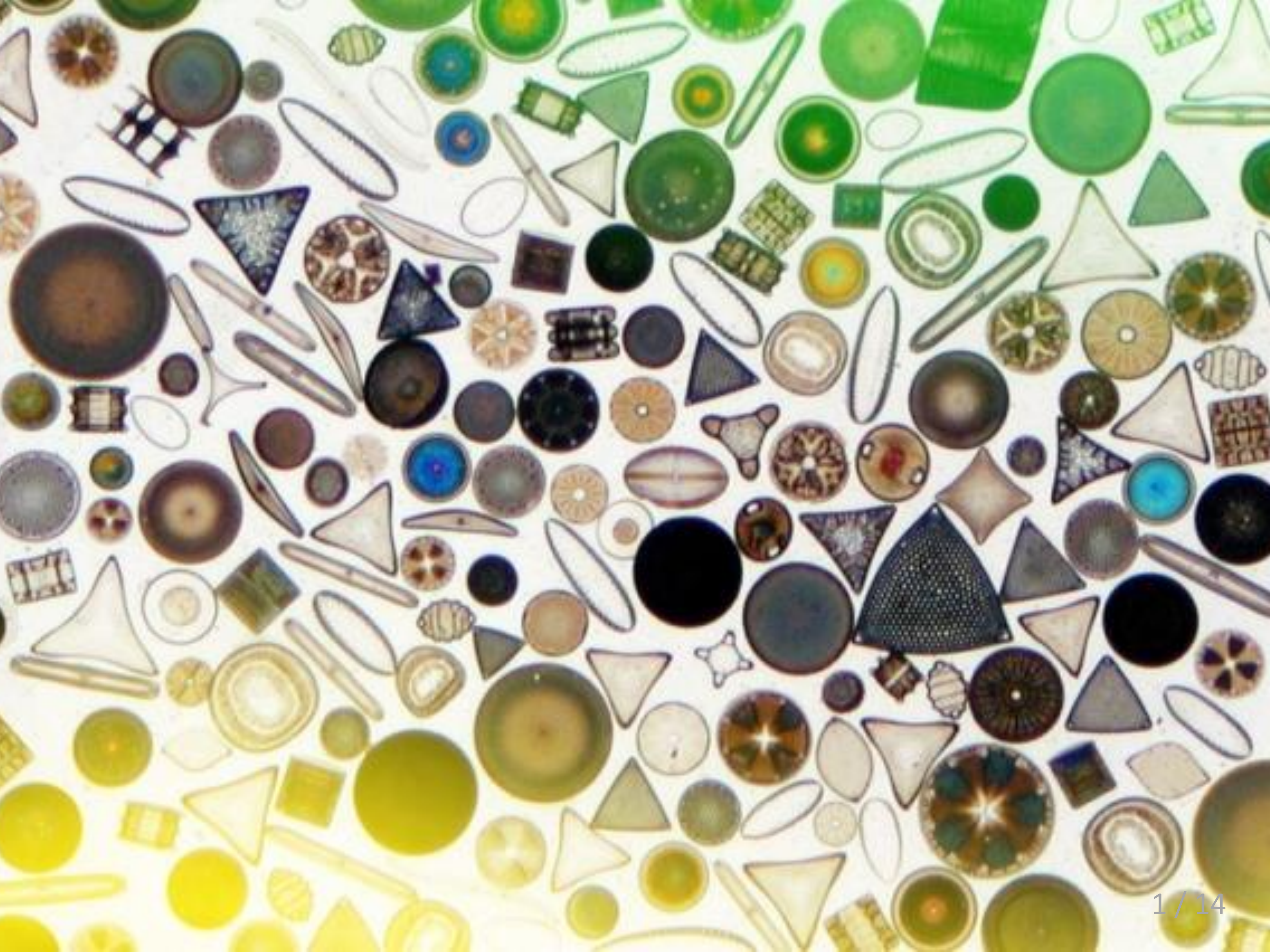
More of the same? Clustering of functional traits under trophic interactions

Matilda Haraldsson

A project together with
Elisa Thebault, Lars Gamfeldt, Erik Selander, Per Jonsson

l'Ecole de recherché MMB, d'Aussois , 21 May 2019



Community assembly

"The process by which **species** from a regional pool **colonize** and **interact** to form local **communities**"

HilleRisLambers et al. 2012

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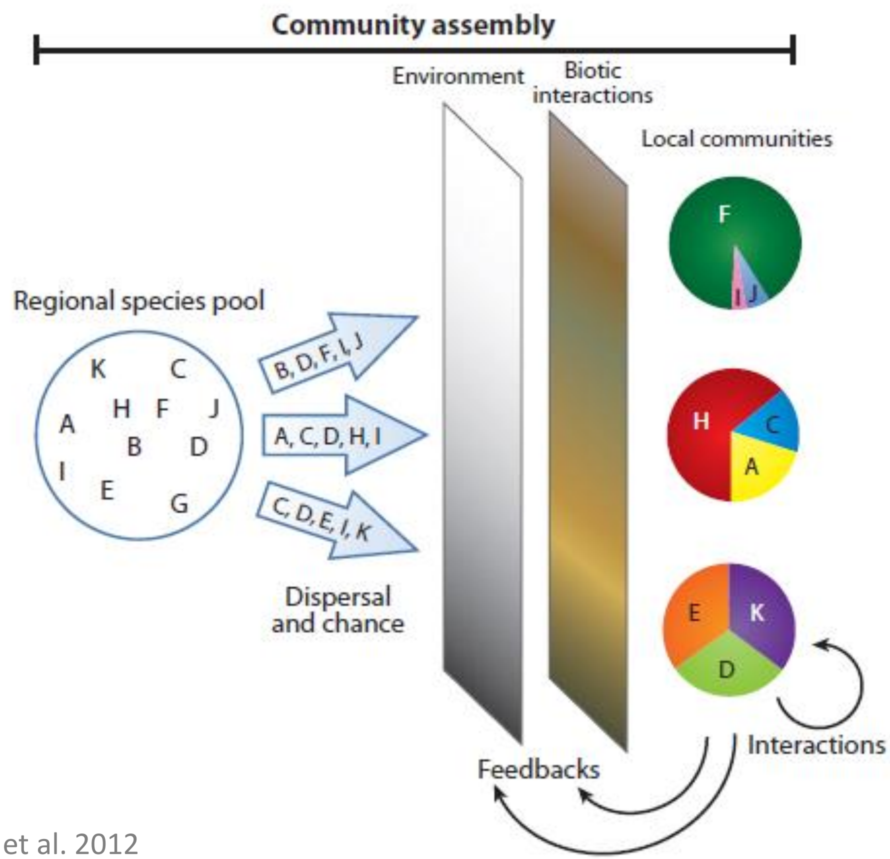
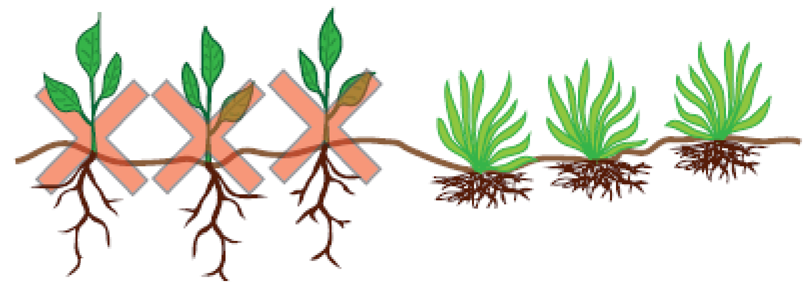


HilleRisLambers et al. 2012

Trait & phylogenetic relatedness

Environmental filter :



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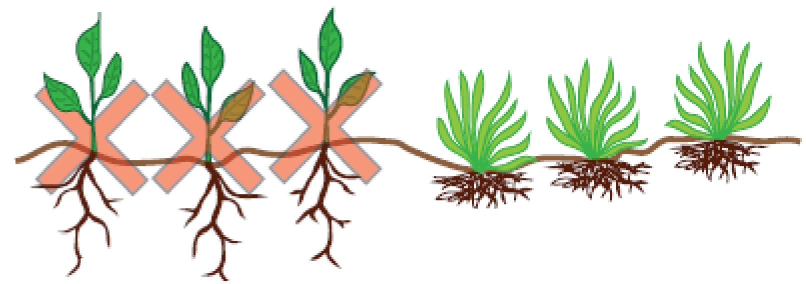
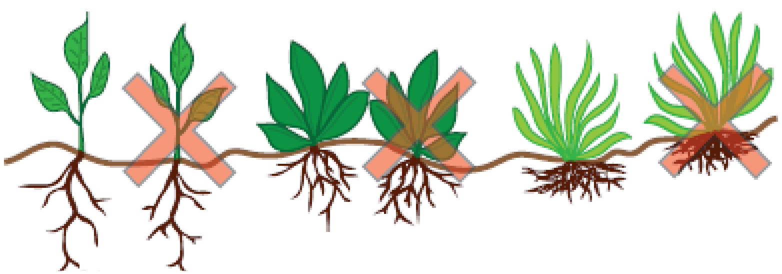


Clustered, or under-dispersed
High similarity
Low functional diversity

Trait & phylogenetic relatedness

Biotic filter :



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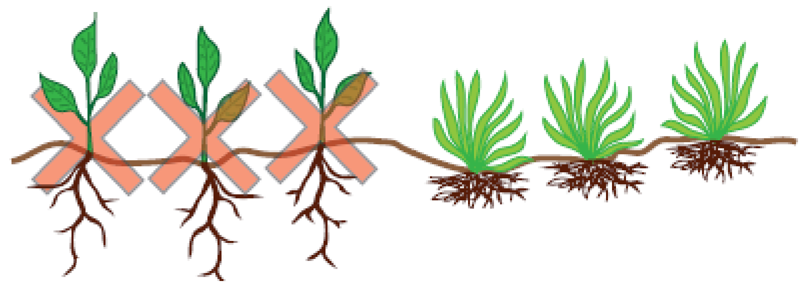

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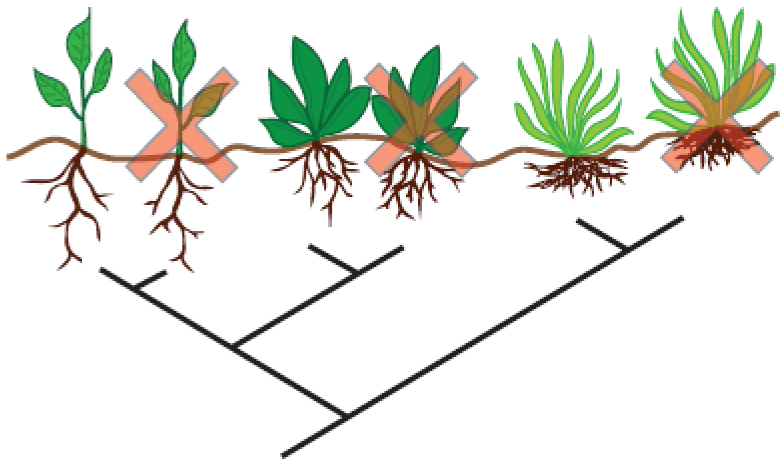

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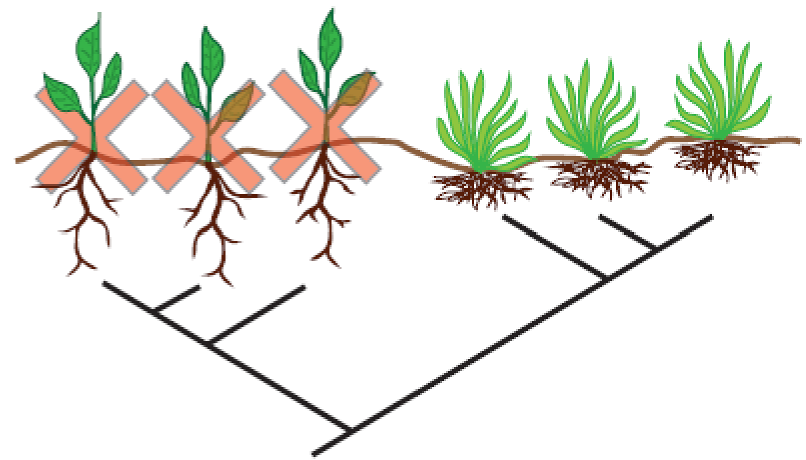

Over-dispersed
Low similarity
High functional diversity

Clustered, or under-dispersed
High similarity
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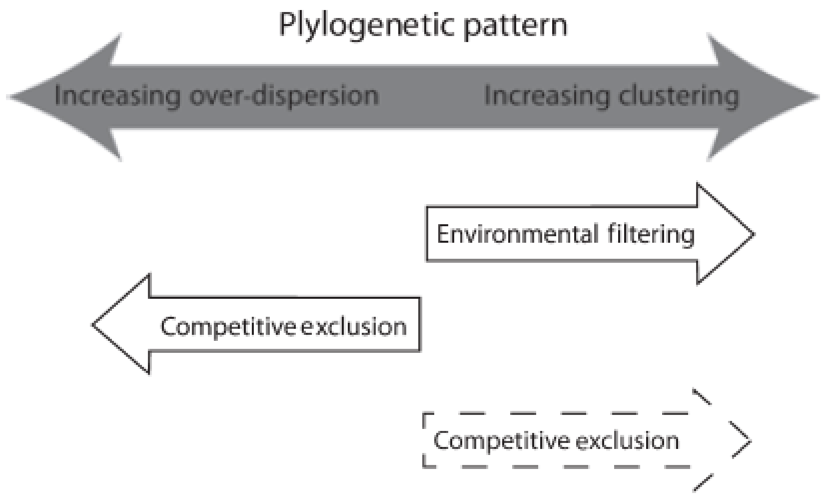
Functional trait approach e.g., Petchey & Gaston 2002, McGill et al. 2006
Phylogenetic approach from Webb 2000, 2002

Critique…

- Strong **critique**, other processes can cause trait/phylogenetic clustering: (e.g., Mayfield & Levine 2010, Kraft et al. 2015, Gerhold et al. 2015, Cadotte et al. 2017)



Mayfield & Levine 2010

Coexistence

Modern coexistence theory by Chesson

- Species **coexistence** depends on **two types** of species **differences**:
  (Chesson 2000, Mayfield & Levine 2010, HilleRisLambers et al. 2012, Barabás et al. 2018)

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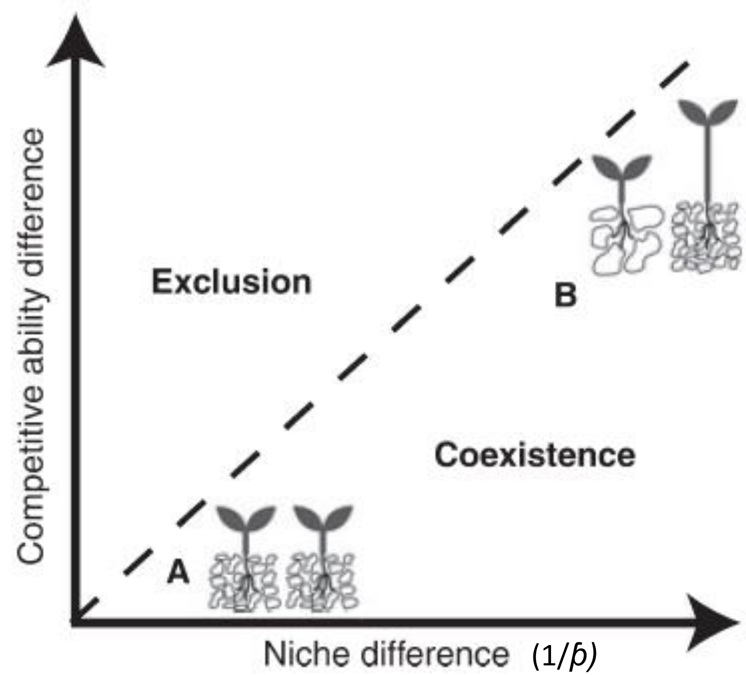
- Stabilizing niche difference

  Intraspecific competition > Interspecific competition

  $\alpha_{ii} > \alpha_{ij}$ or $\frac{\alpha_{ij}}{\alpha_{ii}} < 1$



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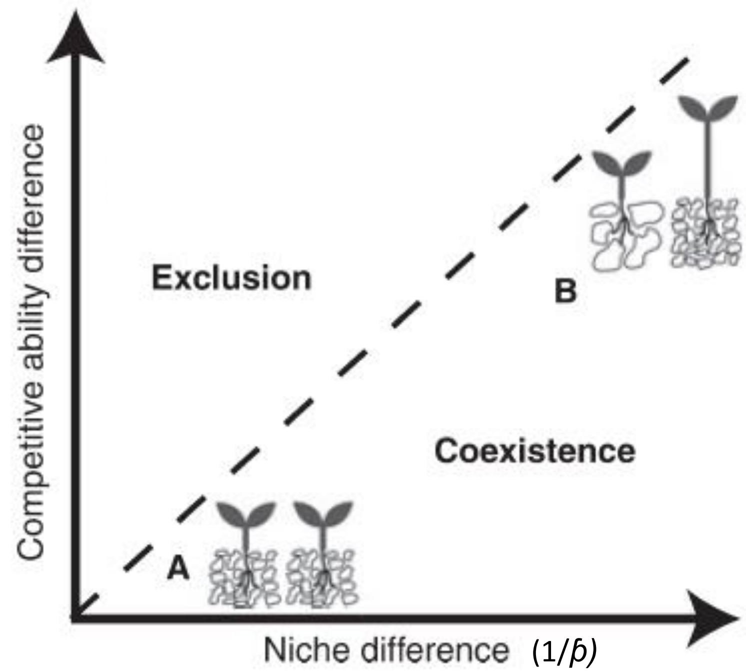

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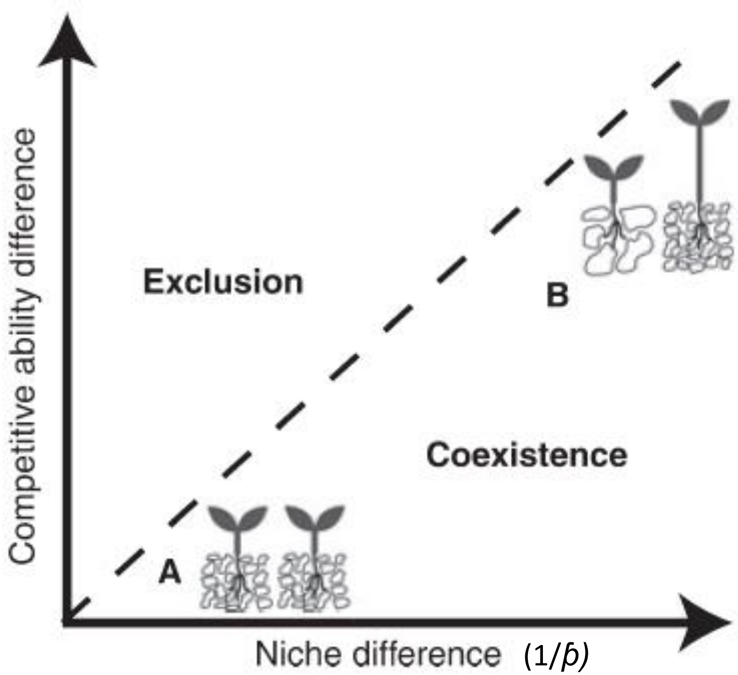
  (or fitness difference)

  $$\frac{f_j}{f_i} = \sqrt{\frac{\alpha_{ij}\alpha_{ji}}{\alpha_{ii}\alpha_{jj}}}$$



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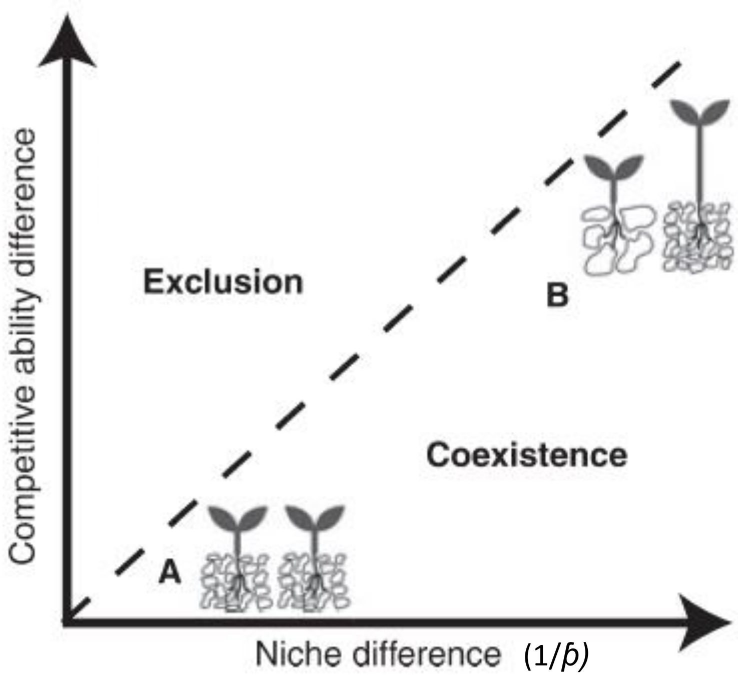
- For stable coexistence $\rho < \frac{f_j}{f_i} < \frac{1}{\rho}$



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Emergent neutrality

Lotka Volterra competition

$$\frac{dN_i}{dt} = rN_i\left(K_i - \sum_j \alpha_{i,j}N_j\right)\Big/K_i \quad i = 1,2,\ldots n;\ \alpha_{i,j} = 1,$$

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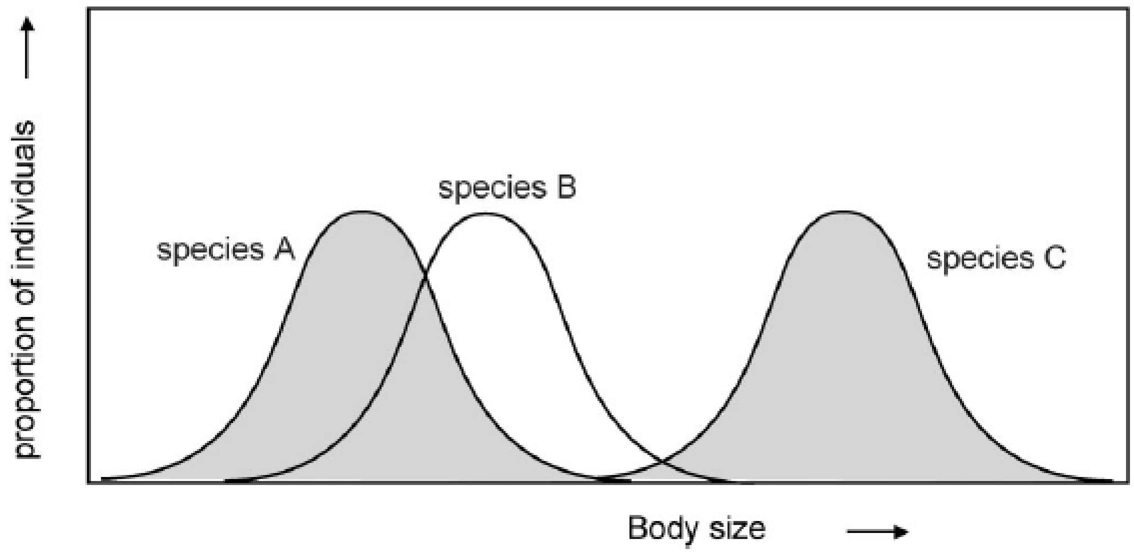

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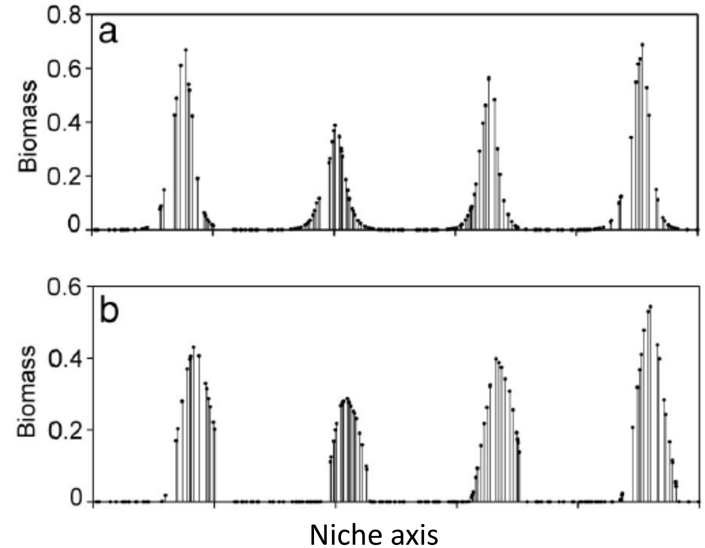

Scheffer & van Nes 2006, PNAS

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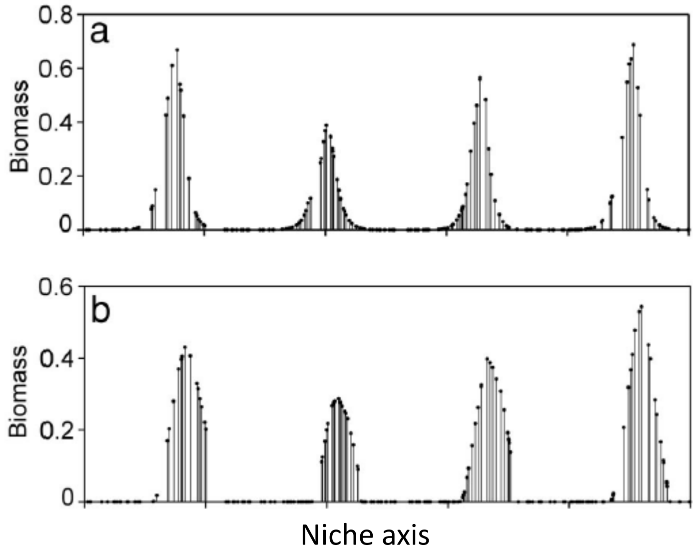
- Emergence of **clusters** containing species with **similar traits**



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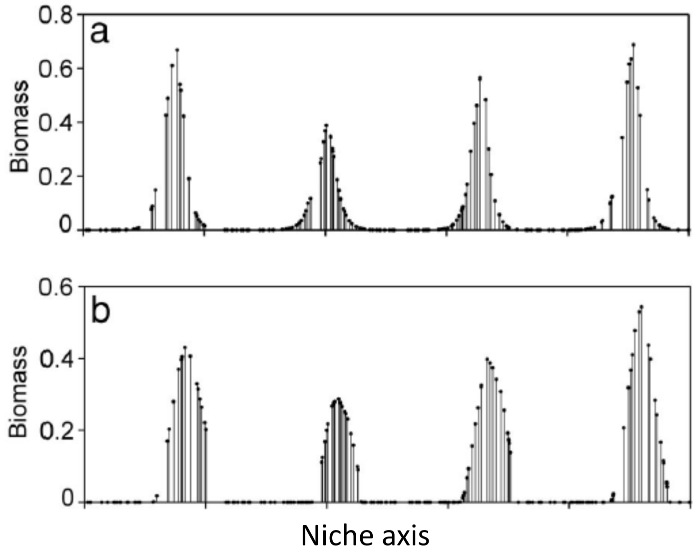
- Emergence of **clusters** containing species with **similar traits**

- Species coexist when **sufficiently different** or **sufficiently similar**

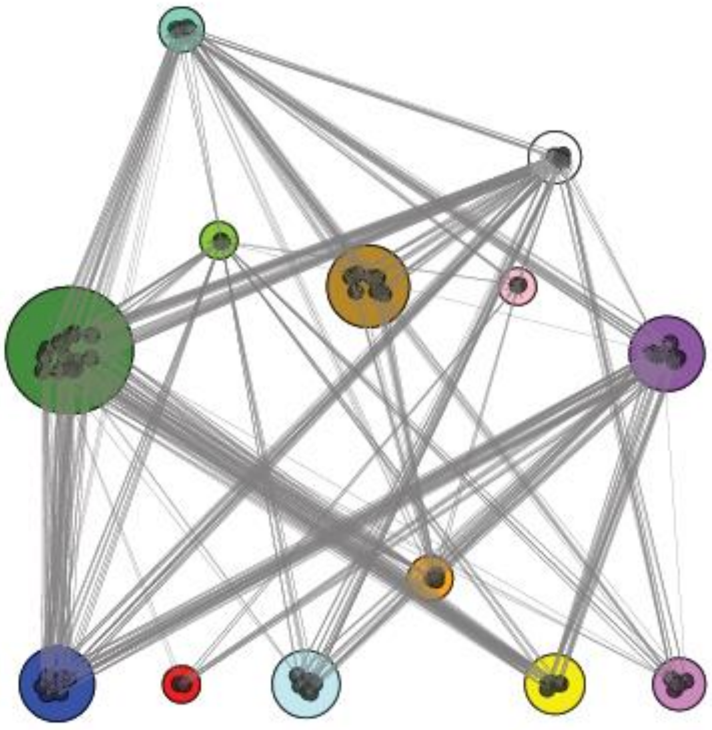


Scheffer & van Nes 2006, PNAS

Trophic groups or guilds

- An important **topological** feature of food webs (Allesina & Pascual 2009)

- Implications for **food web functioning** (Thebault & Fontaine 2010, Stouffer & Bascompte 2011)



Gauzens et al. 2015, J. R. Soc. Interface

Aim

Understand how **trophic interactions** affect **clustering** of **functional traits** in communities and food webs, and thereby the **diversity** of functional traits and the **ecosystem functioning**.

Competition & predation

Lotka Volterra competition

$$\frac{dN_i}{dt} = rN_i\left(K_i - \sum_j \alpha_{i,j}\,N_j\right)/K_i - \mathrm{c} \times \sum_i \beta_{i,k}N_iP_k$$

$$\frac{dP_k}{dt} = ce \times \sum_k \beta_{i,k}N_iP_k - mP_k$$

$$\left\{ \begin{aligned} \alpha_{i,j} &= \frac{\int_0^{Lmax} P_i(L)P_j(L)dL}{\int_0^{Lmax} P_i(L)^2 dL} \\ \beta_{i,k} &= \frac{\int_0^{Lmax} P_i(L)P_k(L)dL}{\int_0^{Lmax} P_i(L)^2 dL} \end{aligned} \right.$$

r : $max.\ per\ capita\ growth\ rate$
K : $carrying\ capacity$
α : $competition\ coefficient$
c : $attack\ rate$
β : $predation\ coefficient$
e : $conversion\ factor$
m : $mortality\ of\ predator$

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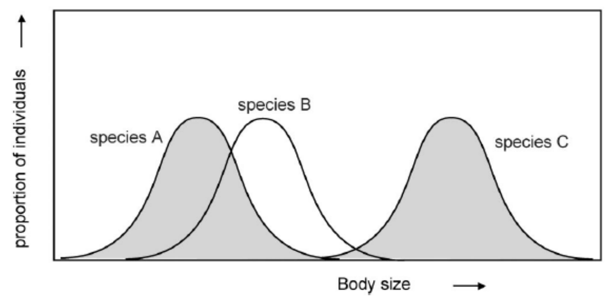

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Research question

How does **resource availability** (bottom up) and **predation** (top down) shape the **clustering** of **functional traits** of coexisting species in **communities** ?

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iii) Level of **specialization** (β)
among predators

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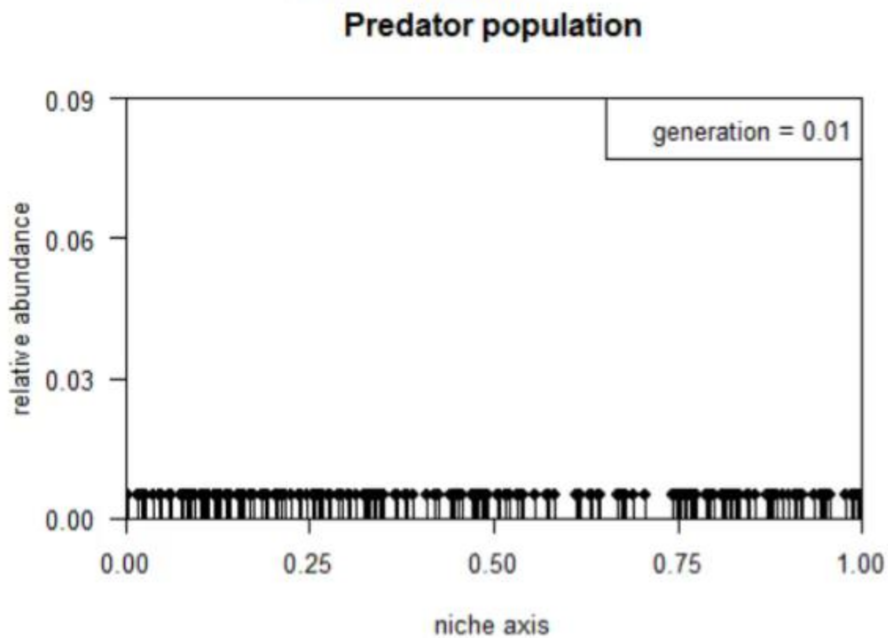
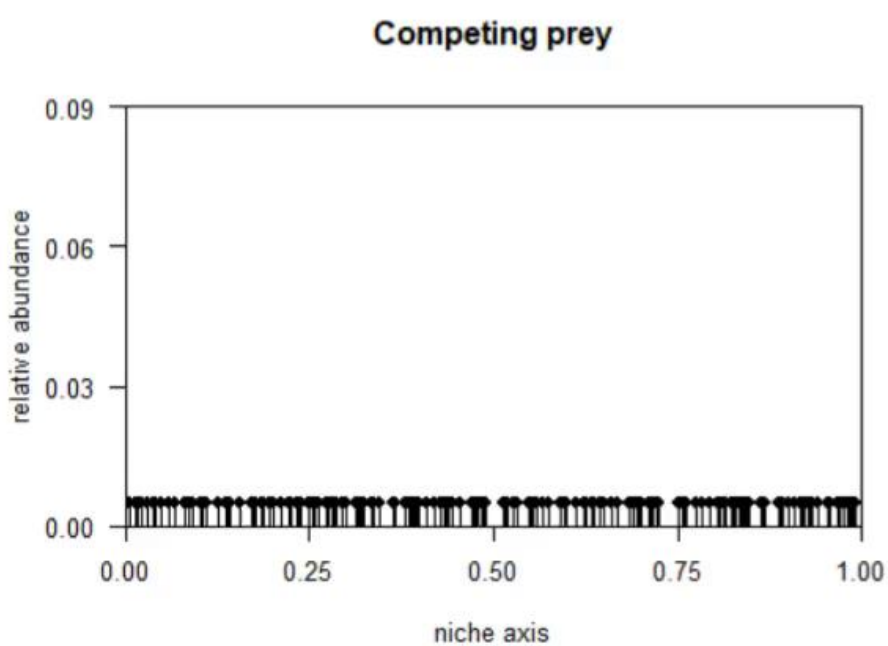
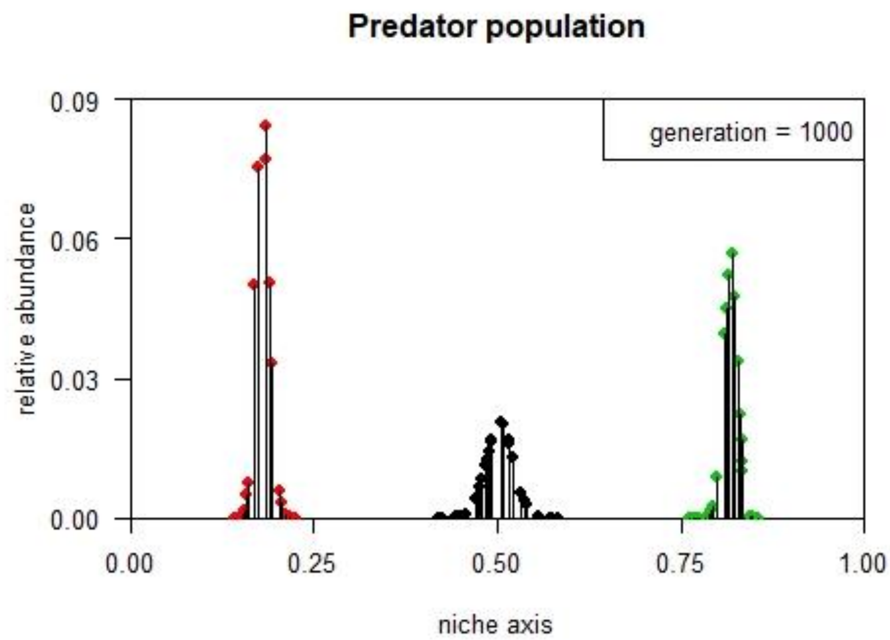
Example simulation

Parameter range:
K : 8 – 13
Sigma (for calculating β) : 0.100 – 0.130

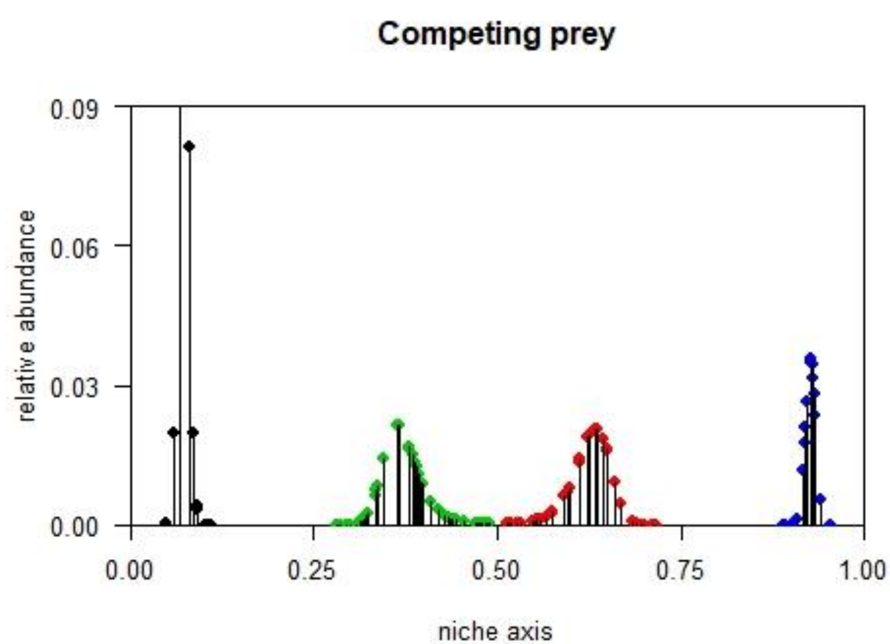




K = 10
Sigma = 0.120



Predator population
generation = 1000
relative abundance
0.09
0.06
0.03
0.00
0.00
0.25
0.50
0.75
1.00
niche axis



Competing prey
relative abundance
0.09
0.06
0.03
0.00
0.00
0.25
0.50
0.75
1.00
niche axis

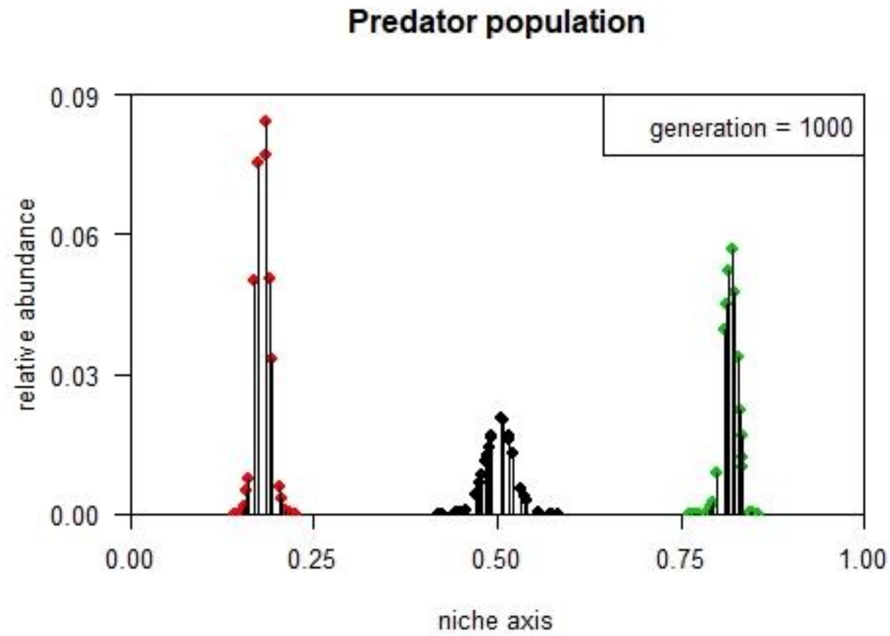
Cluster identification
"Gap statistic"
(D'Andrea et al. 2019)

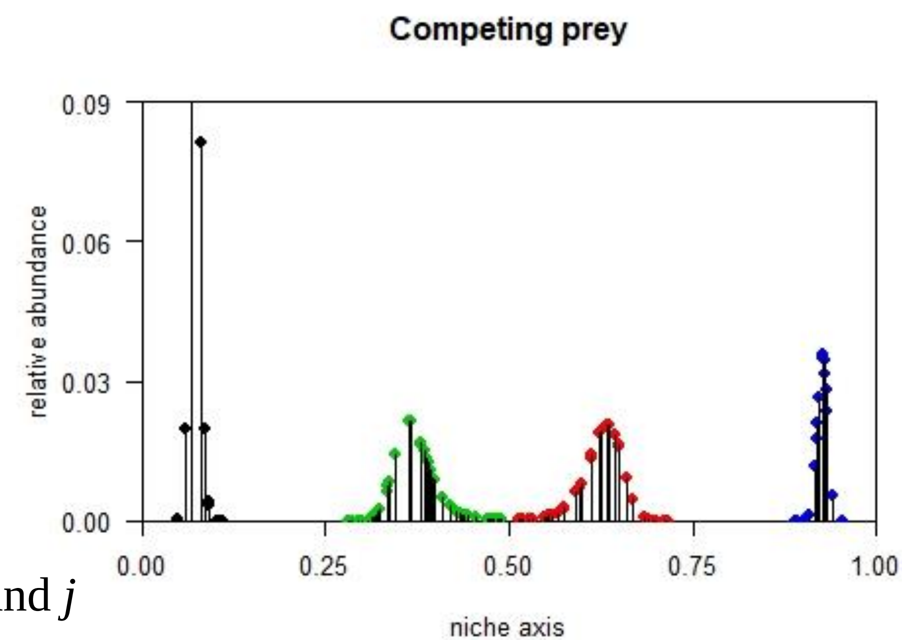
$$D_k = \sum_c \sum_{i,j \epsilon C} n_i n_j d_{ij}$$

$$F_k = -\log(D_k)$$

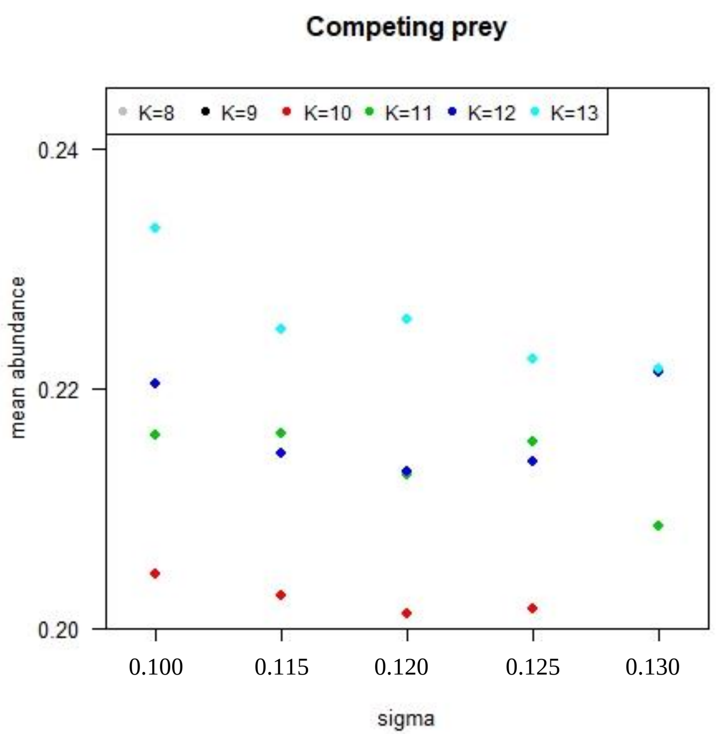
$$G_k = F_k - \bar{F}_{k,null}$$

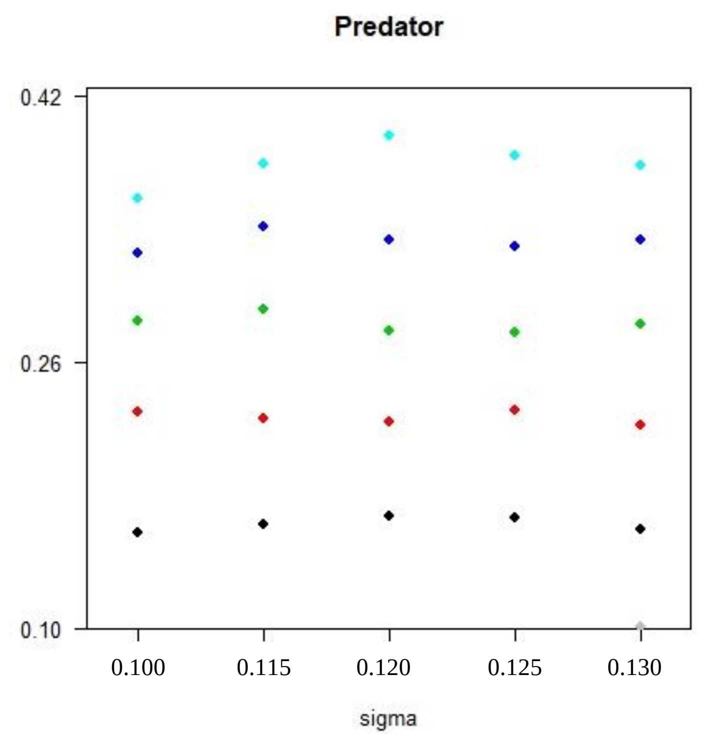
c = clusters ($1 < c <$ k)
n_i = abundance sp. i
d_{ij} = trait distance sp. i and j



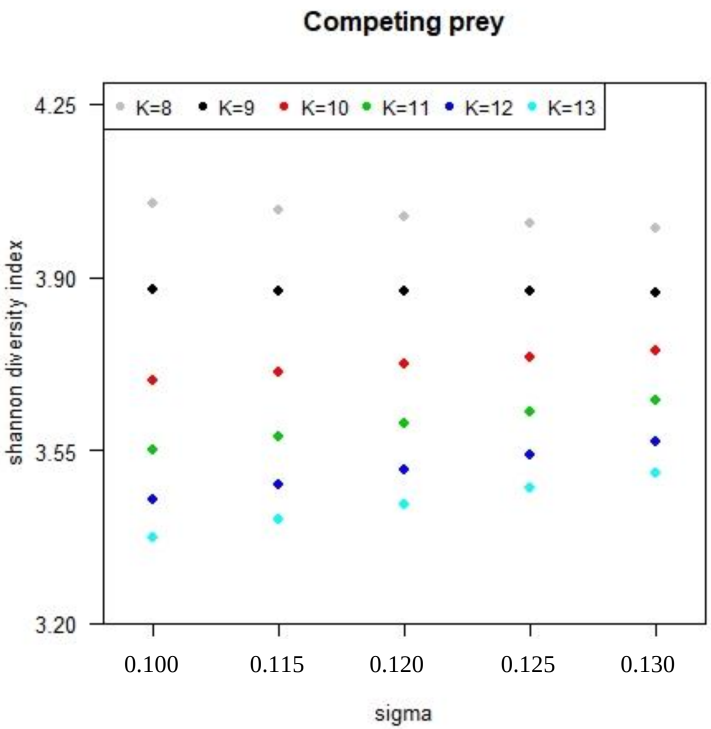


Competition and predation

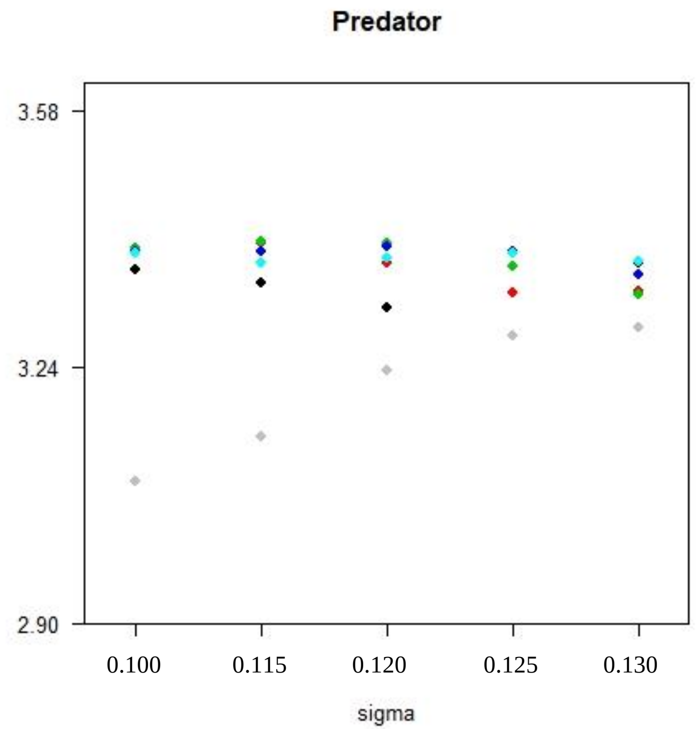




Diversity

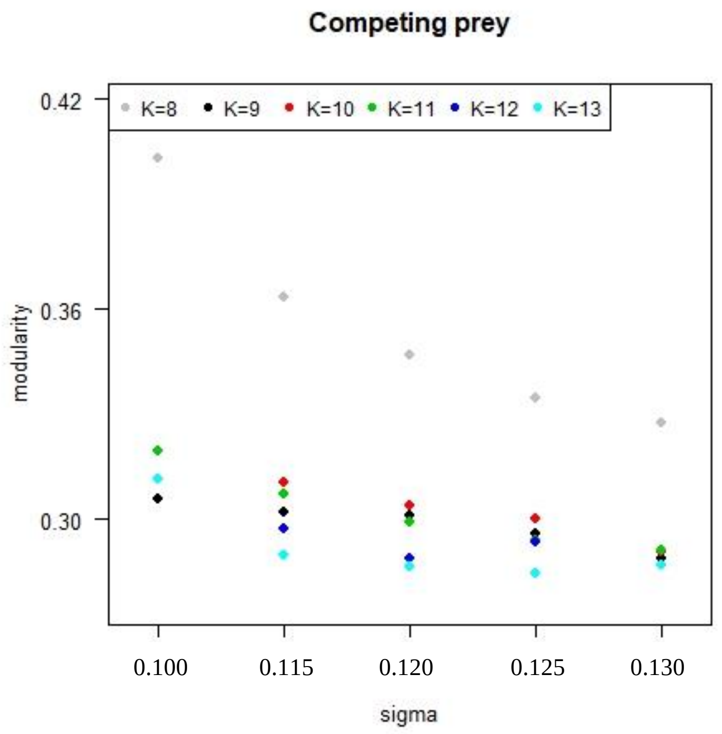


Competing prey
K=8
K=9
K=10
K=11
K=12
K=13
4.25
3.90
3.55
3.20
shannon diversity index
0.100
0.115
0.120
0.125
0.130
sigma

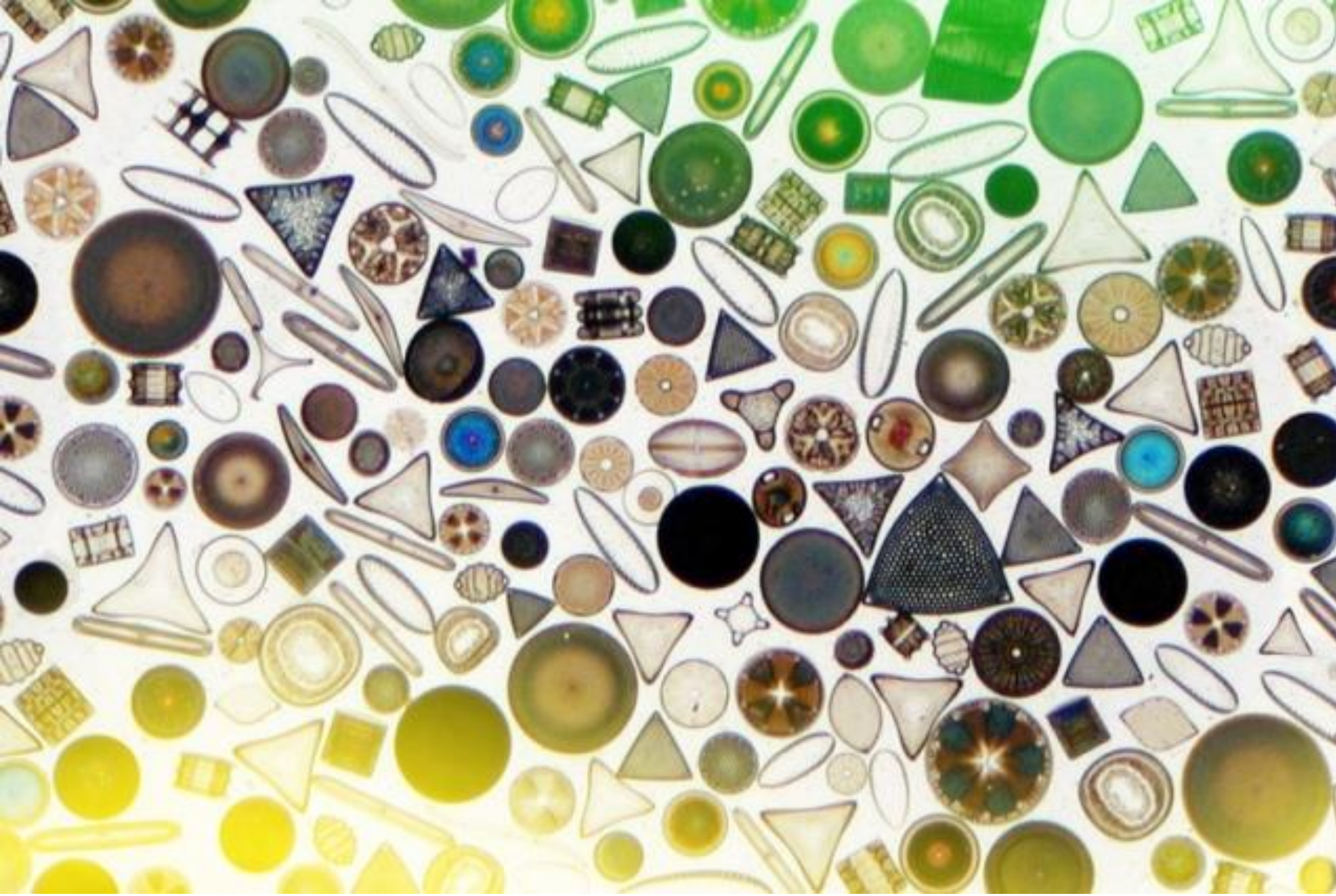


Predator
3.58
3.24
2.90
0.100
0.115
0.120
0.125
0.130
sigma

Modularity



Competing prey
K=8
K=9
K=10
K=11
K=12
K=13
0.42
0.36
0.30
modularity
0.100
0.115
0.120
0.125
0.130
sigma



Thanks for your attention

Scheffer & van Nes method

As a starting point to compute competition coefficients that allow us to mimic competition of species for resources along a niche axis (Fig. 1 and Eq. **1**) we characterize the width of the niche by normal distributions on the niche axis (L)

$$P_i(L) = \frac{1}{\sigma\sqrt{2\pi}} e^{-(L-\mu_i)^2/(2\sigma^2)}. \tag{4}$$

We assume that competition intensity between species i and species j is related to niche overlap, and thus to the probability P that individuals of the two species are at the same position on the niche axis, which is the product of both probabilities

$$\int_{-\infty}^{\infty} P_i(L)P_j(L)dL. \tag{5}$$

We calculate competition coefficients as the ratio of the probability of matching an individual of competing species j and the probability of matching a conspecific (45), which can be solved as follows (cf. 24)

$$\alpha_{i,j} = \frac{\int_{-\infty}^{\infty} P_i(L)P_j(L)dL}{\int_{-\infty}^{\infty} P_i(L)^2 dL} = e^{-\frac{\mu_j^2 - \mu_i^2 - 2\mu_j\mu_i}{4\sigma^2}}. \tag{6}$$

To avoid edge effects, the niche axis is defined circular ("periodic") so that each species has equal numbers of competitors on both sides. Alternatively we checked the effect of having a finite linear niche axis of length $L_{\max}$. In this case, niche overlap is calculated as

$$\int_{0}^{L_{\max}} P_i(L)P_j(L)dL, \tag{7}$$

and the competition coefficients are computed as

$$\alpha_{i,j} = \frac{\int_0^{L_{\max}} P_i(L)P_j(L)dL}{\int_0^{L_{\max}} P_i(L)^2 dL} = e^{-\frac{(\mu_i-\mu_j)^2}{4\sigma^2}} \frac{erf\left(\frac{2L_{\max}-\mu_i-\mu_j}{2\sigma}\right) + erf\left(\frac{\mu_i+\mu_j}{2\sigma}\right)}{erf\left(\frac{L_{\max}-\mu_i}{\sigma}\right) + erf\left(\frac{\mu_i}{\sigma}\right)}. \tag{8}$$

Scheffer & van Nes method

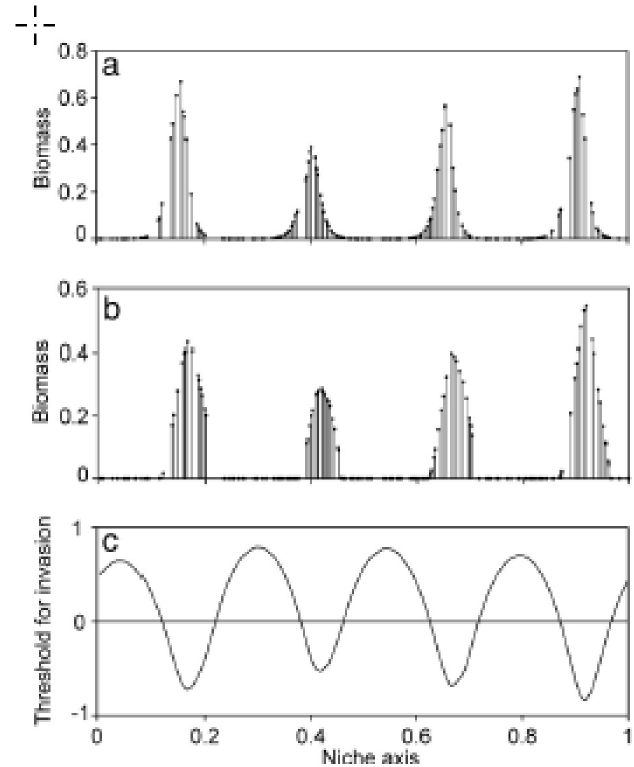


Fig. 2. Self-organized lumpy patterns in the abundance of competing species along a niche axis. (*a*) A transient state after a simulation run of 1,000 generation times. (*b*) A stable pattern of species abundance reached after 5,000 generation times in the presence of mild density-dependent losses ($g = 0.02$, $H = 0.1$, Eq. 2). (*c*) The competitive threshold for invasion of a new species expressed as percentage deviation of its carrying capacity (K) relative to that of the resident species is lowest in the species lumps, showing that these represent relative windows of opportunity for invasion, and attractors in the fitness landscape. Note that the relatively low predation loss at low densities allows starting invaders to enter with a competitive power (K) slightly below that of residents.

Cluster identification with KmeansGap()