interactions are described by matrix  $\mathcal{S}(N)$  $\vec{N}(t+1) = \mathcal{S}(\vec{N}(t))\vec{N}(t)$ 

- Local interactions are slower than individual displacements.
- Two time scales ⇔ two time units: chose the slower one!!

$$\vec{N}(t+1) = S \circ \overbrace{F \circ F}^{k \text{ times}} \left( \vec{N}(t) \right) = S \circ F^{(k)} \left( \vec{N}(t) \right)$$

In our case it reads as

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$
(1)

Being  $F_j$  stochastic implies  $\lim_{k \to \infty} \mathcal{F}_j^k = \mathbf{v}_j \mathbf{1}^T$ 

where  $\mathbf{v}_j$  and  $\mathbf{I}_j^T$  are its left and right main eigenvectors.

$$\lim_{k\to\infty} \mathcal{F}^k = \bar{\mathcal{F}} = \underbrace{\operatorname{diag}(\mathbf{v}_1\cdots\mathbf{v}_c)}_{Ac\times c} \cdot \underbrace{\operatorname{diag}(\mathbf{1}_1^T\cdots\mathbf{1}_c^T)}_{c\times Ac} = \mathcal{E} \cdot \mathcal{G}$$

- Local interactions are slower than individual displacements.
- Two time scales  $\Leftrightarrow$  two time units: chose the slower one!!

$$\vec{N}(t+1) = S \circ \overbrace{F \circ F}^{k \text{ times}} \left(\vec{N}(t)\right) = S \circ F^{(k)}\left(\vec{N}(t)\right)$$

In our case it reads as

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$
(1)

Being  $F_j$  stochastic implies  $\lim_{k\to\infty} \mathcal{F}_j^k = \mathbf{v}_j \mathbf{1}^T$ 

where  $\mathbf{v}_i$  and  $\mathbf{1}_i^T$  are its left and right main eigenvectors.

$$\lim_{k\to\infty} \mathcal{F}^k = \bar{\mathcal{F}} = \underbrace{\operatorname{diag}(\mathbf{v}_1\cdots\mathbf{v}_c)}_{Ac\times c} \cdot \underbrace{\operatorname{diag}(\mathbf{1}_1^T\cdots\mathbf{1}_c^T)}_{c\times Ac} = \mathcal{E} \cdot \mathcal{G}$$

- Local interactions are slower than individual displacements.
- Two time scales ⇔ two time units: chose the slower one!!

$$\vec{N}(t+1) = S \circ \overbrace{F \circ F}^{k \text{ times}} \left( \vec{N}(t) \right) = S \circ F^{(k)} \left( \vec{N}(t) \right)$$

In our case it reads as

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$
(1)

Being  $F_j$  stochastic implies  $\lim_{k \to \infty} \mathcal{F}_j^k = \mathbf{v}_j \mathbf{1}^T$ 

where  $\mathbf{v}_j$  and  $\mathbf{1}_j^T$  are its left and right main eigenvectors.

$$\lim_{k \to \infty} \mathcal{F}^k = \bar{\mathcal{F}} = \underbrace{\operatorname{diag}(\mathbf{v}_1 \cdots \mathbf{v}_c)}_{Ac \times c} \cdot \underbrace{\operatorname{diag}(\mathbf{1}_1^T \cdots \mathbf{1}_c^T)}_{c \times Ac} = \mathcal{E} \cdot \mathcal{G}$$

We approximate the complete system

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$

of dimension  $A \cdot c$  by the auxiliary system

$$\vec{N}(t+1) = S(\bar{\mathcal{F}}\vec{N}(t)) \cdot \bar{\mathcal{F}}\vec{N}(t) = S(\mathcal{E} \cdot \mathcal{G}\vec{N}(t)) \cdot \mathcal{E} \cdot \mathcal{G}\vec{N}(t)$$
(2)

Defining the global variables

$$ec{Y} = \mathcal{G}ec{N}$$
  $y_j = n_{j1} + \dots + n_{jA}$ 

yields the aggregated system, of dimension c,

$$\vec{Y}(t+1) = \mathcal{G} \cdot \mathcal{S}(\mathcal{E}\vec{Y}(t)) \cdot \mathcal{E}\vec{Y}(t)$$
(3)

We approximate the complete system

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$

of dimension  $A \cdot c$  by the auxiliary system

$$\vec{N}(t+1) = S(\bar{\mathcal{F}}\vec{N}(t)) \cdot \bar{\mathcal{F}}\vec{N}(t) = S(\mathcal{E} \cdot \mathcal{G}\vec{N}(t)) \cdot \mathcal{E} \cdot \mathcal{G}\vec{N}(t)$$
(2)

Defining the global variables

$$ec{Y} = \mathcal{G}ec{N}$$
  $y_j = n_{j1} + \dots + n_{jA}$ 

yields the aggregated system, of dimension c,

$$\vec{Y}(t+1) = \mathcal{G} \cdot \mathcal{S}(\mathcal{E}\vec{Y}(t)) \cdot \mathcal{E}\vec{Y}(t)$$
(3)

We approximate the complete system

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$

of dimension  $A \cdot c$  by the auxiliary system

$$\vec{N}(t+1) = S(\bar{\mathcal{F}}\vec{N}(t)) \cdot \bar{\mathcal{F}}\vec{N}(t) = S(\mathcal{E} \cdot \mathcal{G}\vec{N}(t)) \cdot \mathcal{E} \cdot \mathcal{G}\vec{N}(t)$$
(2)

Defining the global variables

$$ec{Y} = \mathcal{G}ec{N}$$
  $y_j = n_{j1} + \dots + n_{jA}$ 

yields the aggregated system, of dimension c,

$$\vec{Y}(t+1) = \mathcal{G} \cdot \mathcal{S}(\mathcal{E}\vec{Y}(t)) \cdot \mathcal{E}\vec{Y}(t)$$
(3)

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$

$$\vec{Y}(t+1) = \mathcal{G} \cdot \mathcal{S}(\mathcal{E}\vec{Y}(t)) \cdot \mathcal{E}\vec{Y}(t)$$

### General results

If  $\vec{Y}^* \in \mathbb{R}^A$  is a hyperbolic fixed point of the reduced system (3) then

•  $\forall k \ge k_0$  the complete system (1) has an unique fixed point  $\vec{X}_k^* \in \bar{B}_r\left(\mathcal{E}\vec{Y}^*\right)$  which is hyperbolic and

$$\lim_{k\to\infty}\vec{X}_k^* = \mathcal{E}\vec{Y}^*$$

*X*<sup>\*</sup> is A.S. (U.) if, and only if *X*<sup>\*</sup><sub>k</sub> (∀k ≥ k<sub>1</sub>) are A.S. (U.)
The basin of attraction of *X*<sup>\*</sup><sub>k</sub> can be described from that of *Y*<sup>\*</sup>

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.

$$\vec{N}(t+1) = \mathcal{S}(\mathcal{F}^k \vec{N}(t)) \cdot \mathcal{F}^k \vec{N}(t)$$

$$\vec{Y}(t+1) = \mathcal{G} \cdot \mathcal{S}(\mathcal{E}\vec{Y}(t)) \cdot \mathcal{E}\vec{Y}(t)$$

### General results

If  $\vec{Y}^* \in \mathbb{R}^A$  is a hyperbolic fixed point of the reduced system (3) then

•  $\forall k \ge k_0$  the complete system (1) has an unique fixed point  $\vec{X}_k^* \in \bar{B}_r\left(\mathcal{E}\vec{Y}^*\right)$  which is hyperbolic and

$$\lim_{k\to\infty}\vec{X}_k^*=\mathcal{E}\vec{Y}^*$$

*X*<sup>\*</sup> is A.S. (U.) if, and only if *X*<sup>\*</sup><sub>k</sub> (∀k ≥ k<sub>1</sub>) are A.S. (U.)
The basin of attraction of *X*<sup>\*</sup><sub>k</sub> can be described from that of *Y*<sup>\*</sup>

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.

### Two patches competing species with fast movements

**Notations:**  $\vec{N} = (N_1^1, N_1^2, N_2^1, N_2^2) = (\vec{N}_1, \vec{N}_2), \quad n_i = N_i^1 + N_i^2$ 

**Fast dynamics:** constant displacement  $0 < p_i, q_i < 1$ 

$$\mathcal{F}_i = \begin{pmatrix} 1 - p_i & q_i \\ p_i & 1 - q_i \end{pmatrix}, \qquad \lim_{k \to \infty} \mathcal{F}_i^k = \begin{pmatrix} \nu_i^* \\ 1 - \nu_i^* \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix} = \bar{\mathcal{F}}_i$$

**Slow dynamics:** local Leslie-Gower competition model  $b_i^j, c_{ij}^k > 0$ 

$$\begin{split} \int & N_1^1(t+1) = \frac{b_1^1}{1 + c_{11}^1 N_1^1(t) + c_{12}^1 N_2^1(t)} N_1^1(t) \\ & N_1^2(t+1) = \frac{b_1^2}{1 + c_{11}^2 N_1^2(t) + c_{12}^2 N_2^2(t)} N_1^2(t) \\ & N_2^1(t+1) = \frac{b_2^1}{1 + c_{21}^1 N_1^1(t) + c_{22}^1 N_2^1(t)} N_2^1(t) \\ & N_2^2(t+1) = \frac{b_2^2}{1 + c_{21}^2 N_1^2(t) + c_{22}^2 N_2^2(t)} N_2^2(t) \end{split}$$

J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson. Some Discrete Competition Models and the Competitive Exclusion Principle *Journal of Difference Equations and Applications*, 10(13-15):1139-1151, 2004.

### Two patches competing species with fast movements

**Notations:**  $\vec{N} = (N_1^1, N_1^2, N_2^1, N_2^2) = (\vec{N}_1, \vec{N}_2), \quad n_i = N_i^1 + N_i^2$ **Fast dynamics:** constant displacement  $0 < p_i, q_i < 1$ 

$$\mathcal{F}_i = \begin{pmatrix} 1 - p_i & q_i \\ p_i & 1 - q_i \end{pmatrix}, \qquad \lim_{k \to \infty} \mathcal{F}_i^k = \begin{pmatrix} \nu_i^* \\ 1 - \nu_i^* \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix} = \bar{\mathcal{F}}_i$$

**Slow dynamics:** local Leslie-Gower competition model  $b_i^j, c_{ij}^k > 0$ 

$$\begin{split} \int & N_1^1(t+1) = \frac{b_1^1}{1 + c_{11}^1 N_1^1(t) + c_{12}^1 N_2^1(t)} N_1^1(t) \\ & N_1^2(t+1) = \frac{b_1^2}{1 + c_{11}^2 N_1^2(t) + c_{12}^2 N_2^2(t)} N_1^2(t) \\ & N_2^1(t+1) = \frac{b_2^1}{1 + c_{21}^1 N_1^1(t) + c_{22}^1 N_2^1(t)} N_2^1(t) \\ & N_2^2(t+1) = \frac{b_2^2}{1 + c_{21}^2 N_1^2(t) + c_{22}^2 N_2^2(t)} N_2^2(t) \end{split}$$

J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson. Some Discrete Competition Models and the Competitive Exclusion Principle Journal of Difference Equations and Applications, 10(13-15):1139-1151, 2004.

### Two patches competing species with fast movements

**Notations:**  $\vec{N} = (N_1^1, N_1^2, N_2^1, N_2^2) = (\vec{N}_1, \vec{N}_2), \quad n_i = N_i^1 + N_i^2$ **Fast dynamics:** constant displacement  $0 < p_i, q_i < 1$ 

$$\mathcal{F}_i = \begin{pmatrix} 1 - p_i & q_i \\ p_i & 1 - q_i \end{pmatrix}, \qquad \lim_{k \to \infty} \mathcal{F}_i^k = \begin{pmatrix} \nu_i^* \\ 1 - \nu_i^* \end{pmatrix} \begin{pmatrix} 1 & 1 \end{pmatrix} = \bar{\mathcal{F}}_i$$

**Slow dynamics:** local Leslie-Gower competition model  $b_i^j, c_{ij}^k > 0$ 

$$\begin{split} \int & N_1^1(t+1) = \frac{b_1^1}{1 + c_{11}^1 N_1^1(t) + c_{12}^1 N_2^1(t)} N_1^1(t) \\ & N_1^2(t+1) = \frac{b_1^2}{1 + c_{11}^2 N_1^2(t) + c_{12}^2 N_2^2(t)} N_1^2(t) \\ & N_2^1(t+1) = \frac{b_2^1}{1 + c_{21}^1 N_1^1(t) + c_{22}^1 N_2^1(t)} N_2^1(t) \\ & N_2^2(t+1) = \frac{b_2^2}{1 + c_{21}^2 N_1^2(t) + c_{22}^2 N_2^2(t)} N_2^2(t) \end{split}$$

 J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson. Some Discrete Competition Models and the Competitive Exclusion Principle Journal of Difference Equations and Applications, 10(13-15):1139-1151, 2004.

### Aggregated model and global variables

Complete model: 
$$\vec{N}(t+1) = S\left(\mathcal{F}^k \vec{N}(t)\right) \cdot \mathcal{F}^k \vec{N}(t)$$

Aggregated system:

$$n_1(t+1) = f(n_1(t), n_2(t))n_1(t)$$
  

$$n_2(t+1) = g(n_1(t), n_2(t))n_2(t)$$
 where

$$f(n_1, n_2) = \left(\frac{b_1^1 \nu_1^*}{1 + c_{11}^1 \nu_1^* n_1 + c_{12}^1 \nu_2^* n_2} + \frac{b_1^2 (1 - \nu_1^*)}{1 + c_{11}^2 (1 - \nu_1^*) n_1 + c_{12}^2 (1 - \nu_2^*) n_2}\right)$$
$$g(n_1, n_2) = \left(\frac{b_2^1 \nu_2^*}{1 + c_{21}^1 \nu_1^* n_1 + c_{22}^1 \nu_2^* n_2} + \frac{b_2^2 (1 - \nu_2^*)}{1 + c_{21}^2 (1 - \nu_1^*) n_1 + c_{22}^2 (1 - \nu_2^*) n_2}\right)$$

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

J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson. Some Discrete Competition Models and the Competitive Exclusion Principle Journal of Difference Equations and Applications, 10(13-15):1139-1151, 2004.

### Aggregated model and global variables

Complete model: 
$$\vec{N}(t+1) = S\left(\mathcal{F}^k \vec{N}(t)\right) \cdot \mathcal{F}^k \vec{N}(t)$$

Aggregated system:

$$n_1(t+1) = f(n_1(t), n_2(t))n_1(t)$$
  

$$n_2(t+1) = g(n_1(t), n_2(t))n_2(t)$$
 where

 $f(n_1, n_2) = \left(\frac{b_1^1 \nu_1^*}{1 + c_{11}^1 \nu_1^* n_1 + c_{12}^1 \nu_2^* n_2} + \frac{b_1^2 (1 - \nu_1^*)}{1 + c_{11}^2 (1 - \nu_1^*) n_1 + c_{12}^2 (1 - \nu_2^*) n_2}\right)$  $g(n_1, n_2) = \left(\frac{b_2^1 \nu_2^*}{1 + c_{21}^1 \nu_1^* n_1 + c_{22}^1 \nu_2^* n_2} + \frac{b_2^2 (1 - \nu_2^*)}{1 + c_{21}^2 (1 - \nu_1^*) n_1 + c_{22}^2 (1 - \nu_2^*) n_2}\right)$ 

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

J.M. Cushing, S. Levarge, N. Chitnis, S.M. Henson. Some Discrete Competition Models and the Competitive Exclusion Principle Journal of Difference Equations and Applications, 10(13-15):1139-1151, 2004.

### Results from the aggregated system:

- The trivial equilibrium point (0,0).
- The semitrivial equilibrium points  $(n_1^*, 0)$ ,  $(0, n_2^*)$  always exist and can be explicitly calculated.
- No explicit expression for positive equilibrium (if any)

Equilibrium	Asint stable	Unstable	
(0, 0)	$0 < b_{ij}^r < 1$	$b_{ij}^{r} > 1$	
$(n_1^*, 0)$	$g(n_1^*, 0) < 1$	$g(n_1^*, 0) > 1$	
$(0, n_2^*)$	$f(0, n_2^*) < 1$	$f(0, n_2^*) > 1$	
		global coex	

Are there displacements-competition tradeoffs? Assume: \* Spatial homogeneity

\* Asymmetric competition

### Results from the aggregated system:

- The trivial equilibrium point (0,0).
- The semitrivial equilibrium points  $(n_1^*, 0)$ ,  $(0, n_2^*)$  always exist and can be explicitly calculated.
- No explicit expression for positive equilibrium (if any)

Equilibrium	Asint stable	Unstable	
(0, 0)	$0 < b_{ij}^r < 1$	$b_{ij}^{r} > 1$	
$(n_1^*, 0)$	$g(n_1^*, 0) < 1$	$g(n_1^*, 0) > 1$	
$(0, n_2^*)$	$f(0, n_2^*) < 1$	$f(0, n_2^*) > 1$	
		global coex	

Are there displacements-competition tradeoffs? Assume: \* Spatial homogeneity

\* Asymmetric competition

### Results from the aggregated system:

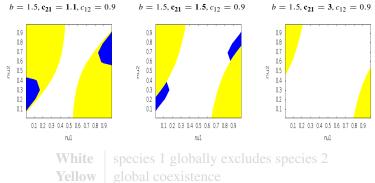
- The trivial equilibrium point (0,0).
- The semitrivial equilibrium points  $(n_1^*, 0)$ ,  $(0, n_2^*)$  always exist and can be explicitly calculated.
- No explicit expression for positive equilibrium (if any)

Equilibrium	Asint stable	Unstable
(0,0)	$0 < b_{ij}^r < 1$	$b_{ij}^{r} > 1$
$(n_1^*, 0)$	$g(n_1^*, 0) < 1$	$g(n_1^*, 0) > 1$
$(0, n_2^*)$	$f(0, n_2^*) < 1$	$f(0, n_2^*) > 1$
		global coex

Are there displacements-competition tradeoffs? Assume:

- \* Spatial homogeneity
- \* Asymmetric competition

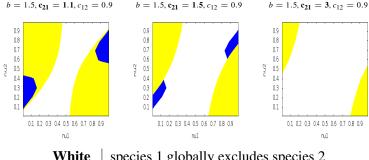
### Numerical experiments



ue species 2 globally excludes species 1

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? Journal of Theoretical Biology, 266:256-263, 2010.

### Numerical experiments



Whitespecies 1 globally excludes species 2Yellowglobal coexistenceBluespecies 2 globally excludes species 1

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? Journal of Theoretical Biology, 266:256-263, 2010.

# Thanks; questions?

### About approximate aggregation of discrete systems

- R. Bravo de la Parra, M. Marvá, E. Sánchez, L. Sanz Reduction of Discrete Dynamical Systems with Applications to Dynamics Population Models Mathematical Models of Natural Phenomena, (to appear).
- 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.

### About approximate aggregation, including ODEs and PDEs

P. Auger, R. Bravo de la Parra, J.-C. Poggiale, E. Sánchez, T. and Nguyen-Huu Aggregation of variables and applications to population dynamics In P. Magal, S. Ruan (Eds.), Structured Population Models in Biology and Epidemiology, Lecture Notes in Mathematics 1936, Mathematical Biosciences Subseries, Springer Verlag, Berlin, 2008, 209–263.