

Clusters, exclusion and patterns in models of species competition

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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, or for space ...
 - **Population dynamics.**
 - **Sympatric speciation.**
 - **Evolutionary dynamics**

Lotka-Volterra type competition.

(Volterra 1926, Lotka 1932)

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

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
- K_i – carrying capacity of species i
- G_{ij} – 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: $\dot{N}_i = N_i f_i(R_1(N), \dots, R_n(N))$
 $i=1, \dots, m$, with **number of resources $n <$ number of species m**

For example: 2 species, 1 resource ($R(N_1, N_2) = A - BN_1 - BN_2$)

$$\dot{N}_1 = R(N_1, N_2)N_1 - d_1N_1 = N_1(A - BN_1 - BN_2 - d_1)$$

$$\dot{N}_2 = R(N_1, N_2)N_2 - d_2N_2 = N_2(A - BN_1 - BN_2 - d_2)$$

competitive exclusion occurs.

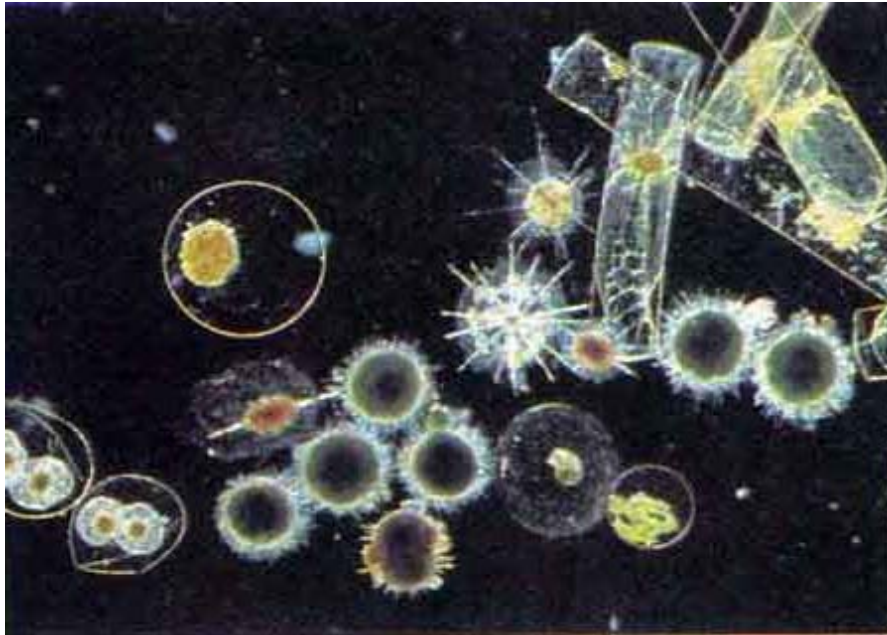
But it does not apply to

$$\dot{N}_1 = N_1(A - BN_1 - CN_2 - d_1)$$

$$\dot{N}_2 = N_2(A - CN_1 - BN_2 - d_2)$$

if $B > C$

Nor to unsteady solutions ...



But coexistence occurs !!!

(e.g. the Plankton paradox,
Hutchinson, Am. Nat. 1961)

Many additional explanations:

Time-dependent dynamics

Temporal forcing

Predation, other interactions ...

Spatial inhomogeneities

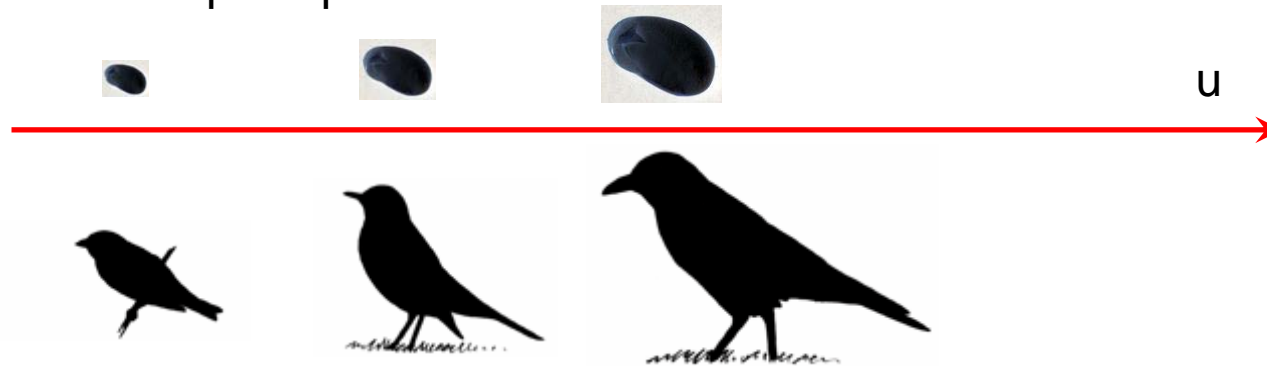
Flow effects

...

What does it mean 'the same' or
'similar' resources?

(Hutchinson, 1959; MacArthur & Levin, 1967)

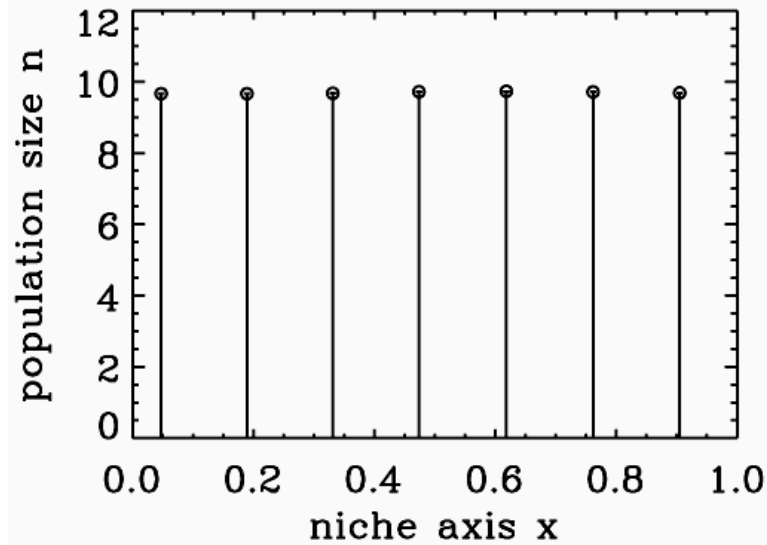
Resources arranged in a continuum: the niche space (size of prey, its location, ...)
 Species distribute according to their phenotype on such space. Continuous or discrete distributions are in principle allowed



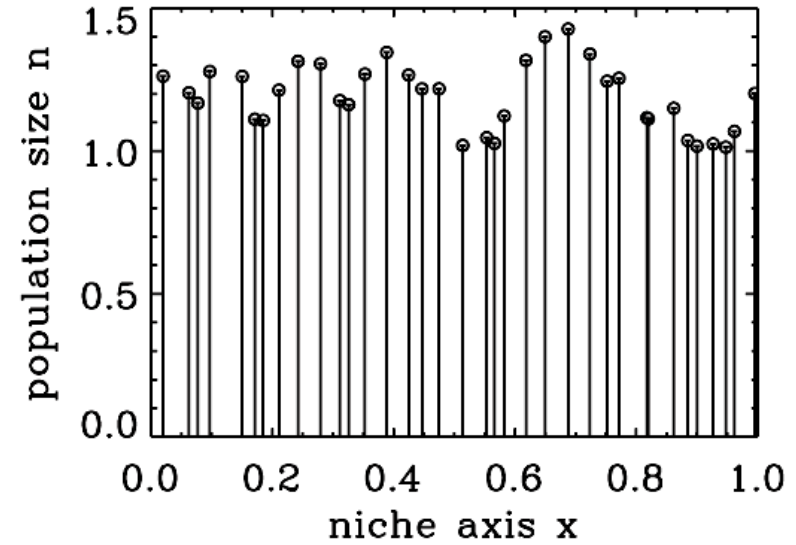
$$\partial_t \psi(u, t) = r(u) \psi(u, t) \left[1 - \frac{1}{K(u)} \int G(u, v) \psi(v, t) dv \right]$$

Principle of **competitive exclusion** → Existence of a **Limiting similarity**

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

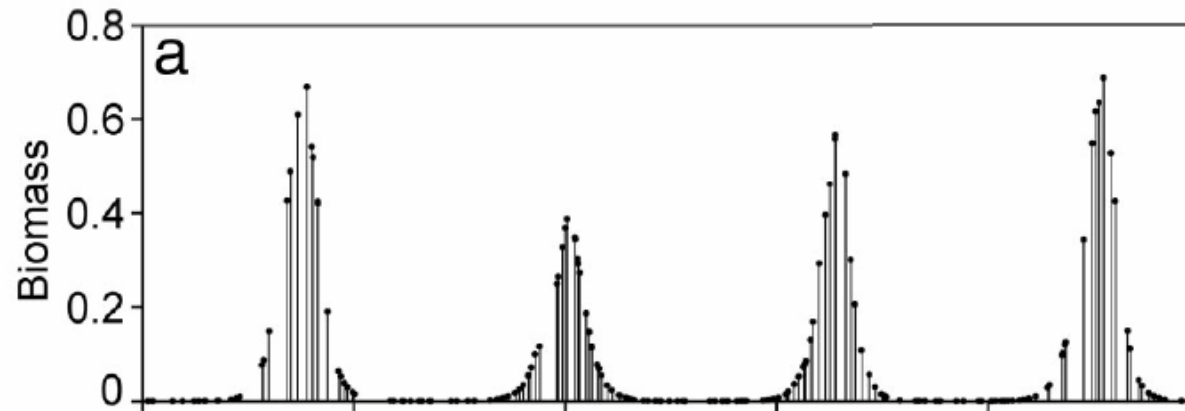


Limiting similarity scenario



No limiting similarity

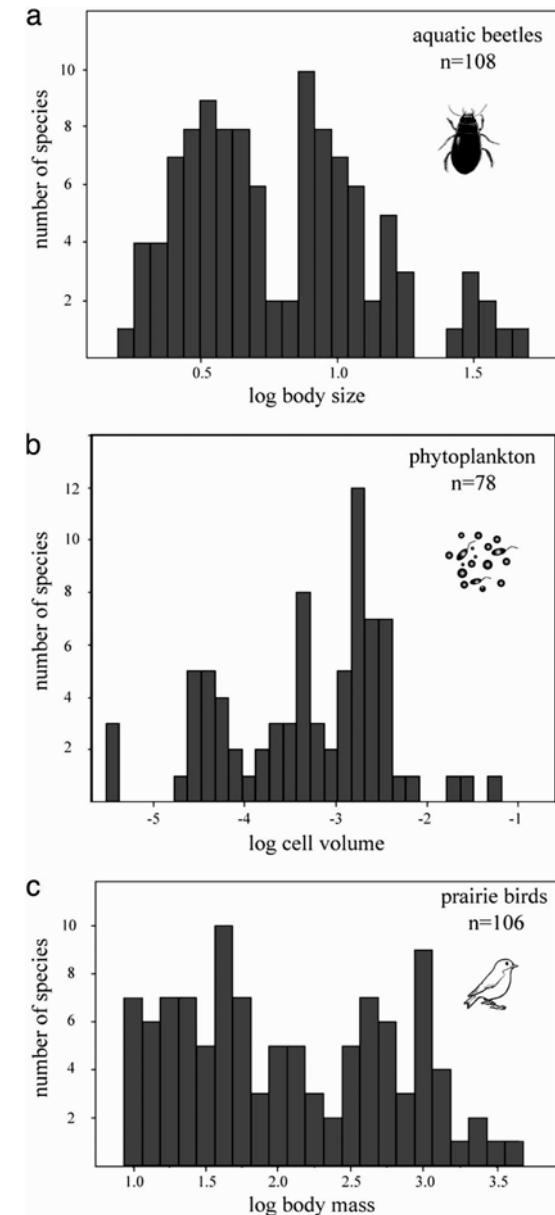
LV dynamics with constant carrying capacity supports both scenarios depending on the interactions G .

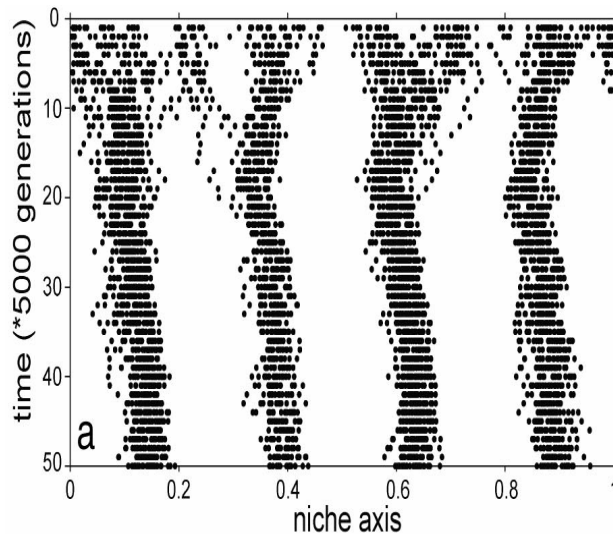


LV model with Gaussian competition $G(|u-v|)$.

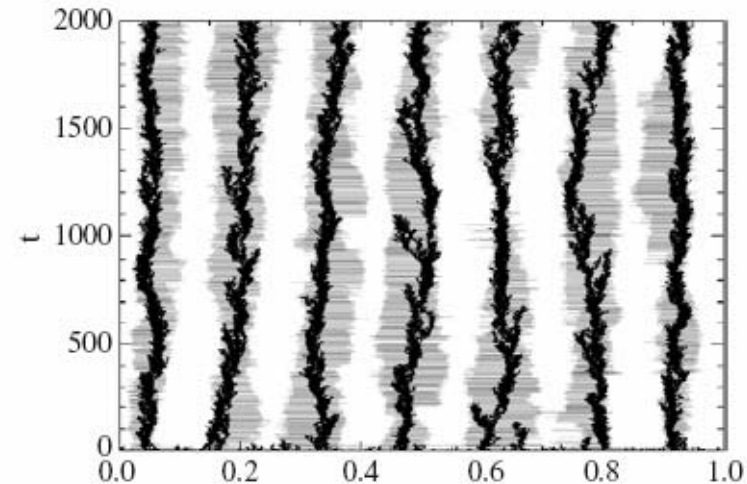
Scheffer & Van Nes, PNAS 103, 6230 (2006).
Self-organized similarity, the evolutionary emergence
of groups of similar species

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

→ 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

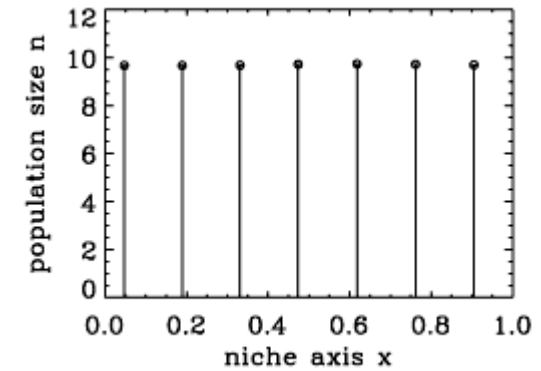
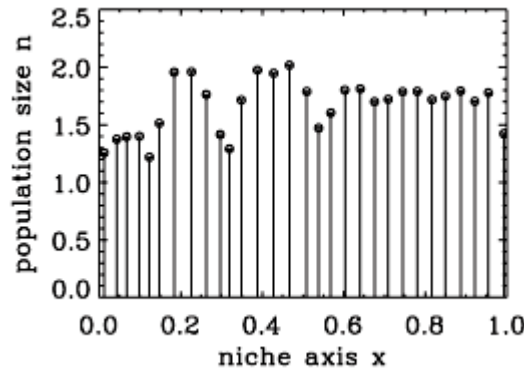
uniformity of carrying capacity and of linear growth rate

$\sigma=1$

$\sigma=4$

$$G(u, v) =$$

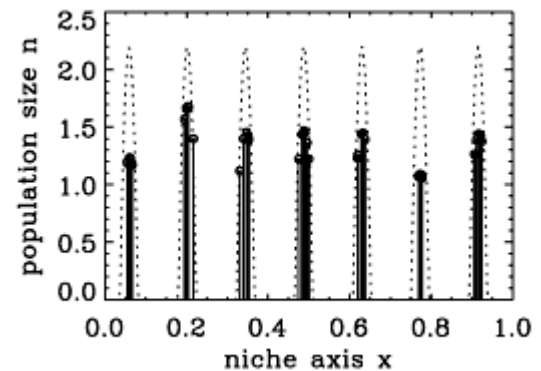
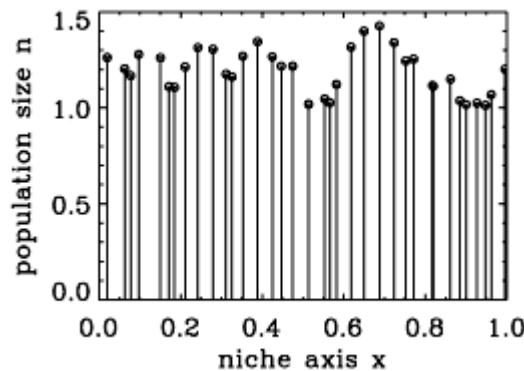
$$g_\sigma(|u - v|) = e^{-\left(\frac{|u-v|}{r}\right)^\sigma}$$



$$G(u, v) =$$

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

(enhanced self-competition)





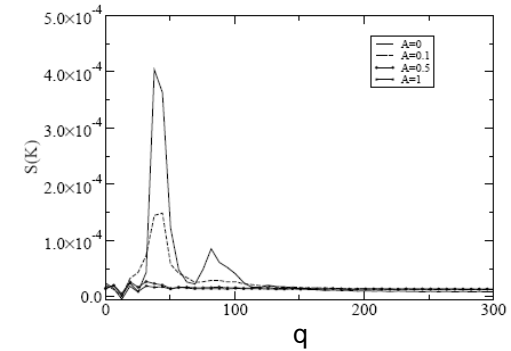
Pattern formation in LV dynamics

For the family of interaction kernels

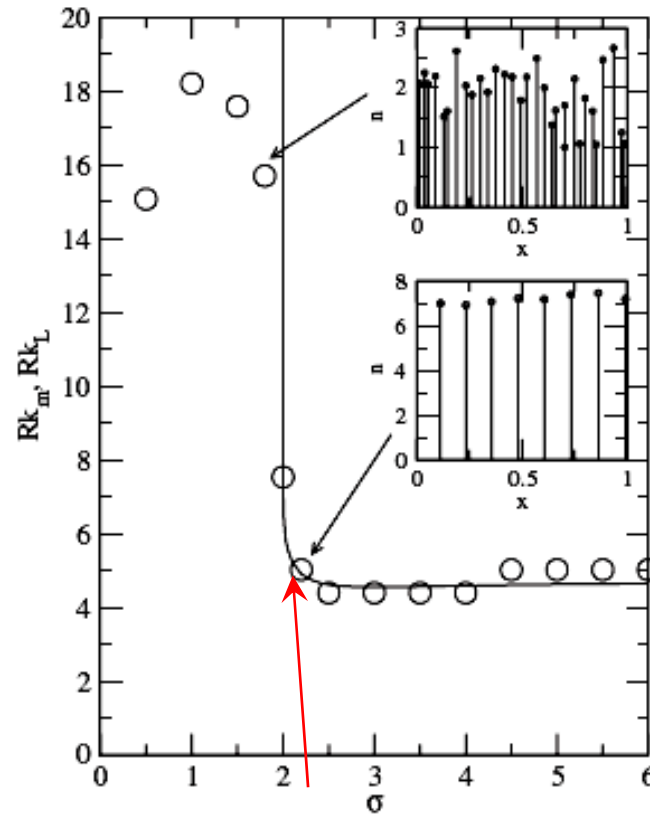
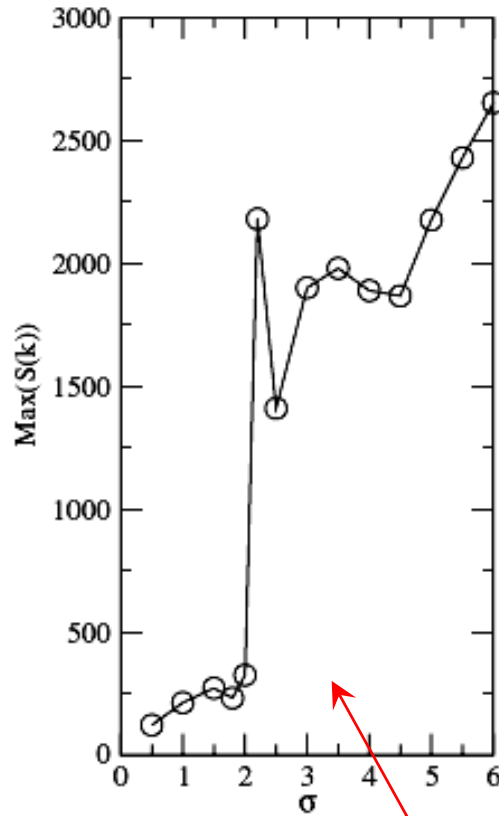
$$g_\sigma(x) = \exp[-(|x|/r)^\sigma]$$

$$S(q) = \langle |\hat{\psi}(q)|^2 \rangle$$

structure function



max(S(q))



q:
wavenumber
of the
periodicity

(periodicity of
the order
of 2r)

transition for $\sigma=2$: the **Gaussian kernel**



Analytic results (constant r_0 and K_0):

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

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

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

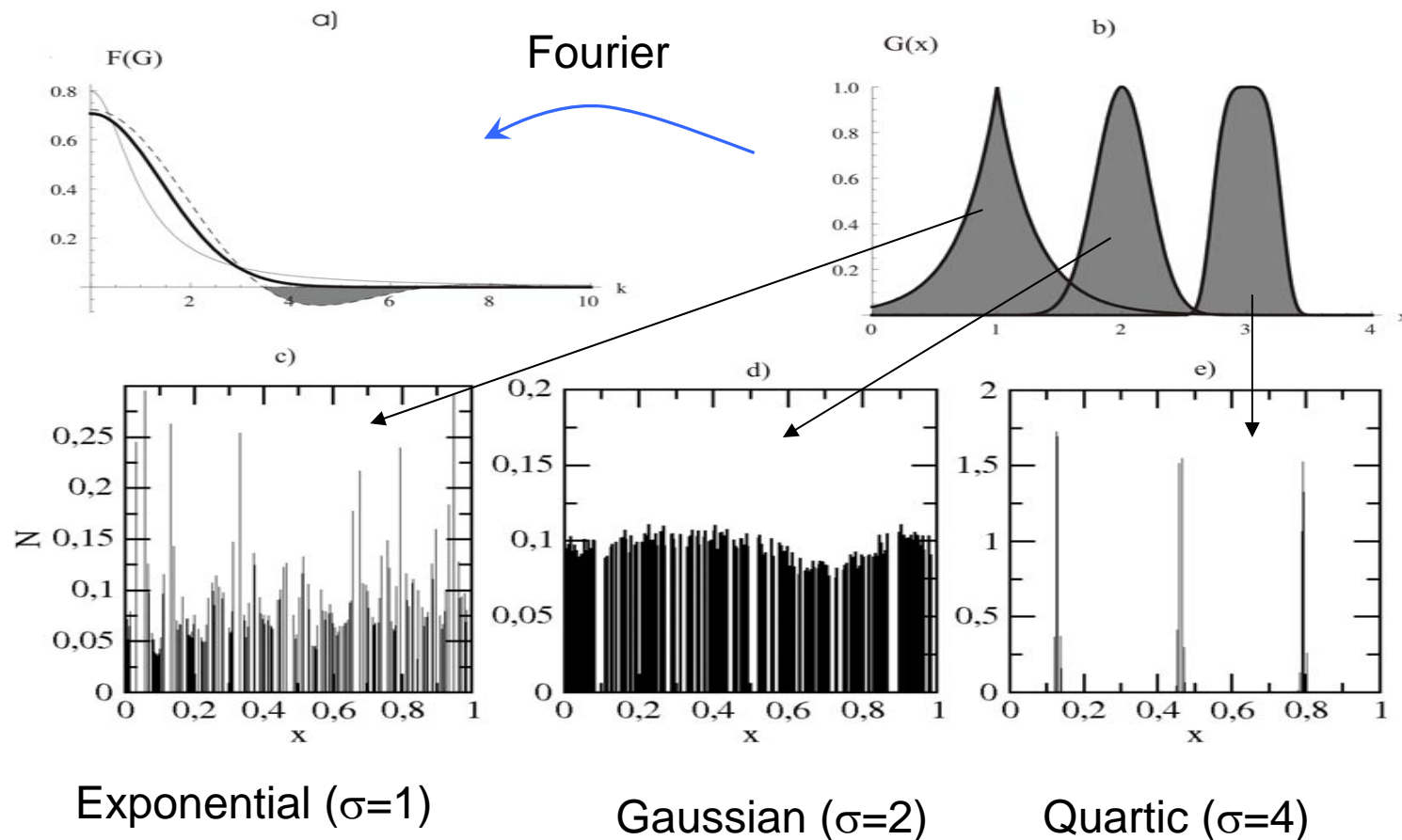
Thus, if the **Fourier transform of the interaction kernel has negative values**

(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 $0 \leq \sigma \leq 2$



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 Lyapunov 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** $\forall u$ exist (species coexistence):

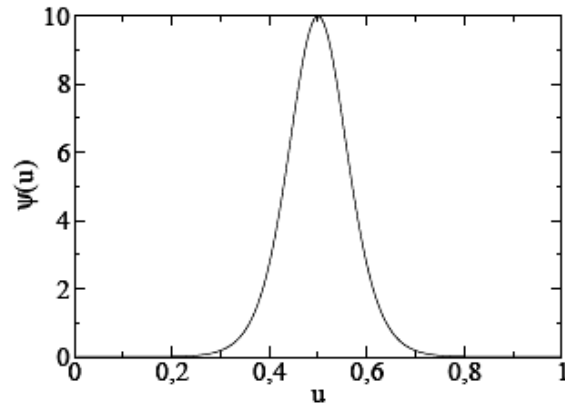
$$\int dv G(u, v) \psi^N(v) = K(u)$$

$$\hat{\psi}_g^N = \frac{\hat{K}_g}{\hat{G}_g}$$

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

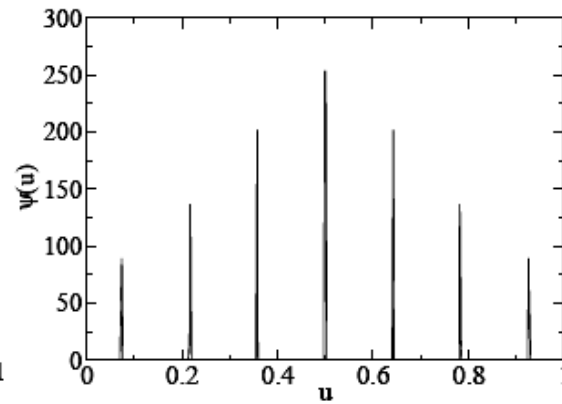
Thus, **limiting similarity scenarios** and **non-limiting similarity scenarios** appear, respectively, for **non-positive** and for **positive-definite competition kernels**



$G=g_\sigma^1$
(exponential interaction)
 $K=\text{sech}(u/\sigma)$

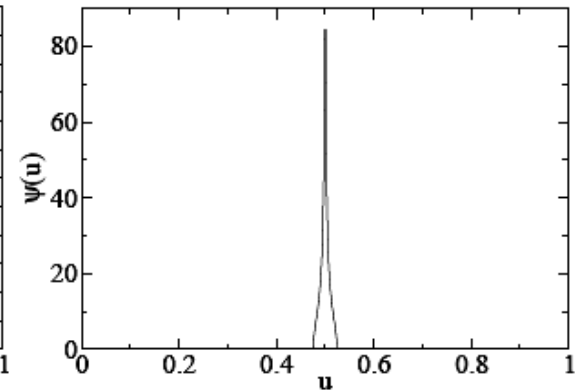
$$\Psi(u)=(1/\sigma)\text{sech}^3(u/\sigma)$$

G positive definite +
positive natural solution
exists:
COEXISTENCE



$G=g_\sigma^4$
 $K=g_\sigma^{0.5}$

G non positive definite
EXCLUSION



$G=g_\sigma^{0.5}$
 $K=g_\sigma^1$

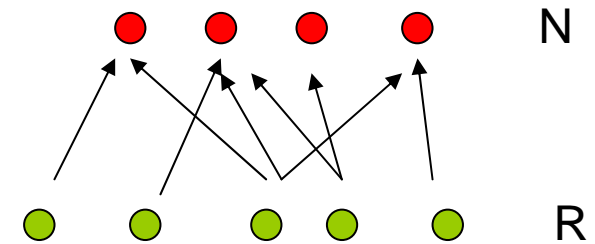
G positive definite
but natural solution
(inverse Fourier transform
of $\hat{\psi}_q^N = \frac{\hat{K}_q}{\hat{G}_q}$)
non-positive

Is the Gaussian Kernel, or positive-definite, or negative-definite interactions more 'realistic' than others?

NO, one can obtain many types of interactions from more fundamental models which include the dynamics of the shared resources R:

$$\dot{R}_\alpha = -R_\alpha \sum_i a_{\alpha i} N_i + \beta_\alpha R_\alpha \left(1 - \frac{R_\alpha}{Q_\alpha}\right)$$

$$\dot{N}_i = N_i \sum_\alpha S_{i\alpha} R_\alpha - d_i N_i$$



By adiabatic elimination of the resources (dR/dt ≈ 0):

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

All the types of interactions can be achieved

$$G_{ij} = \frac{C_{ij}}{C_{ii}} = \frac{\sum_\alpha S_{i\alpha} D_{\alpha j}}{\sum_\alpha S_{i\alpha} D_{\alpha i}} \quad K_i = r_i / C_{ii}$$

$$r_i = \sum_\alpha S_{i\alpha} Q_\alpha \quad C_{ij} = \sum_\alpha S_{i\alpha} D_{\alpha j}$$

$$D_{\alpha i} = Q_\alpha a_{\alpha i} / \beta_\alpha$$

The Gaussian Kernel.

But Scheffer & van Ness (2006) found exclusion zones (\approx 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

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

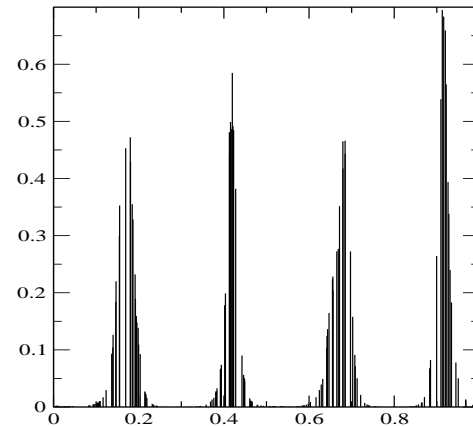
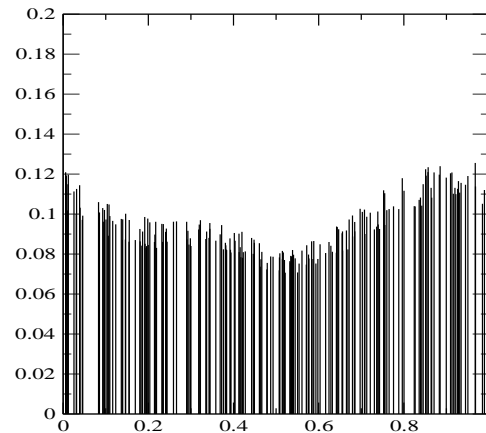
← Almost identical →

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.**

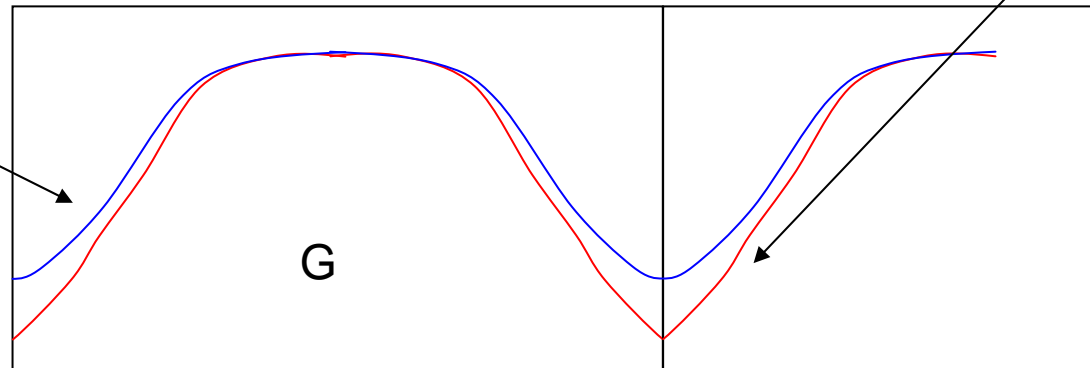
$$g(y) = \sum_n g(y - nL)$$

L system size and
 $n=0, +-1, +-2, \dots$



Scheffer & Van Nes.

Our work



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

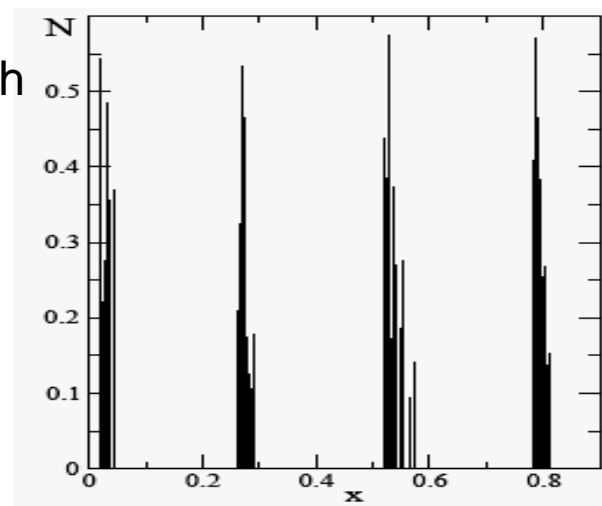
We have added several additional mechanisms to study the stability of the niche model with Gaussian competition.

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



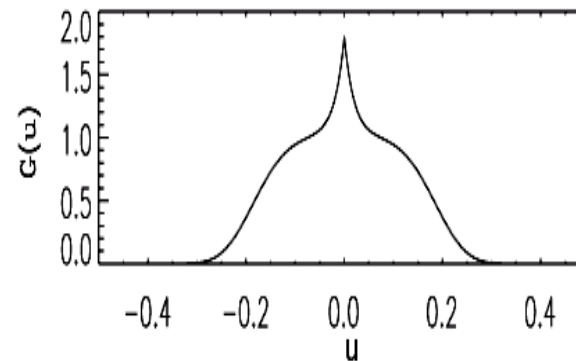
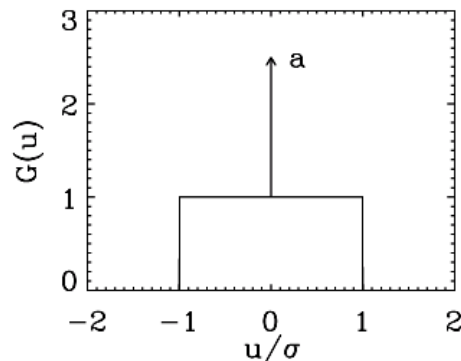
Take-home message:

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

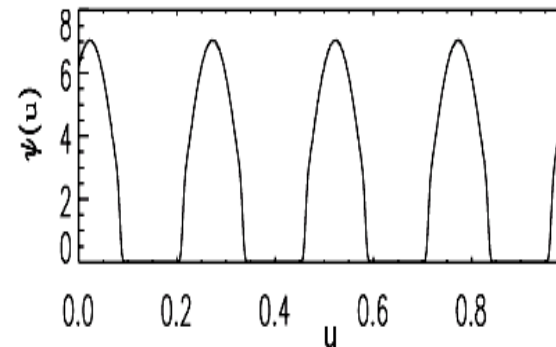
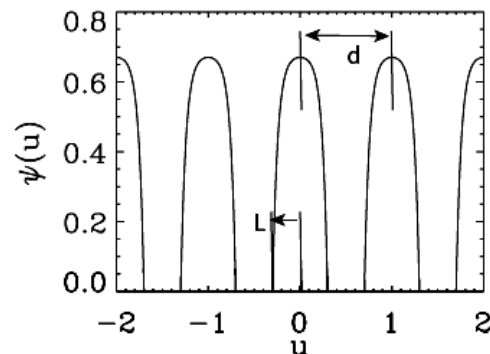
Do the 'lumped solutions' (the mixed state of clusters of close species separated by exclusion zones) only exist because of marginality of the Gaussian interaction?

NO.

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

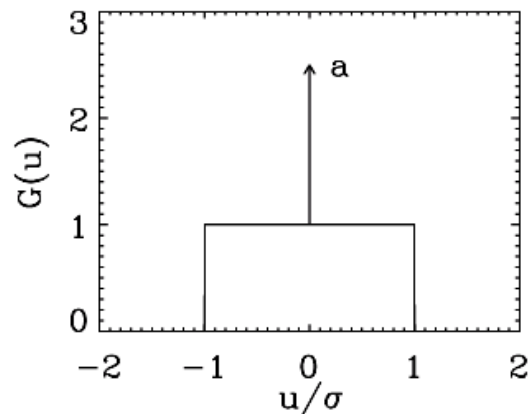


$$G = g_4 + g_1$$



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:



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

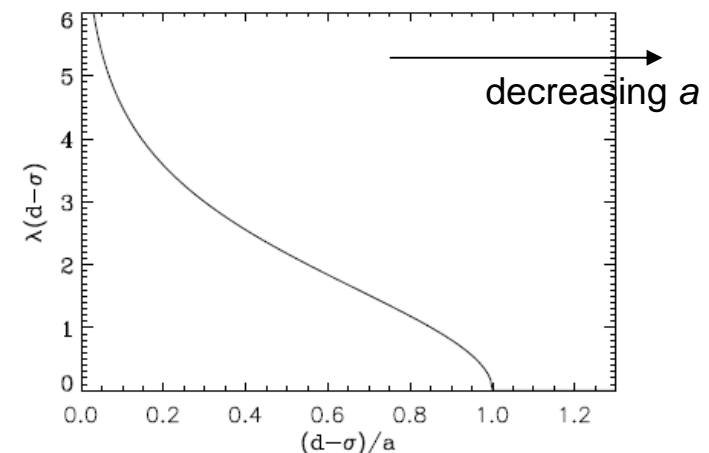
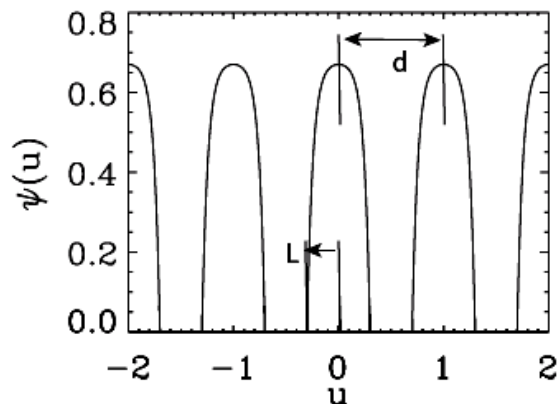
$$f(u) = \begin{cases} A \left(1 - \frac{\cosh(\lambda u)}{\cosh(\lambda L)} \right) & \text{if } u \in [-L, L] \\ 0 & \text{elsewhere} \end{cases}$$

with

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

$$a\lambda = \sinh(\lambda(d - \sigma))$$

$\lambda \approx$ inverse width



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

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