Species clustering in models of biological competition

EMILIO HERNÁNDEZ-GARCÍA
CRISTÓBAL LÓPEZ
Instituto de Física Interdisciplinar y Sistemas Complejos
IFISC (CSIC-UIB), Palma de Mallorca, Spain

SIMONE PIGOLOTTI
The Niels Bohr Institute, Copenhagen, Denmark

KEN H. ANDERSEN
National Institute of Aquatic Resources, Copenhagen, Denmark

IFISC

Competition processes:
Interactions between different entities competing for the same resources

- Multimode optical devices in which different lasing modes are driven by the same population inversion.
- Spin wave patterns, crystalization fronts, multiwave competition …
- Technology substitution in which users decide between alternative products.
- language competition
-Scientist competing for funding …
- **Population dynamics.**
- **Sympatric speciation.**
- **Evolutionary dynamics**

Lotka-Volterra type competition.

(Volterra 1926, Lotka 1932)

$$\dot{N}_i = r_i N_i \left(1 - \frac{1}{K_i} \sum_{j=1}^{m} G_{ij} N_j \right), \quad i = 1, ..., m.$$

Lotka-Volterra (LV) type competition

(Volterra 1926, Lotka 1932)

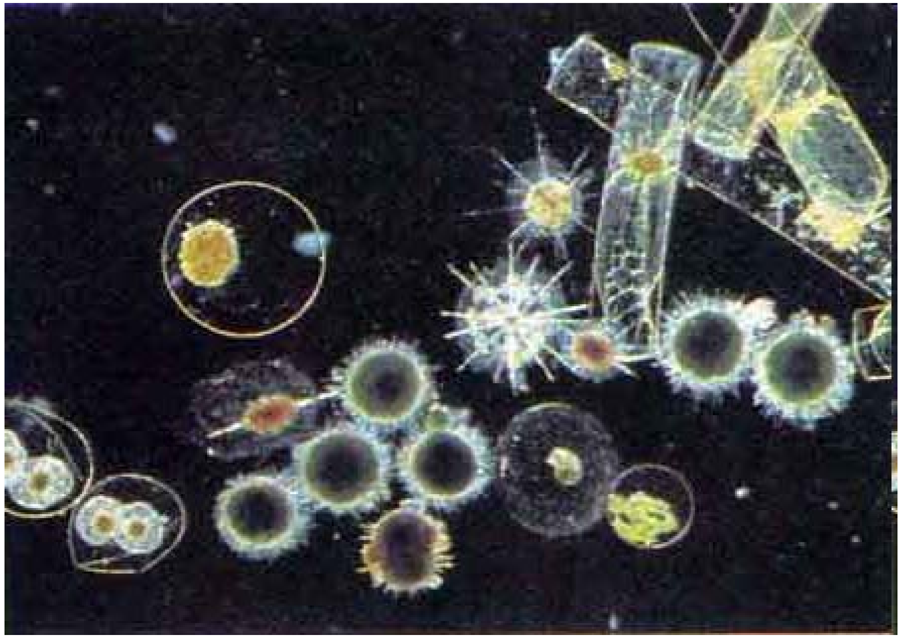
- competition among *m* species
- N_i – population of species *i*
- r_i – linear growth rate of species *i*
- *Ki* – carrying capacity of species *i*
- *Gij* – impact of species j on the growth of *i*

(Gause, 1934; Hardin, 1960)

The principle of competitive exclusion:
two species competing for the same resource
will not coexist: one will become extinct or displaced

Supported by LV in a particular case: $\dot{N}_i = N_i f(R_1(N),\ldots,R_n(N))$

with **number of resources *n* < number of species *m***



But coexistence occurs !!!

(e.g. the Plankton paradox)

Many explanations:

Time-dependent dynamics

Temporal forcing

Predation, other interactions …

Spatial inhomogeneities

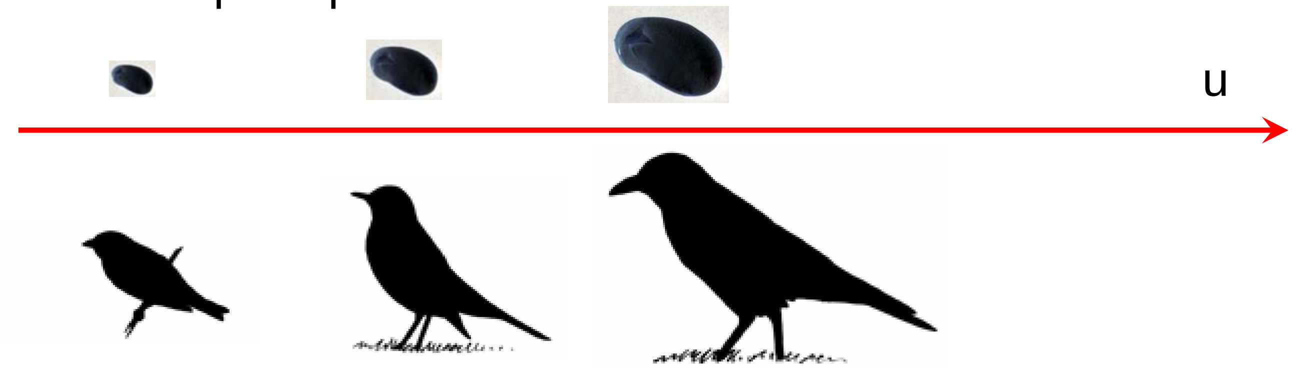
Flow effects

…

What does it means ‘the same’ or ‘similar’ resources?

(Hutchinson, 1959; MacArthur & Levin, 1967)

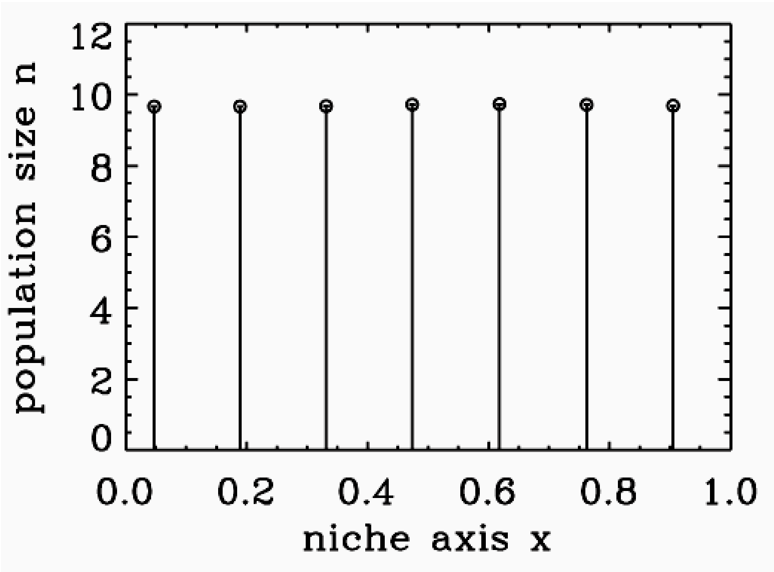
Resources arranged in a continuum: the niche space (size of prey, its location, …)
Species distribute according to their phenotype on such space. Continuous or discrete distributions are in principle allowed



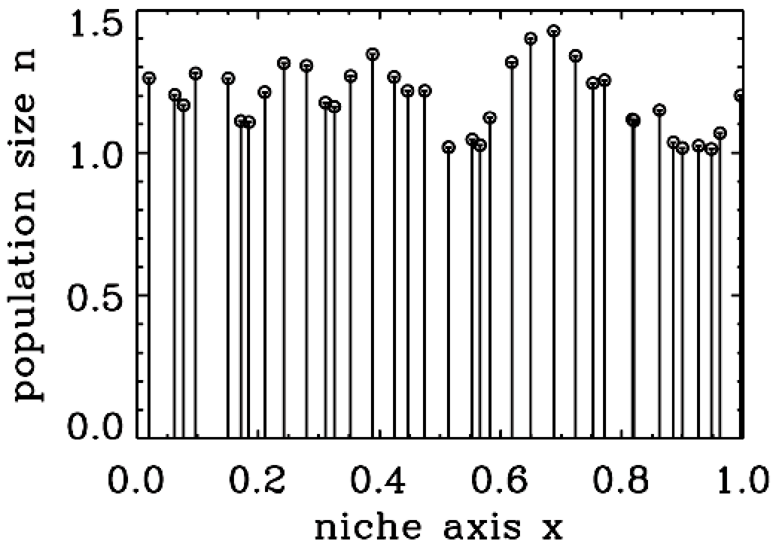
$$\partial_t \psi(u,t) = r(u)\psi(u,t) \left[1 - \frac{1}{K(u)} \int G(u,v)\psi(v,t)dv\right]$$

Principle of **competitive exclusion** $\rightarrow$ Existence of a **Limiting similarity**

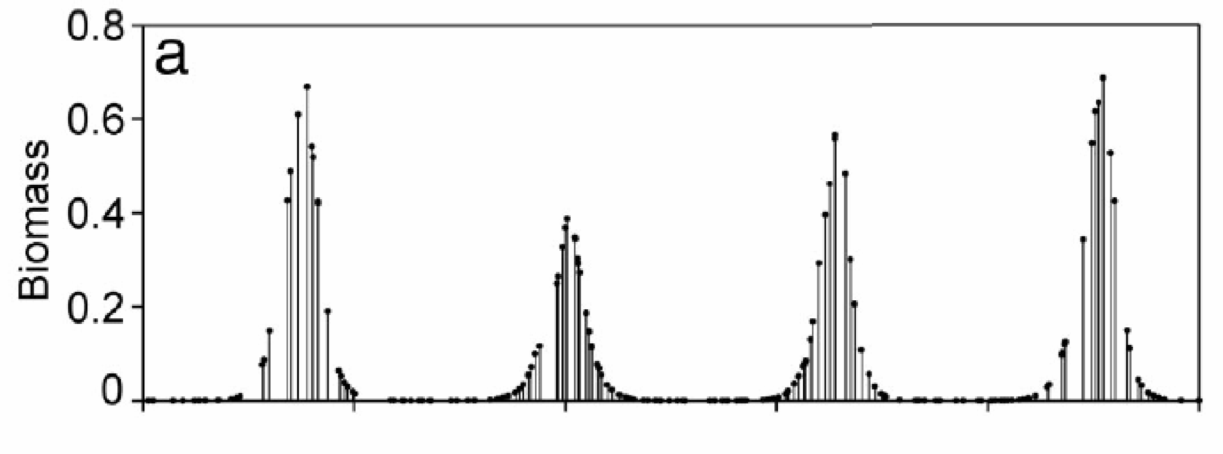
Stronger competition G(u,v) among species specialized in resources close in niche space   G≈G (|u-v|)



Limiting similarity scenario

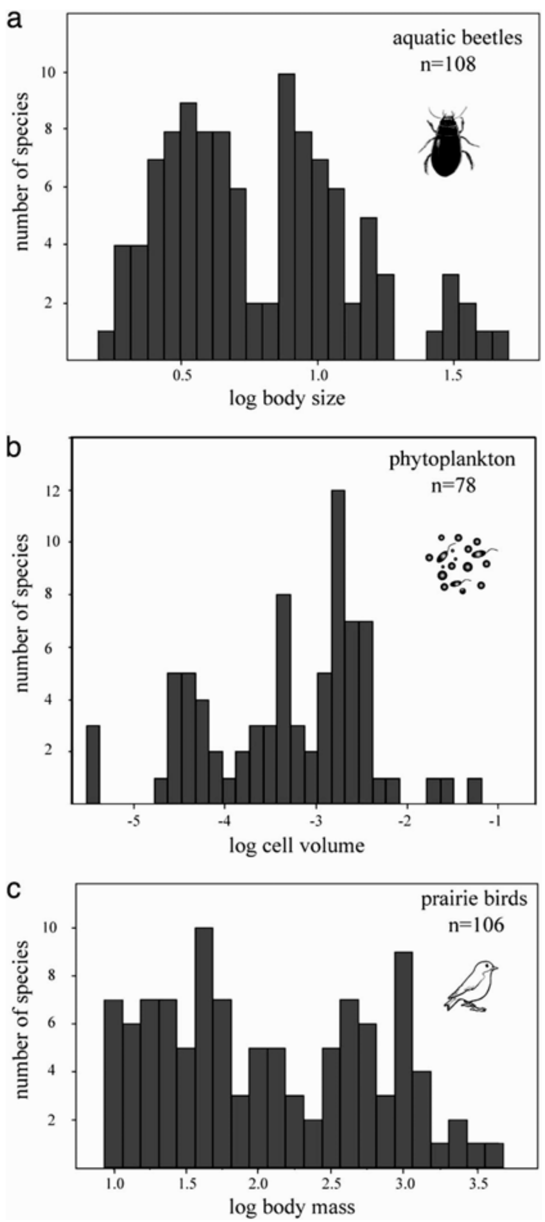


No limiting similarity

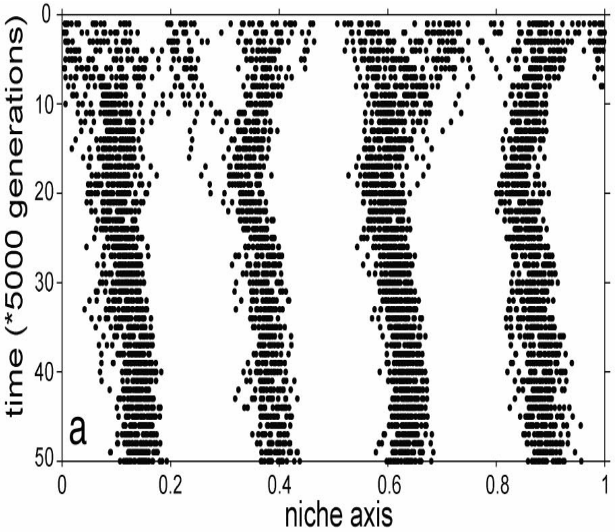


LV model with Gaussian competition G(|u-v|).

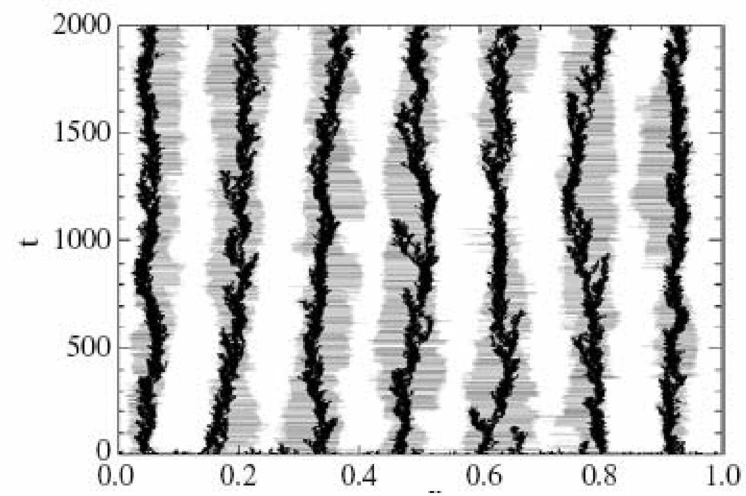
Scheffer & Van Nes, PNAS 103, 6230 (2006).
Self-organized similarity, the evolutionary emergence of groups of similar species



Neither a limiting similarity scenario nor the opposite. Mixed behavior:
CLOSE COEXISTENCE + EXCLUSION ZONES



Competing species in niche space
(+evolutionary diffusion)
Scheffer & van Ness, 2006



Brownian bugs competing in space
Hernandez-Garcia & Lopez,
Phys. Rev. E 70, 016216 (2004)
Physica D 199, 223-234 (2004)

$$\partial_t \phi(\mathbf{x},t) = \mu\phi(\mathbf{x},t) + D\nabla^2\phi(\mathbf{x},t) - g\phi(\mathbf{x},t)\int_S G(\mathbf{x}-\mathbf{y})\phi(\mathbf{y},t)d\mathbf{y} \ .$$

birth date decreasing with the number of neighbors
$\rightarrow$ LV type of dynamics for spatial distribution of walkers

Fuentes, Kuperman & Kenkre, PRL 91, 158104 (2003)

AIM:

- Understanding this mixed scenario in terms of a pattern forming instability
- Discussing the role of the interaction function (in theoretical ecology the interaction kernel is always taken Gaussian, and the discussion is on the role of the carrying capacity K(u))

OUTLINE

- Pattern formation for Lotka-Volterra competition in niche space.
- The Gaussian interaction kernel.
- The lumped (mixed) solutions.

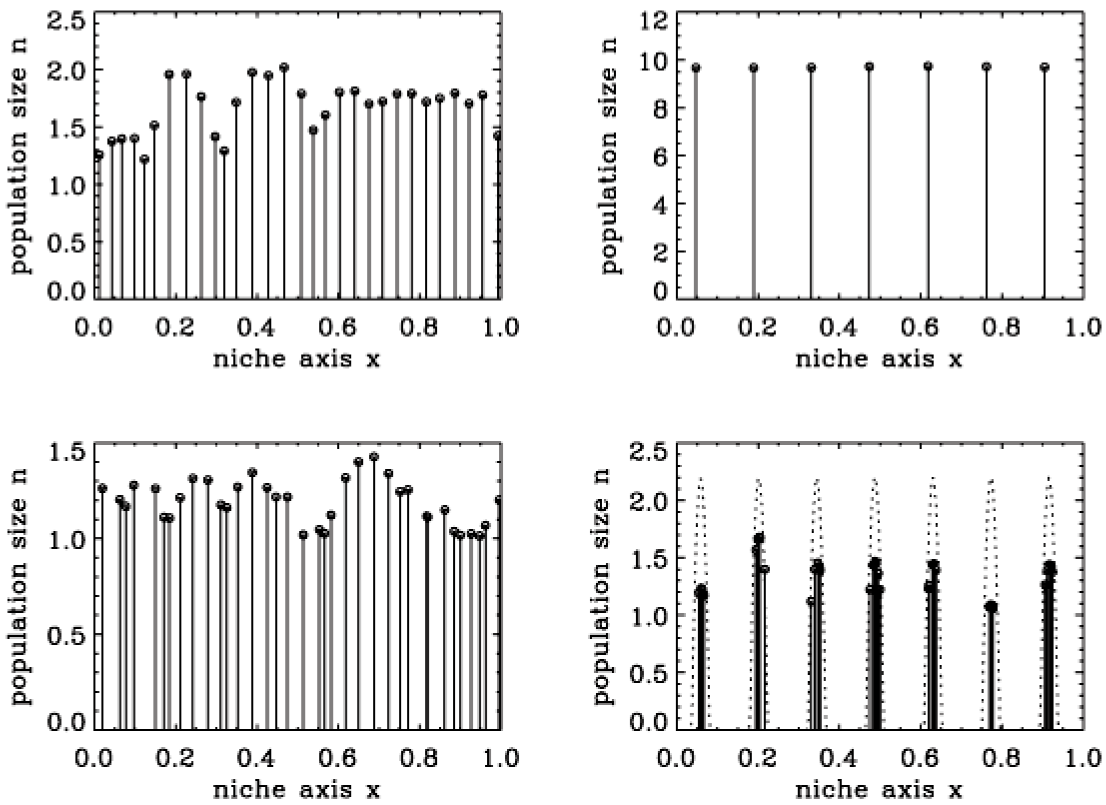
LV dynamics (no diffusion) in continuous niche space (with periodic boundary conditions) + random immigration
+ extinction if population < N_m
uniform carrying capacity and linear growth rate

$$G(u,v) = g_\sigma(|u-v|) = e^{-\left(\frac{|u-v|}{r}\right)^\sigma}$$

$$G(u,v) = g_\sigma(|u-v|) + \delta(u-v)$$

(enhanced self-competition)

σ=1 σ=4



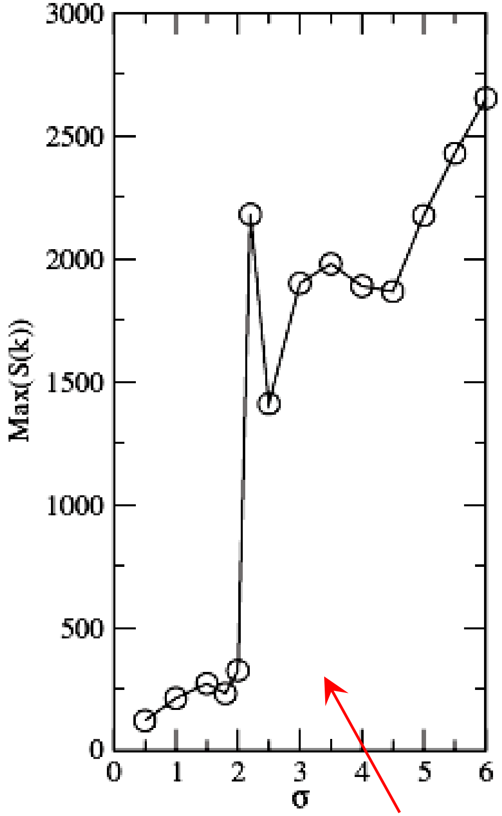
For the family of interaction kernels

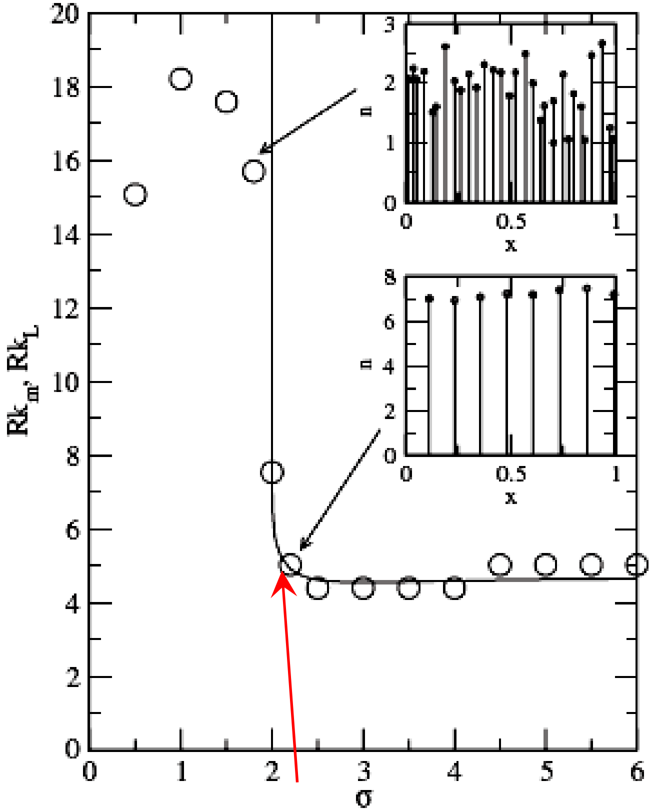
$$g_\sigma(x) = \exp[-(|x|/r)^\sigma]$$

$S(q) = <|\hat{\psi}(q)|^2>$

structure function

max(S(q))





q: wavenumber of the periodicity

(it is of the order of 2 r)

transition for σ=2: the **Gaussian kernel**

Analytic results (constant r_0 and K_0):

Homogeneous species distribution: $\psi_0 = K_0/\hat{G}_0$

Linear stability analysis $\psi(u,t) = \psi_0 + \delta\psi(u,t)$

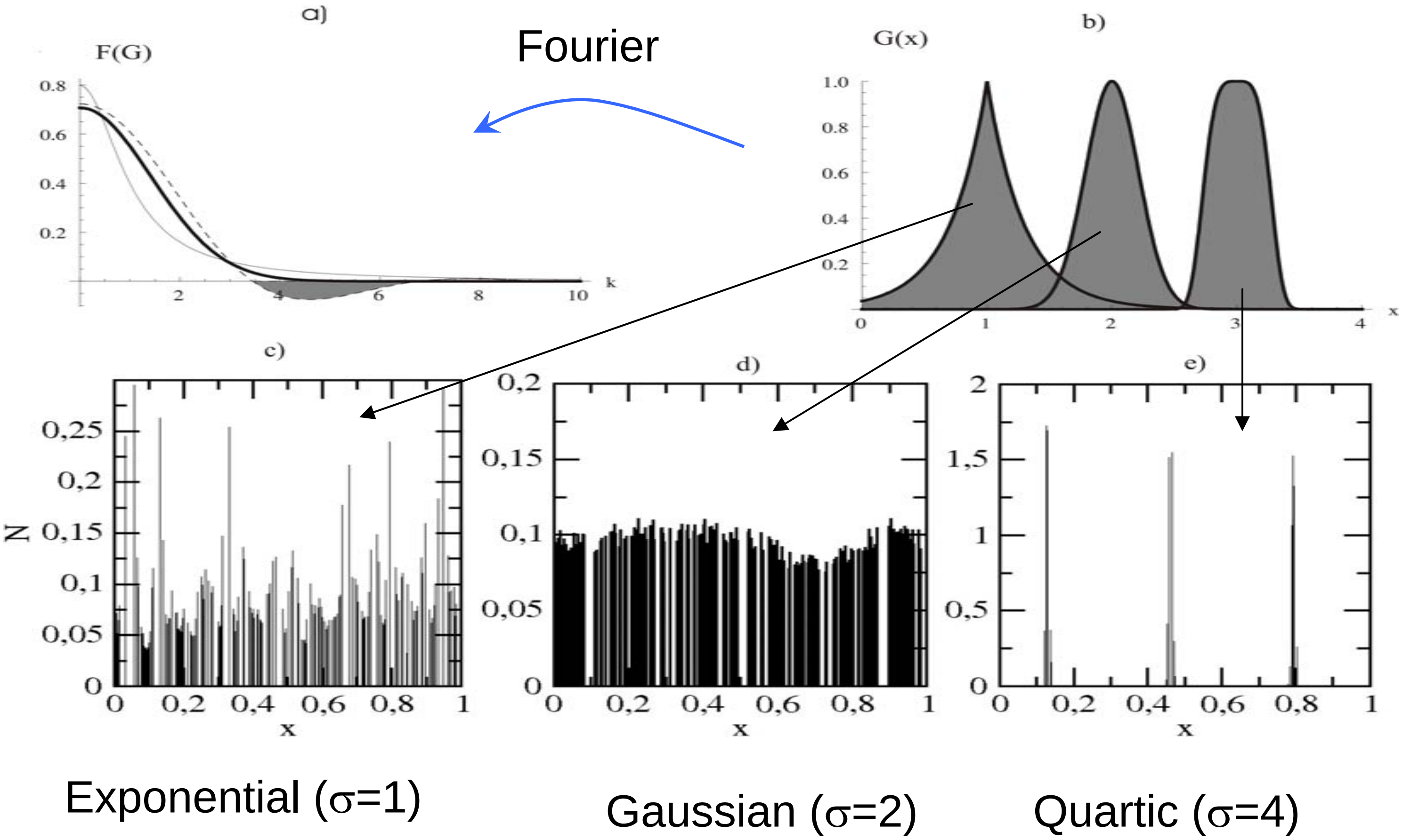
$$\delta\hat{\psi}_q(t) = \delta\hat{\psi}_q(0)e^{\lambda_q t} \text{ , with } \boxed{\lambda_q = -r_0\frac{\hat{G}_q}{\hat{G}_0}}$$

Thus, if the **Fourier transform of the interaction kernel has negative values** (for some q_c), the homogeneous distribution will be unstable:

a **pattern** will occur (typically of a periodicity determined by q_c)

Otherwise, some homogeneous distribution is expected.

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



The result can be extended to **non-uniform** carrying capacity K(u) and linear growth rate r(u)

by using that, if the kernel is symmetric (G(u,v)=G(v,u)) the equation has a Lyapunv potential:

$$\partial_t \psi(u,t) = -r(u)\frac{\psi(u,t)}{K(u)}\frac{\delta V[\psi]}{\delta \psi(u)}$$

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

$$V = -\int du K(u)\psi(u,t) + 1/2\int dudv G(u,v)\psi(u)\psi(v)$$

If K and G are such that a steady solution which is positive ∀u exist (species coexistence) , then it is stable if G is positive definite

($\sum x_i \, G(x_i,x_j) \, x_j \geq 0 \;\forall \{x_i\}$)

For non-symmetric kernels a similar (but only local) stability result also holds

Thus, limiting similarity scenarios and non-limiting similarity scenarios appear, respectively, for non-positive and for positive-definite competition kernels

The Gaussian Kernel.

But Scheffer & van Ness (2006) found exclusion zones (≈limiting similarity) for the Gaussian case, at variance with us !!

The Gaussian Kernel is the one traditionally used in the ecological community.

IT IS POSITIVE DEFINITE AND THUS DOES NOT GIVE RISE TO SPECIES PATTERNS. BUT IT IS A MARGINAL CASE:

Very sensitive to numerical issues and to

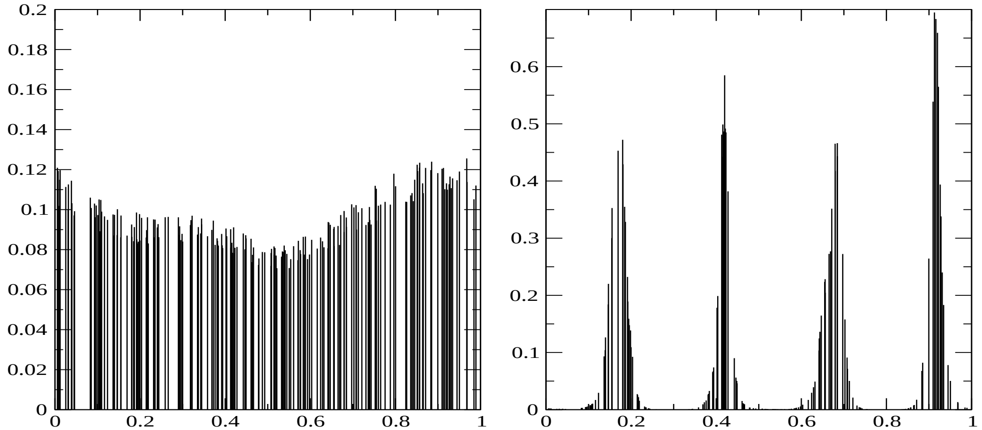
ecological second-order effects

$$g_{2.01}(x) = \exp[(-x/R)^{2.01}] \qquad g_2(x) = \exp[(-x/R)^2]$$

Almost identical

But one produces patterns and the other should not

Scheffer & Van Nes, PNAS 103, 6230 (2006). Use a Gaussian Kernel and they obtain a lumpy distribution?? **It is a numerical effect arising from the way periodic boundary conditions are implemented.**

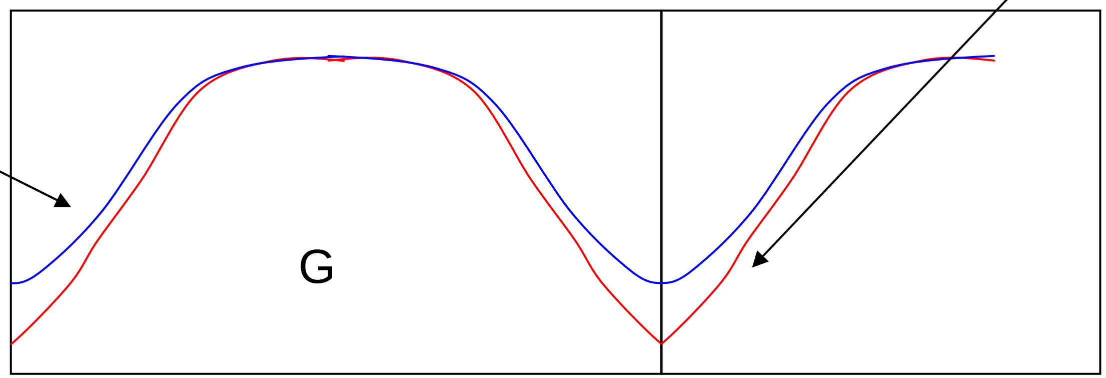


$$g(y)=\sum_{n} g(y-nL)$$

L system size and *n=0, +-1, +-2,…*

Scheffer & Van Nes.

Our work



This sensibility is not so strong for other non-marginal kernels

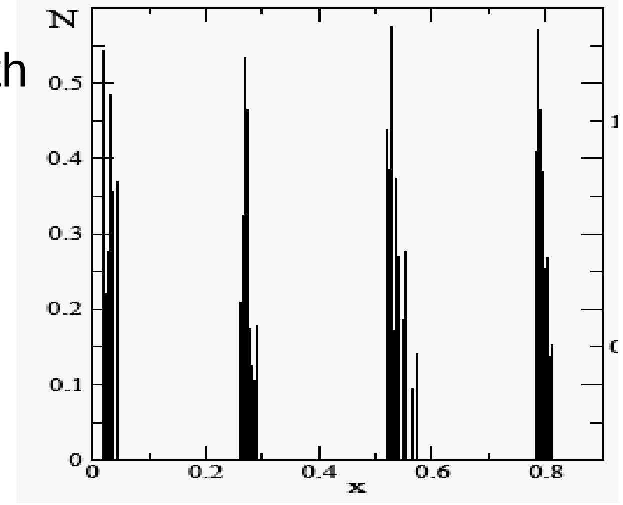
We have added several additional mechanisms to study the stability of the niche model with Gaussian competition.

It turns out that some small ecological mechanisms are able to change the qualitative behavior of the Gaussian kernel. This does not happen with non-marginal ones.

Example: Species extinction and speciation (evolutionary diffusion):

eliminate species below a given population threshold and introduced new ones at a given rate close to already existing species

Gaussian kernel with 'perfect' periodic boundary conditions



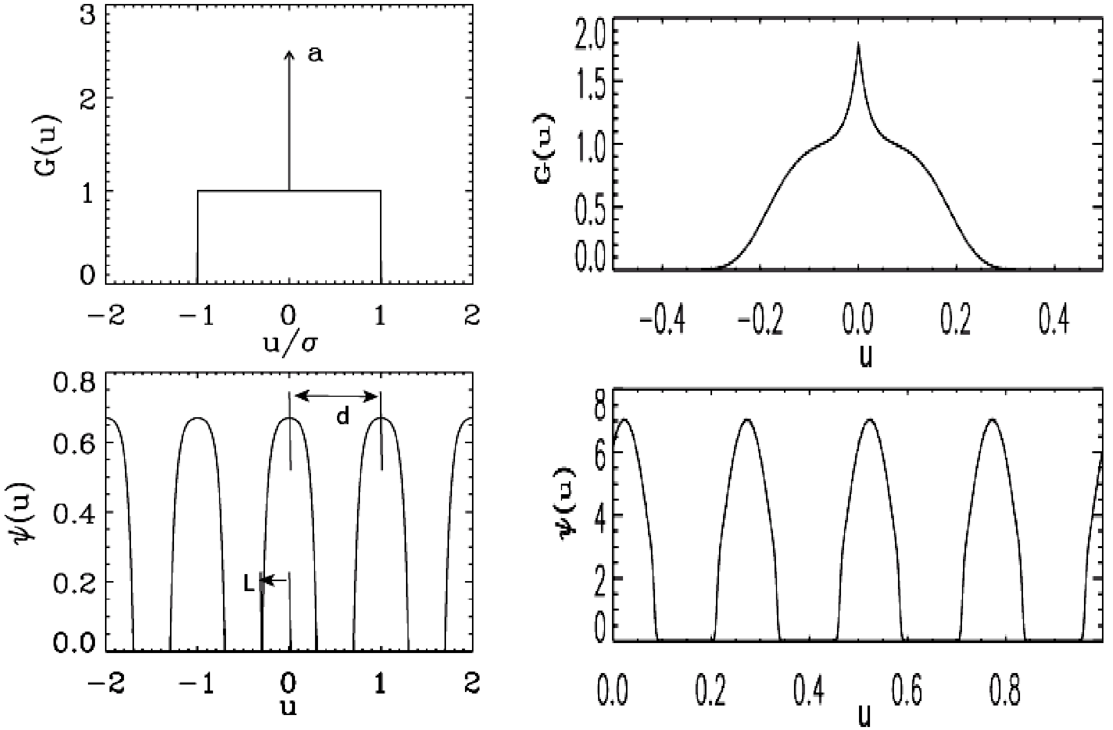
Take-home message:

Do not use always structurally unstable interactions if you want to know what are you doing

Do the ‘lumped solutions’ (the mixed state of clusters of close species separated by exclusion zones) only exist because of marginality of the Gaussian interaction?

NO.

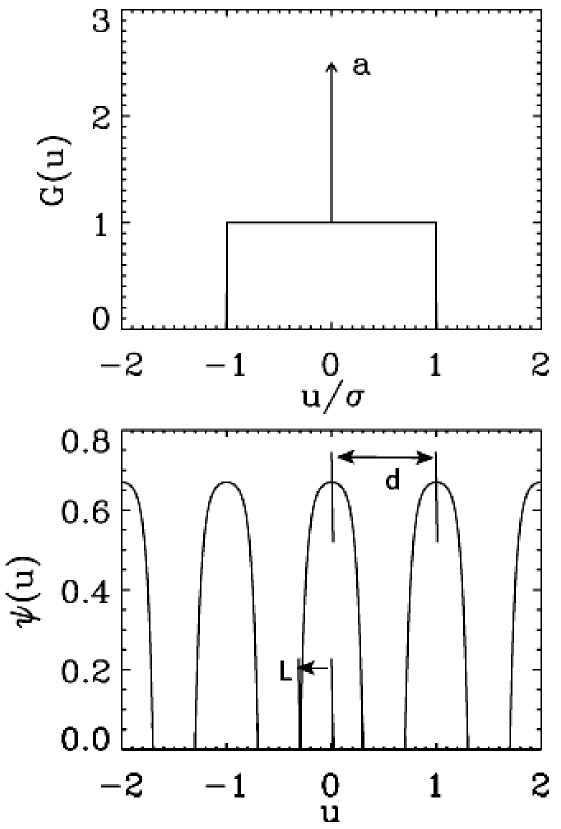
$G=g_{\infty}+\delta$



$G=g_4+g_1$

It arises also when adding enhanced intraspecific competition (which prevent excessive accumulation of individuals in a single species) to a situation of pattern forming leading to exclusion zones

In a simple case the lumped solution can be found analitically:



$$\psi(u) = \sum_{n=-\infty}^{\infty} f(x - nd)$$

$$\begin{aligned} f(u) &= A\left(1 - \frac{\cosh(\lambda u)}{\cosh(\lambda L)}\right) \text{ if } u \in [-L, L] \\ &= 0 \qquad \text{elsewhere} \end{aligned}$$

with

$$A = \frac{K_0}{a\,(1 - \operatorname{sech}(\lambda L)) + \frac{2}{\lambda}\,(\lambda L - \tanh(\lambda L))}$$

$$a\lambda = \sinh\left(\lambda(d - \sigma)\right) \ .$$

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 coexistence is estable (if the coexisting solution exists and is positive), otherwise there is a pattern forming instability leading to exclusion zones where species cannot develop, or even clusters of species.
- The widely used Gaussian interaction is a marginal case. Much care have to be taken in numerical work. Also, second-order ecological effects may completely change the scenario.
- Lumps of species arise from enhanced intraspecific competition on top of a pattern forming kernel

Pigolotti, S., López, C. & Hernández-García, E. [2007] "Species clustering in competitive Lotka-Volterra models." *Phys. Rev. Lett.* **98**, 258101.

Pigolotti, S., López, C., Hernández-García, E. & Andersen, K. H. [2008] "How competition leads to lumpy or homogeneous species distributions." preprint

Hernández-García, E., López, C., Pigolotti, S. & Andersen, K. H. [2008] "Species competition: coexistence, exclusion and clustering." preprint

All available from http://ifisc.uib-csic.es/publications/