Competing species in niche space: the role of the competition kernel.

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Outline:

- Introduction.

- Lotka-Volterra competition model in niche space. Results.

- The Gaussian or Normal distribution Kernel.

- Simple ecological system giving rise to non-positive kernel.

- Conclusions.

PATRES

Interactions between different entities competing for the same resources arise in a large variety of physical, chemical, biological, social and economical systems.

Lotka-Volterra competition.

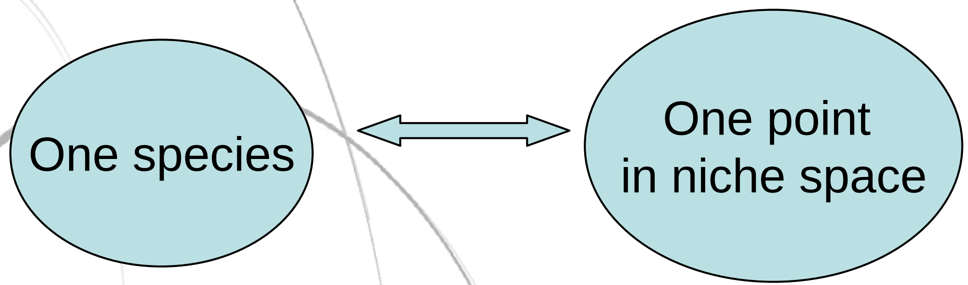
- Population dynamics.
- Sympatric speciation.
- Multimode optical devices in which different lasing modes are driven by the same population inversion.
- Technology substitution in which users decide between alternative products.
- Spin-wave patterns.
- Mode interaction in crystallization fronts.
- Evolutionary dynamics.
- Food web assembly.
- Groups competing for their technical niche in the Flicker??

This talk will be in the context of ecosystem dynamics.

-A central concept in Ecology is “limiting similarity”.

- It states that species can coexist if they are sufficiently different from competing species.

- The way to quantify this difference is by using the niche space, whose coordinates signal the phenotypic traits of an species relevant for the consumption of resources.

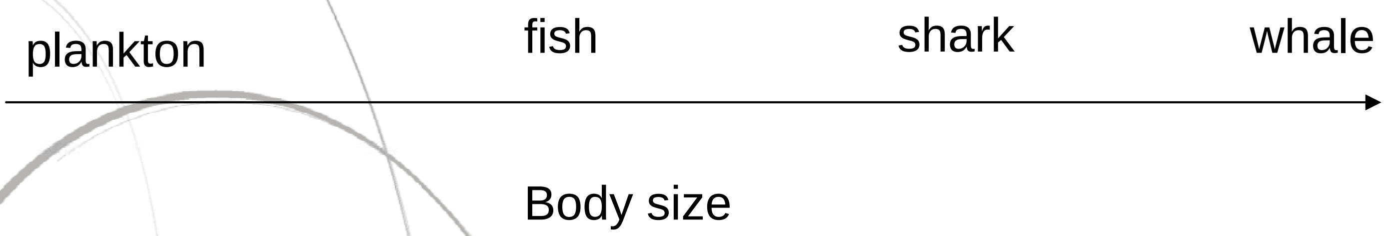


Phenotypic traits: body size, peak size, preferred food, etc…

I.e, any observed quality of an organism:

Genotype+environment+randomness → phenotype

Marine ecosystem.



-Species experience stronger competition with close species in niche space.

COMPETITIVE EXCLUSION PRINCIPLE (CEP)
Species can only survive if they maintain A minimum distance with others in niche space.

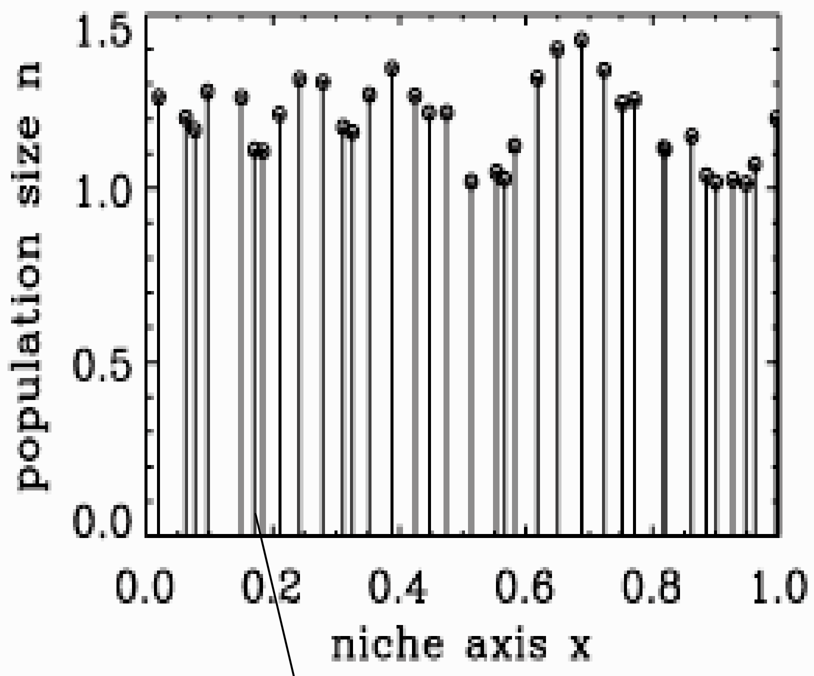
In niche space the scenario: Homogenous distribution of species more or less equidistants filling the whole niche space.

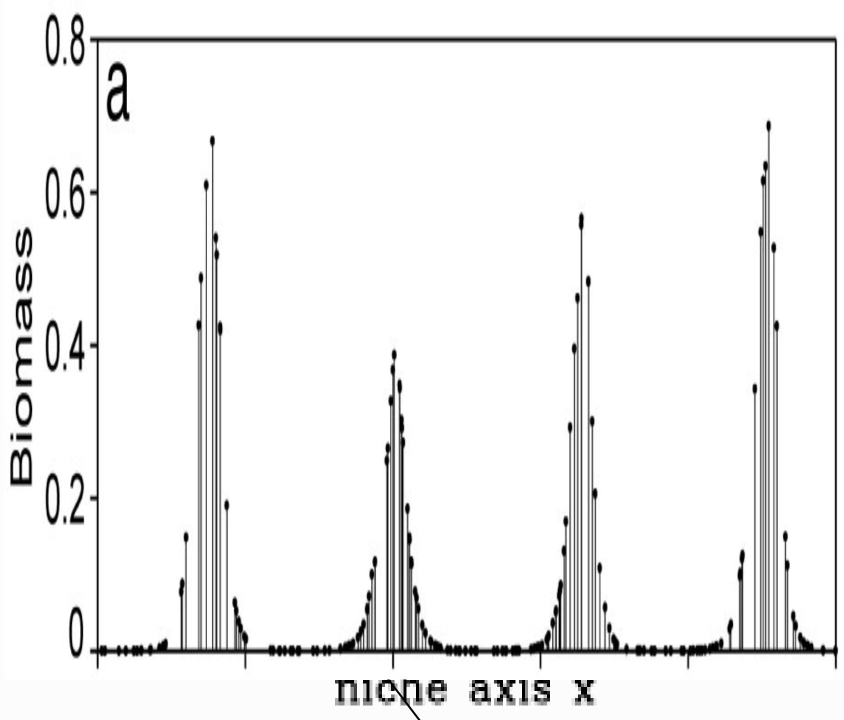
Contradiction ⟷

Ecologist: why are there so many similar species in Nature?
I.e. arbitrarily close in niche space

Scheffer & Van Nes, PNAS 103, 6230 (2006). LV model with Gaussian competition. Result is against CEP.

CEP





There are no exclusion zones

Exclusion zones

Lotka-Volterra competion model in niche space

The Lotka-Volterra symmetric competition model in niche space. (Classical and simplest model).

$$\frac{dN_i}{dt} = N_i\left[1-\frac{1}{K}\sum_{j=1}^{N} g(|x_i - x_j|)N_j\right], i = 1,\dots, N$$

N total number of species; N_i population of species *i*; *K* carrying capacity; *x* coordinate in niche space; *g* is the competition kernel

Typical analysis (Scheffer & Van Nes; Szabo & Meszena*: Fix the Kernel to Gaussian and study the role of homogenous and non-homogenous carrying capacity.

P. Szabo & G. Meszena, OIKOS 112, 612 (2006).

OUR STUDY IS SOMEWHAT DIFFERENT.

WE FOCUSS ON THE ROLE OF THE COMPETITION KERNEL.

Numerical results for LV:

- Runge-Kutta simulation of the LV model.

-Consider extinct and remove from the system if a population is below a threshold value.

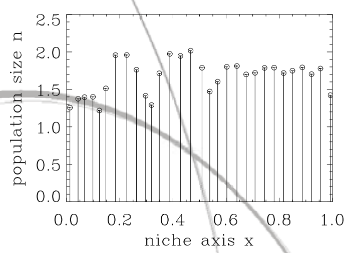
- Immigration mechanism by which new species are introduced in the system at a given rate. To reach a stationary value we switch off it after some time.

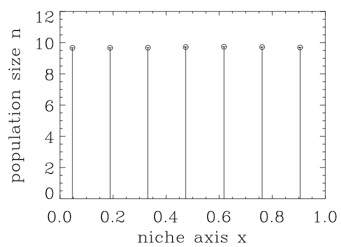
- We consider a family of kernels given by:

$$g_\sigma(x) = \exp[-(|x|/R)^\sigma]$$

R= Competition range

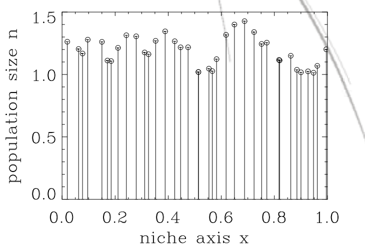
$\sigma = 1$

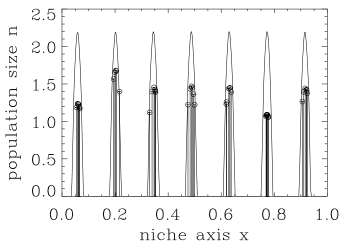




$\sigma = 4$

Enhanced self-competition

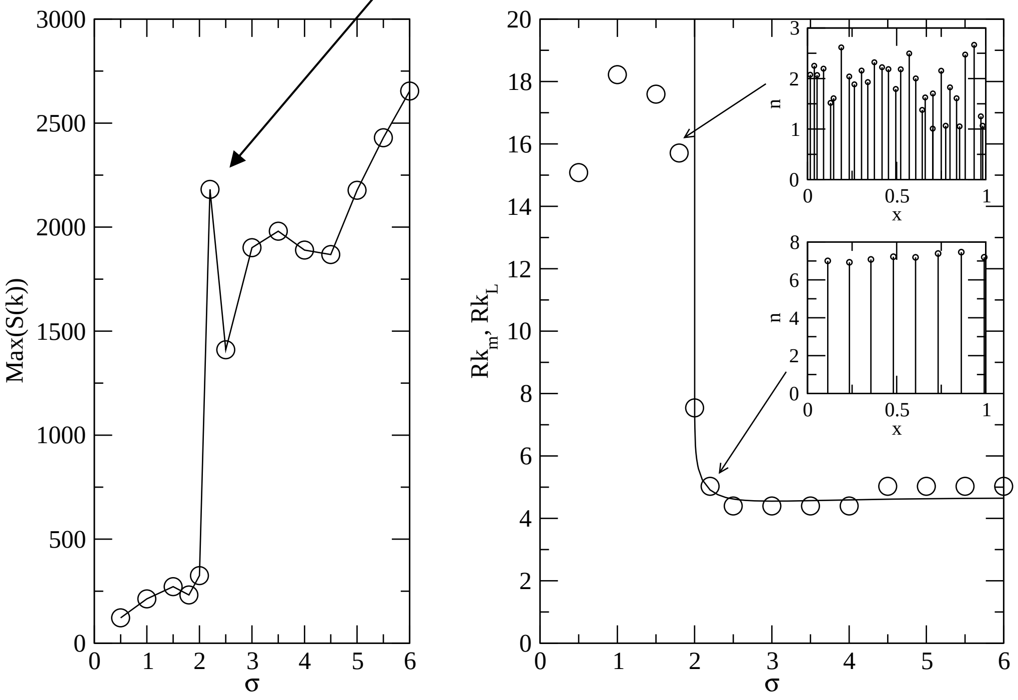




For the family of kernels

$$g_\sigma(x) = \exp[-(|x|/R)^\sigma]$$

Transition for the Gaussian Kernel



Analytical results:

- Let us consider that the number of species is large and differences between neighboring phenotypes small. We can consider a continuus evolution equation for the expected density of individuals at any given point of the continuus niche space:

$$\partial_t \phi(x,t) = \phi(x,t)\left[1 - 1/K \int dy g(|x-y|)\phi(y,t)\right] + s$$

Stationary homogenous solutions for s=0: $\phi_0 = 0; \phi_0 > 0$

Instability analysis of the positive solution: $\phi = \phi_0 + \varepsilon e^{\lambda t + iqx}$

$$\lambda(q) = -\frac{\bar{g}(q)}{\int g(x)\,dx}$$

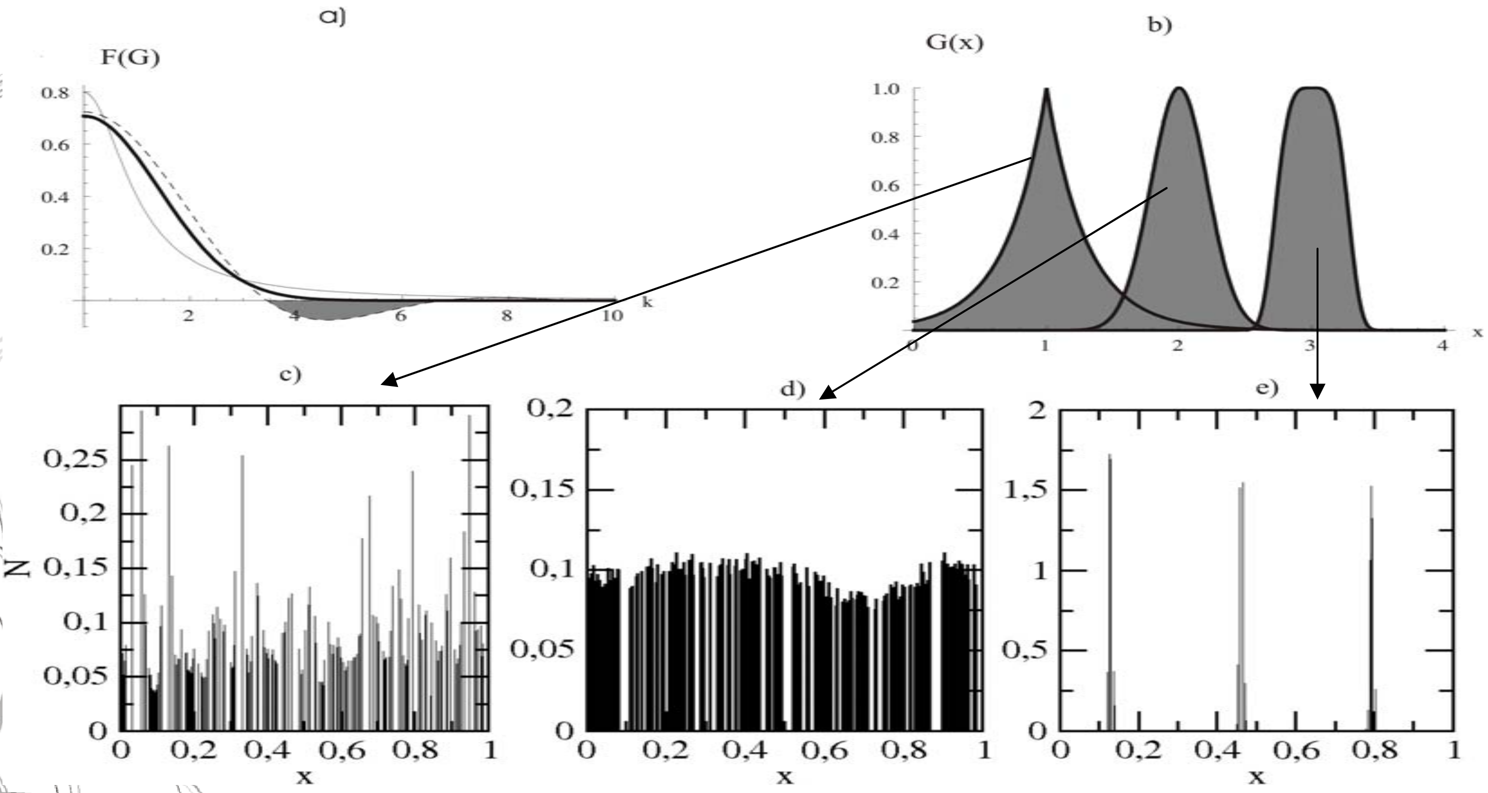
KERNEL FOURIER TRANSFORM

$$\lambda \geq 0 \Leftrightarrow \bar{g}(q) \geq 0 \quad \text{for} \quad \text{some} \quad q$$

Condition for pattern forming transition

ONLY DEPENDS ON THE KERNEL AND NOT ON ANY OTHER PARAMETER OF THE SYSTEM.

It is well-known that for the family of stretched-exponential functions their Fourier transform never takes negative values for, (i.e., ***NO CLUSTERING OF SPECIES WITH EXCLUSSION ZONES OCCUR)*** $0 \leq \sigma \leq 2$



Exponential Gaussian Quartic

Non-constant (phenotype-dependent) carrying capacity:

$$\partial_t \phi(x,t) = \phi(x,t)\left[1 - 1/K(x)\int dy\, g(|x-y|)\phi(y,t)\right]$$

If the kernel is symmetric (our case of interest) the equation is potential:

$$\partial_t \phi(x,t) = -\frac{\phi(x,t)}{K(x)}\frac{\delta V(\phi)}{\delta \phi}$$

$$V = -\int dx K(x)\phi(x,t) + 1/2\int dx dy\, g(x,y)\phi(x)\phi(y)$$

Lyapunov potential $\frac{dV}{dt} \leq 0$

Natural stationary solution: is the one which is positive and non-vanishing for all *x*, that is, the solution of:

$$\left(\frac{\delta V}{\delta \phi}\right)_{\phi^N} = 0$$

$$K(x) = \int dy g(x,y)\phi^N(y) \Leftrightarrow \overline{\phi}^N(q) = \frac{\overline{K}(q)}{\overline{g}(q)}$$

These Fourier transforms and their inverses should exist and lead to positive populations. This is not always the case (for e.g. when both *K* and *g* are superexponentials and the exponent of *K* is larger than the one of *g*).

When the natural solution exists, its stability depends, since *V* is a quadratic potential (form), on the positive-definiteness* of the kernel. ITS STABILITY DOES NOT DEPEND ON THE CARRYING CAPACITY.

We can extend these results to non-symmetric kernels.

$* \sum_i a_i M_{ij} a_j \geq 0; \; for \quad any \quad set \quad \{a_i\}$

SUMMING UP THIS SECTION:

IN THE LV COMPETITION MODEL THERE IS A UNIFORM DISTRIBUTION OF CLOSE SPECIES IF THE KERNEL IS POSITIVE DEFINITE. WHEN THIS IS NOT THE CASE A LUMPY DISTRIBUTION OF SPECIES, WITH EXCLUSION ZONES, APPEAR.

NOTE THAT POSITIVE-DEFINITENESS IS EQUIVALENT TO REQUIRE THAT THE FOURIER TRANSFORM OF THE KERNEL TAKES ONLY POSITIVE VALUES.

FOR THE FAMILY OF KERNELS $g_\sigma(x) = \exp[(-x/R)^\sigma]$

THIS HAPPENS FOR $$0 \leq \sigma \leq 2$$

THE GAUSSIAN KERNEL IS A FRONTIER CASE THAT GIVES RISE TO A HOMOGENOUS DISTRIBUTION.

The Gaussian Kernel.

The Gaussian Kernel is the one traditionally used in the ecological community. To my knowledge is the one exclusively used.

WHY?

-It is ecologically sound: it fits to data.

- Analytically manageable.

- MOST IMPORTANTLY: Next section.

BUT IT IS A MARGINAL CASE AS WE HAVE JUST SEEN (BEING POSITIVE DEFINITE AND THUS NOT GIVING RISE TO CLUSTERS OF SPECIES)

How is it sensitive to numerical issues and to ecologically second-order effects?

Almost identical

1)

$$g_2(x) = \exp[(-x/R)^2]$$

Positive definite

Homogenous
distribution of species

$$g_{2.1}(x) = \exp[(-x/R)^{2.1}]$$

Non-positive definite

Lumpy distribution

2)

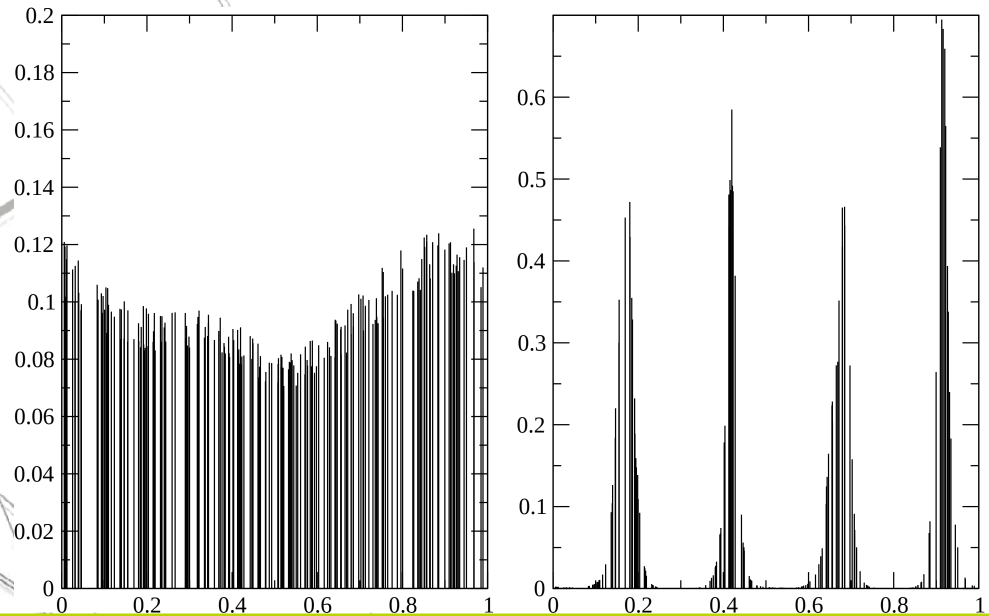
Scheffer & Van Nes, PNAS 103, 6230 (2006).
Use a Gaussian Kernel and they obtain a Lumpy distribution??

It is a numerical error of taking wrongly the periodic boundary conditions (PBC).

$$g(y) = \sum_n g(y - nL)$$

L system size and *n=0, +-1, +-2,…*

Correct PBC



Wrong PBC as in Scheffer & Van Nes.

This does not happen e.g. exponential.

3) Ecological mechanisms (second order effects):

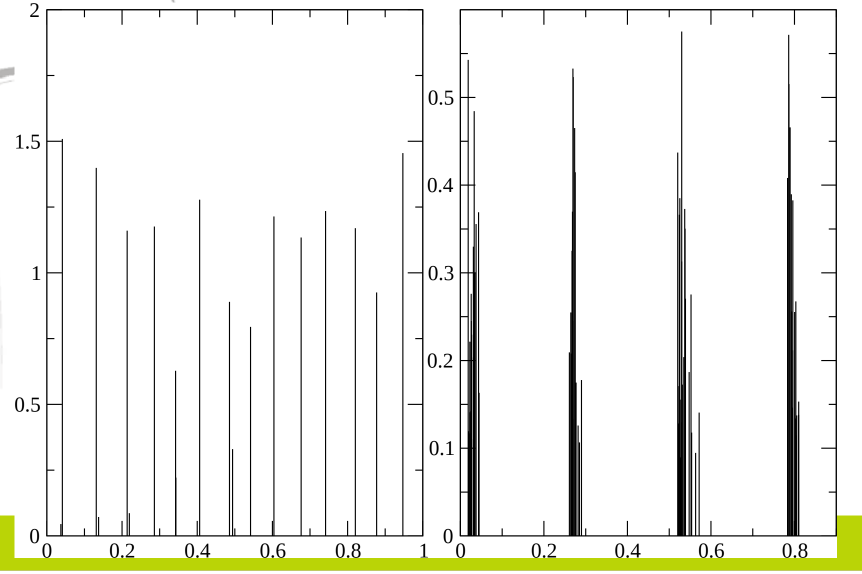
- We have added several mechanisms to study the stability of the niche model with Gaussian competition

- *Small immigration* DOES NOT LUMP THE SPECIES DISTRIBUTION.

- *Adding noise or an extinction threshold* DOES NOT FORM CLUSTER but impose some limit to similarity (for any kernel).

- Species extinction and speciation: eliminate species below a given population threshold and introduced new ones at a given rate close to already existing species (evolutionary diffusion in other contexts).

Exponential



Gaussian with perfect PBC

-Summing up this section:

The Gaussian competition function is rather marginal. It is a borderline between a family of kernels giving rise to lumpy species distributions (non positive definite) and a family (like the Gaussian itself) that results in homogenous distributions.

Message: take care in numerical work. Second order ecological effects may also have a very strong influence.

SIMPLE ECOLOGICAL MODELS GIVING RISE TO NON-POSITIVE DEFINED KERNELS

-The LV model is some kind of effective model where competition coefficients are postulated to be of a particular functional form (Gaussian, exponential, etc..).

- At a more fundamental level species utilize a common distributed resource *x* according to an utilization funcion $u_i(x)$

- The competition coefficients are calculated as the probability that consumer *i* meets consumer *j*

$$g(|x_i - x_j|) = g_{ij} = \frac{\int dx u_i(x) u_j(x)}{\int dx u_i^2(x)}$$

In particular, for Gaussian utilization functions we get Gaussian coefficients (kernel)

IMPORTANT: ONE CAN SHOW THAT ANY INTERACTION KERNEL CONSTRUCTED FROM CONVOLUTION OF TWO UTILIZATION FUNCTIONS IS POSITIVE DEFINITE.

- Non-sense our study for kernels (non-positive) giving rise to lumpy distribution of species??

ANSWER: NO. We can construct a simple ecological model with a non-positive defined kernel.

Meszena et al have pointed out that one should consider two different utilization-like functions:

a) A sensitivity function describing the effect of resource *x* on species *i*. $S_i(x)$

b) An impact function describing the depletion of resource *x* by species *i*. $D_i(x)$

$$g_{ij} = \int dx S_i(x) D_j(x)$$

Not neccesarily positive defined.

Let us obtain this sensitivity and impact functions from a simple ecological model of predators competing for different types of preys or resources:

Resources →

$$\frac{dR_\alpha}{dt} = -R_\alpha \sum_i a_{\alpha i} N_i + \beta_\alpha R_\alpha (1 - \frac{R_\alpha}{Q_\alpha})$$

$$\frac{dN_i}{dt} = N_i \sum_\alpha S_{i\alpha} R_\alpha - d_i N_i$$

If the time scale of the evolution of resources is much larger than that of the preys, i.e, dR/dt=0. One obtains a LV equation:

$$\frac{dN_i}{dt} = N_i (r_i - \sum_j C_{ij} N_j)$$

$$C_{ij} = \sum_k S_{ik} D_{kj}$$

$$D_{kj} \propto a_{kj}$$

Example: a situation in which consumer k grows only by consumer its optimal resource at k, but it depletes also the neighbouring resources

$$Q_\alpha = Q \,;\, \beta_\alpha = \beta \,;\, d_i = d \,;$$
$$S_{i\alpha} = g\,\delta_{i\alpha}$$
$$a_{\alpha j} = a\,\delta_{\alpha j} + b\,(\delta_{\alpha j-1} + \delta_{\alpha j+1})$$

The LV dynamics is

$$\frac{dN_i}{dt} = Qi + gN_i(1 - 1/\beta(aN_i + bN_{i+1} + bN_{i-1}))$$

Whose natural solution and stability eigenvalues

$$N_i^N = \frac{\beta}{a+2b}$$
$$\lambda_q = -(Qg/\beta)(a + 2b\cos q)$$

They can be positive or negative depending on a and b

Conclusions:

-The competition kernel plays a fundamental role in the stationary spatial structure of competing species/agents.

- We have shown that if it is positive-defined the distribution is homogenous (coexistance o species), otherwise there are exclusion zones where species cannot develop, or even clusters of species.

- The Gaussian Kernel is a frontier case. Much care have to be taken in numerical work. Also, second-order ecological effects may completely change the scenario.