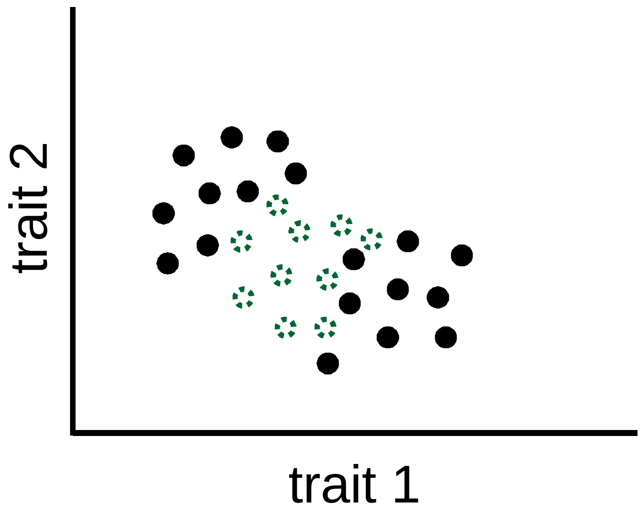
# On the origin of species




gaps not filled by interbreeding:
reproductive isolation

gaps not filled by other species:
limiting similarity

# Limiting similarity

A classical approach based on Lotka-Volterra competition

# Lotka-Volterra competition

- Population dynamics:

$$\frac{dN_i}{dt} = r_i N_i \left[ 1 - \frac{\sum_j \alpha_{ij} N_j}{K_i} \right]$$

- Equilibrium: $\mathbf{AN} = \mathbf{K}, \quad [\mathbf{A}]_{ij} = \alpha_{ij}, [\mathbf{K}]_i = K_i$

$\mathbf{N} = \mathbf{A}^{-1}\mathbf{K}$ positive?

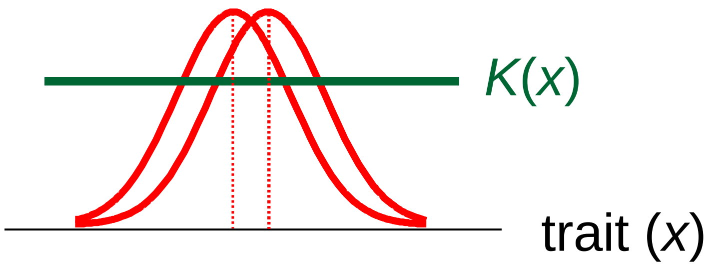
- Trait-dependent competition: $\alpha_{ij} = \alpha(x_i, x_j) = \exp\left( -\frac{(x_i - x_j)^2}{2\sigma^2} \right)$

- Equidistant spp: $\alpha_{i,i\pm 1} = \exp\left( -\frac{d^2}{2\sigma^2} \right) = \alpha < 1, \ \alpha_{i,i\pm k} = \alpha^{k^2}$

# Constant carrying capacity

- Constant carrying capacity: $K_i = K(x_i) \equiv 1 \quad (\mathbf{K} = \mathbf{1})$
- 2 species: $\mathbf{A} = \begin{pmatrix} 1 & \alpha \\ \alpha & 1 \end{pmatrix}$

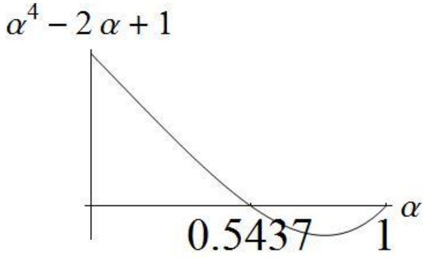
$$\mathbf{N} = \mathbf{A}^{-1}\mathbf{K} = \frac{1}{1-\alpha^2}\begin{pmatrix} 1 & -\alpha \\ -\alpha & 1 \end{pmatrix}\begin{pmatrix} 1 \\ 1 \end{pmatrix} = \begin{pmatrix} 1/(1+\alpha) \\ 1/(1+\alpha) \end{pmatrix} > 0$$



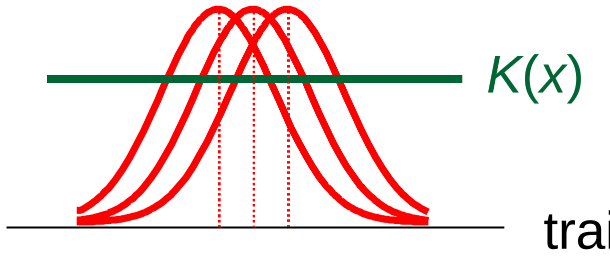

no limiting similarity

# Constant carrying capacity

- 3 species: $$\mathbf{A} = \begin{pmatrix} 1 & \alpha & \alpha^4 \\ \alpha & 1 & \alpha \\ \alpha^4 & \alpha & 1 \end{pmatrix}, \quad \mathbf{N} = \mathbf{A}^{-1}\mathbf{K} = \begin{pmatrix} 1-\alpha \\ 1-2\alpha+\alpha^4 \\ 1-\alpha \end{pmatrix}$$ ← ?

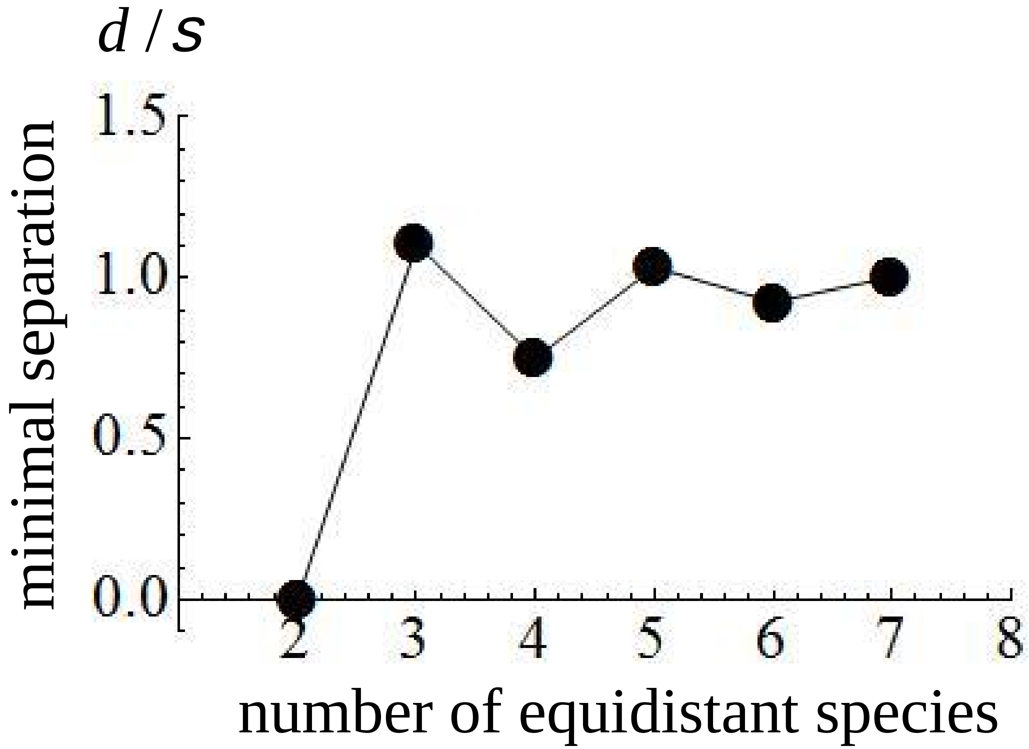



$$\alpha = \exp\left(-\frac{d^2}{2\sigma^2}\right) < 0.5437 \quad \Leftrightarrow \quad d/\sigma > 1.104$$

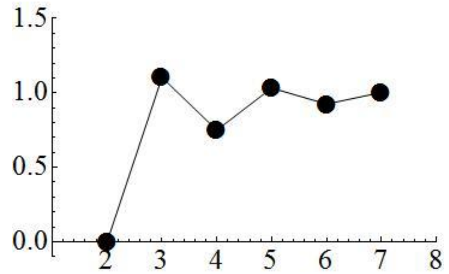



limiting similarity

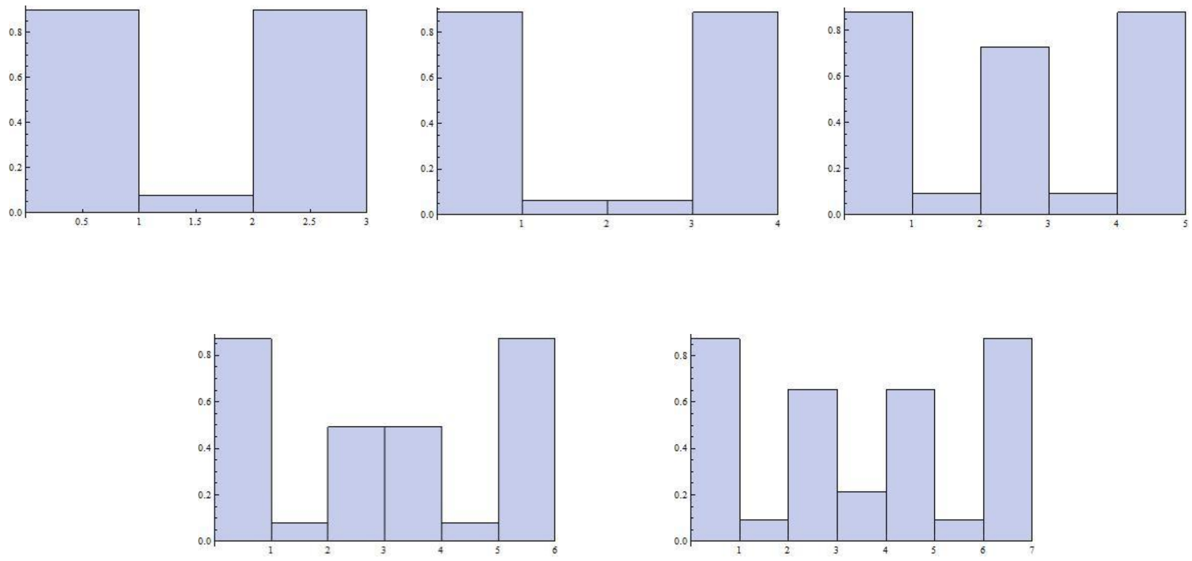
# Constant carrying capacity



# Constant carrying capacity



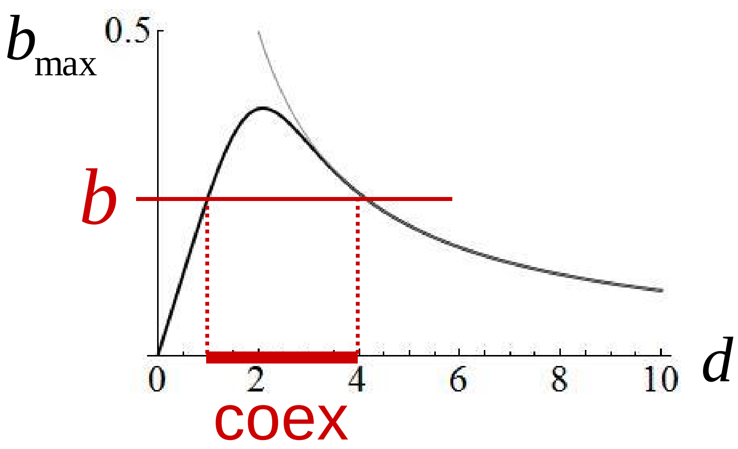

Equilibrium densities near the minimal separation



# Non-constant carrying capacity

- Linear $K$: $K(x) = 1 + 2bx$
- 2 species: $x_1 = -d/2,\ x_2 = d/2;\ \sigma = 1$; recall $\alpha = \exp\left(-d^2/2\sigma^2\right)$

$$\mathbf{N} = \mathbf{A}^{-1}\mathbf{K} = \frac{1}{1-\alpha^2}\begin{pmatrix} 1 & -\alpha \\ -\alpha & 1 \end{pmatrix}\begin{pmatrix} 1-bd \\ 1+bd \end{pmatrix} = \frac{1}{1-\alpha^2}\begin{pmatrix} 1-\alpha-(1+\alpha)bd \\ 1-\alpha+(1+\alpha)bd \end{pmatrix}$$ ← ?

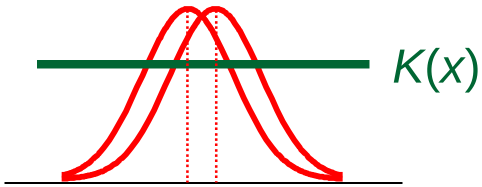



limiting similarity for 2 spp

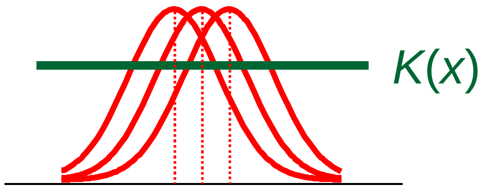
also maximum separation
(sp 2 is favoured)
$K$ too steep: no coexistence

# Can similar species coexist?

### Constant $K$

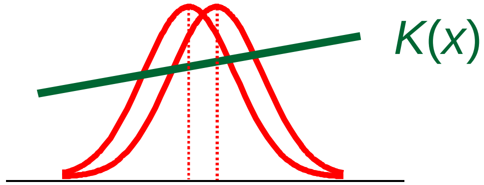



yes

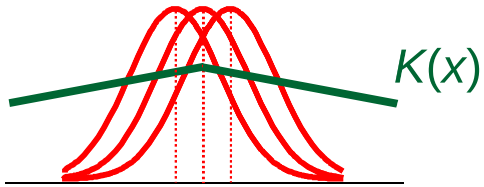



no

### Non-constant $K$




no




yes, if $K$ chosen properly

# Can similar species coexist?

- I can make *any* species coexist (and at any densities)!
  if I may choose the $K$´s

$$\mathbf{K} = \mathbf{A}\mathbf{N}$$

Fine tuning of parameters makes coexistence possible

- If there are more consumer species than resources, then
  - $\mathbf{A}$ is singular (neutral coexistence)
  - $\mathbf{K}$ must be in the range of $\mathbf{A}$, which has zero volume; the slightest perturbation destroys coexistence

# Can similar species coexist?

- $a_{ij} = a(x_i, x_j)$ depends on the trait values continuously

  if $x_\mathrm{i}$ and $x_\mathrm{k}$ are similar, then $a_{ij}$ » $a_{kj}$ for all $j$
  and therefore $\mathbf{A}$ is nearly singular

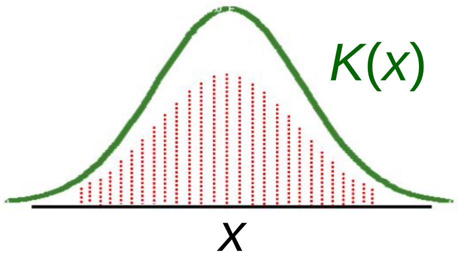
- $\mathbf{K}$ must be in the range of $\mathbf{A}$, which has small volume;
  a small perturbation destroys coexistence

Coexistence of similar species is possible **but not robust**

(Meszéna et al. 2006, Theor. Pop. Biol.)

# Can infinitely many species coexist?

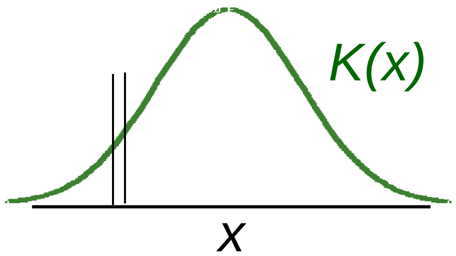
- Gaussian *K:* infinitely many species can coexist




$$K(x) = \int_{-\infty}^{\infty} a(x' - x)N(x')dx'$$

convolution of Gaussians is Gaussian:
$N(x)$ is Gaussian with $\sigma_N^2 = \sigma_K^2 - \sigma^2$

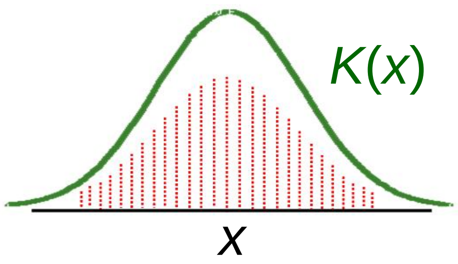
- but 2 similar species cannot (unless near the peak)




~ linear *K*

# Can infinitely many species coexist?

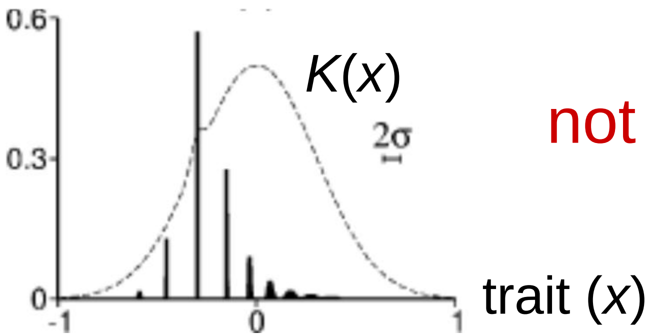
- Gaussian *K:* infinitely many species can coexist




$$K(x) = \int_{-\infty}^{\infty} a(x' - x)N(x')\,dx'$$

convolution of Gaussians is Gaussian:
$N(x)$ is Gaussian with $\sigma_N^2 = \sigma_K^2 - \sigma^2$

- but not if the Gaussian *K* is perturbed




not structurally stable

# Limiting similarity

The more similar the species are, the smaller is the region of parameter space where they coexist, making coexistence unlikely (= not robust).

(Meszéna et al. 2006, Theor. Pop. Biol.)