Niche theory in ecology and evolution: *A mathematical exercise, or help in biology*?

Géza Meszéna

Eötvös University, Budapest

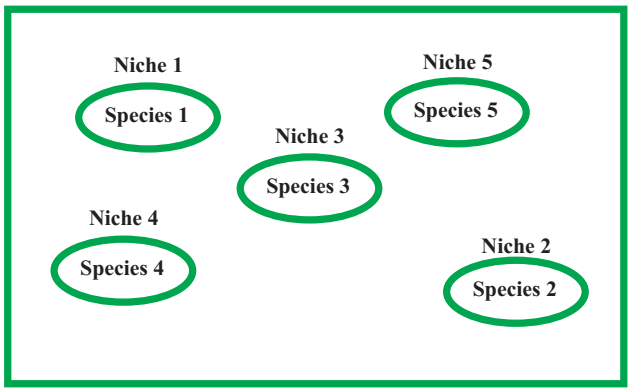
MBA15:
Linking Mathematical Theories with Empirical Realities
Leicester, 2015

Outline

Why are there so many kinds of animals?

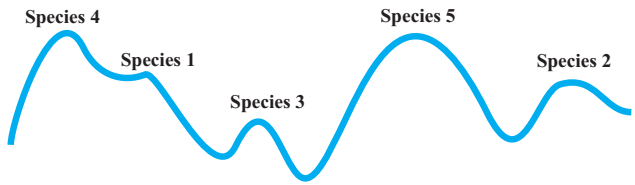
Different pictures in ecology and evolution:
we need a mathematical unification.

Niche space



Species occupy different
niches.

Adaptive landscape



Species occupy different
peaks of landscape.

Tension: "wittest wins" *versus* "coexistence with reduced competition"

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Karen C. Abbott
- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales

ESA14 Ignite: Theory vs. Empiricism

- Frederick R. Adler: Go to the ant, thou theorist
- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales
- Bradley J. Cardinale: Team Empiricism: If a model is written in a forest, and no one hears it, does it make a sound?

ESA14 Ignite: Theory vs. Empiricism

- Greg Dwyer: Models without data can be useful, data analysis without mechanistic models often is not
- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales
- Bradley J. Cardinale: Team Empiricism: If a model is written in a forest, and no one hears it, does it make a sound?
- John J. Stachowicz: Empirical rules. A picture is worth a thousand words. . . or equations

ESA14 Ignite: Theory vs. Empiricism

- Annette M. Ostling: The case for general theory development as a guiding force in ecology
- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales
- Bradley J. Cardinale: Team Empiricism: If a model is written in a forest, and no one hears it, does it make a sound?
- John J. Stachowicz: Empirical rules. A picture is worth a thousand words. . . or equations
- Alison G. Power: Bridging the gap between theory and data: Is empiricism the driver or the passenger?

ESA14 Ignite: Theory vs. Empiricism

- Jeremy W. Fox: When does data settle arguments and when does it not?
- Mercedes Pascual: Team Theory: When we can't experiment and we need to tackle long and large scales
- Bradley J. Cardinale: Team Empiricism: If a model is written in a forest, and no one hears it, does it make a sound?
- John J. Stachowicz: Empirical rules. A picture is worth a thousand words... or equations
- Alison G. Power: Bridging the gap between theory and data: Is empiricism the driver or the passenger?
- Shahid Naeem: Condensation and ignition in ecological research: Making sense of biodiversity's demise

Is there such thing, as niche theory?

- Once upon a time we have it:
  - Gause's principle & limiting similarity
  - Lotka-Volterra model & resource utilization function
  - Hutchinson's niche space
- Before long, the picture fell apart:
  - Ecology became too complicated for Lotka-Volterra.
  - Mechanistic models did not lead general results.
  - No clear conclusion on Gause and limiting similarity.
- Since, theoretical ecology has grown up:
  - Beyond the specific models (eg. Caswell).
  - Renewed interest in coexistence theory (eg. Chesson).
  - Niche has remained controversial.

Is there such thing, as niche theory?

- Once upon a time we have it:
  - Gause's principle & limiting similarity
  - Lotka-Volterra model & resource utilization function
  - Hutchinson's niche space
- Before long, the picture fell apart:
  - Ecology became too complicated for Lotka-Volterra.
  - Mechanistic models did not lead general results.
  - No clear conclusion on Gause and limiting similarity.
- Since, theoretical ecology has grown up:
  - Beyond the specific models (eg. Caswell).
  - Renewed interest in coexistence theory (eg. Chesson).
  - Niche has remained controversial.

Is there such thing, as niche theory?

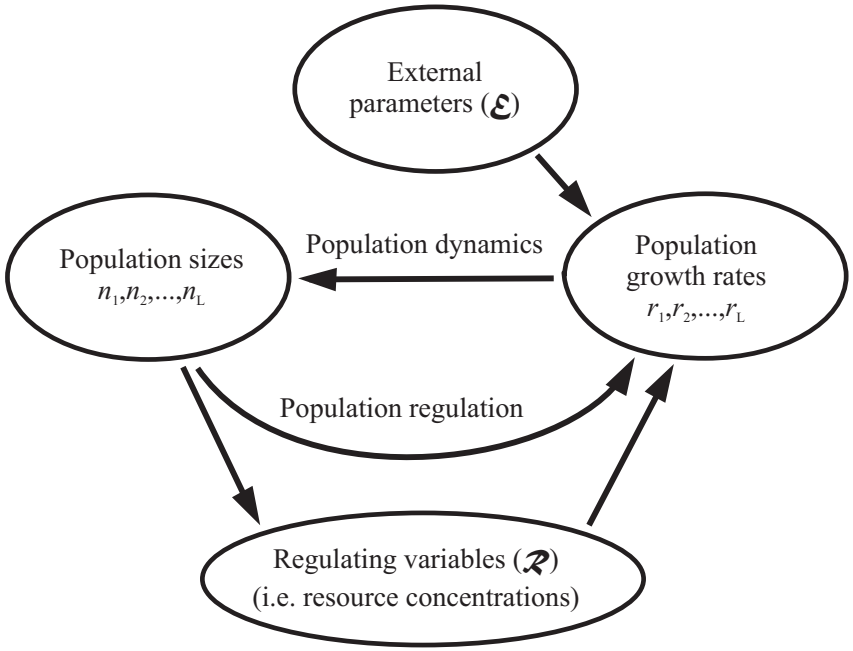
- Once upon a time we have it:
  - Gause's principle & limiting similarity
  - Lotka-Volterra model & resource utilization function
  - Hutchinson's niche space
- Before long, the picture fell apart:
  - Ecology became too complicated for Lotka-Volterra.
  - Mechanistic models did not lead general results.
  - No clear conclusion on Gause and limiting similarity.
- Since, theoretical ecology has grown up:
  - Beyond the specific models (eg. Caswell).
  - Renewed interest in coexistence theory (eg. Chesson).
  - Niche has remained controversial.

Goal: Clarity to niche theory!

- Needed: a comprehensive mathematical theory of ecological niche.
- It should be applicable to any ecological situation.
- It should provide biological insight.

Steps from LV & classical niche to modern theory

1. Resources ⇒ Regulating variables
2. Lotka Volterra ⇒ linearization of dynamics
3. Resource utilization ⇒ impact & sensitivity
4. Limit of similarity ⇒ Robustness of coexistence



Steps from LV & classical niche to modern theory

1. Resources ⇒ Regulating variables
2. Lotka Volterra ⇒ linearization of dynamics
3. Resource utilization ⇒ impact & sensitivity
4. Limit of similarity ⇒ Robustness of coexistence

Any model can be linearized!

Lotka-Volterra competition:

$$r_i = r_{0i} - \sum_j a_{ij} n_j$$

Generalized competition coefficient:

$$a_{ij} = -\frac{\partial r_i}{\partial n_j}$$

Steps from LV & classical niche to modern theory

1. Resources ⇒ Regulating variables
2. Lotka Volterra ⇒ linearization of dynamics
3. Resource utilization ⇒ impact & sensitivity
4. Limit of similarity ⇒ Robustness of coexistence

Classical niche theory (*ad hoc*):

$$a_{ij} \sim \sum_k u_{ik} u_{jk}$$

Resource utilization

Proposed theory (derived):

$$-a_{ij} = \frac{\partial r_i}{\partial n_j} = \sum_k \frac{\partial r_i}{\partial \mathcal{R}_k} \frac{\partial \mathcal{R}_k}{\partial n_j} = \boldsymbol{S}_i \cdot \boldsymbol{I}_j$$

Sensitivity of Species i

Impact of Species j

Steps from LV & classical niche to modern theory

1. Resources $\Rightarrow$ Regulating variables
2. Lotka Volterra $\Rightarrow$ linearization of dynamics
3. Resource utilization $\Rightarrow$ impact & sensitivity
4. Limit of similarity $\Rightarrow$ Robustness of coexistence

Equilibrium:

$$\boldsymbol{r}(\boldsymbol{\mathcal{R}}(\boldsymbol{n}), \boldsymbol{\mathcal{E}}) = 0$$

Perturbation:

$$\frac{\partial \boldsymbol{n}}{\partial \boldsymbol{\mathcal{E}}} = \boldsymbol{a}^{-1} \frac{\partial \boldsymbol{r}}{\partial \boldsymbol{\mathcal{E}}}$$

Robustness:

$$\det \boldsymbol{a} = \det(\boldsymbol{S}_i \boldsymbol{I}_j)$$

must be large!

$\Rightarrow$ Species should be different!

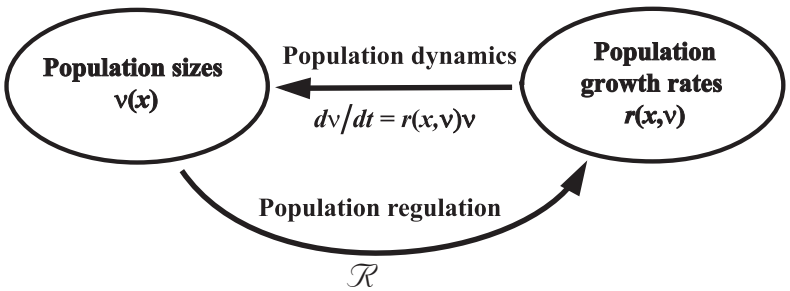
Steps from LV & classical niche to modern theory

1. Resources $\Rightarrow$
   Regulating variables
2. Lotka Volterra $\Rightarrow$
   linearization of dynamics
3. Resource utilization $\Rightarrow$
   impact & sensitivity
4. Limit of similarity $\Rightarrow$
   Robustness of coexistence

Larger similarity in
*I*mpact or *S*ensitivity
$\Downarrow$
Weaker robustness
of coexistence

[No absolute limit of similarity!]

Structural instability of continuous coexistence



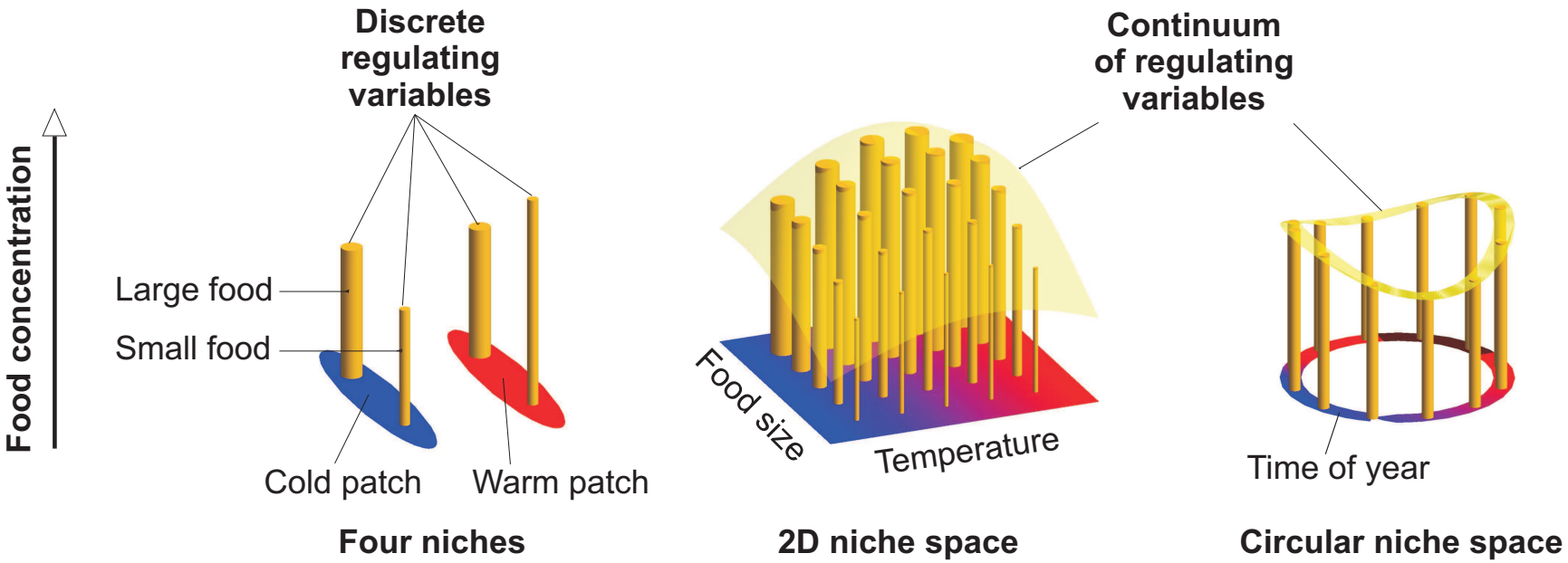
Theorems proven:

- Compactness of the operator of regulation: coexistence of infinitely many *fixed* types is structurally unstable.
- + analicity in 1D: the *possibility* of a coexistence with limit point is structurally unstable

(Meszéna & Gyllenberg, JMB, 2005; Barabás et al., 2012, EER)

Niche space: Ways of niche segregation

Varieties for niche space:



Niche space: set of regulating variables.
Not necessarily an Euclidean space of a few dimension!

Complications abound

What about

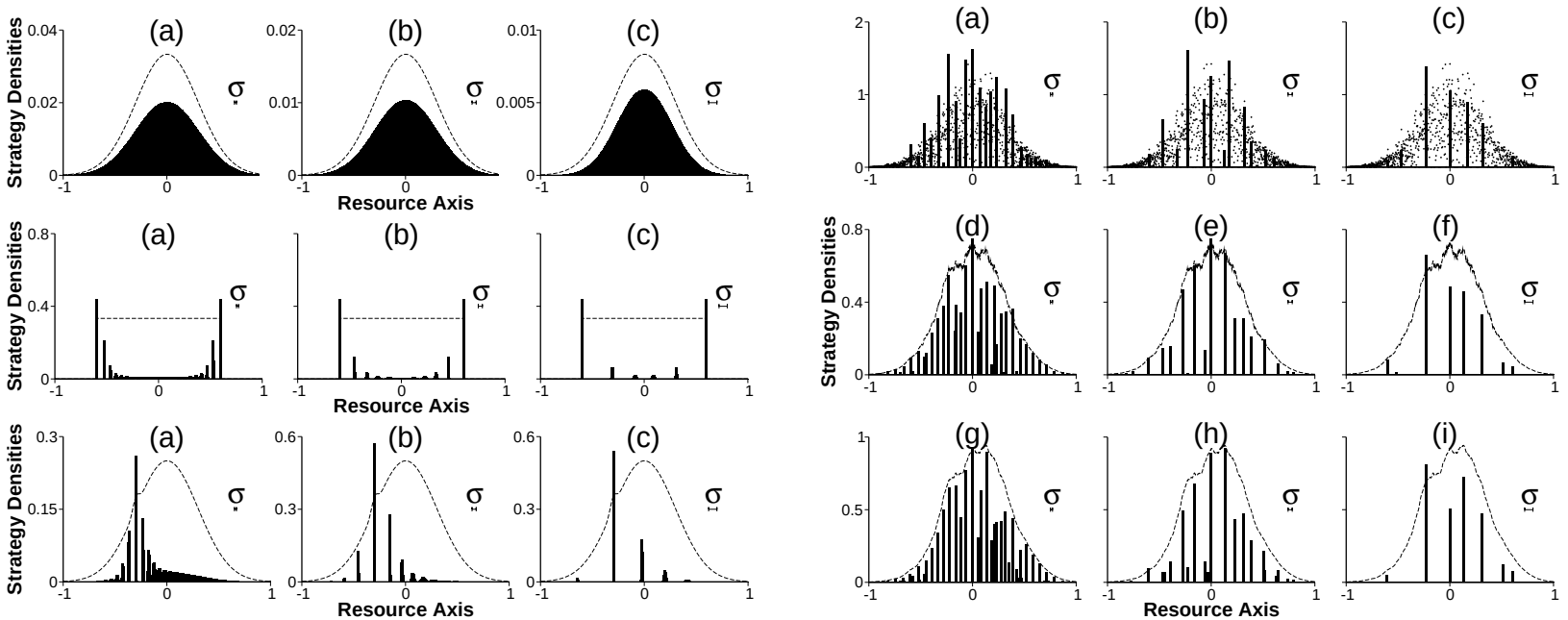
- population structure?
- spatial structure?
- temporal structure?
- facilitation?
- etc.

We have papers about them...

Structural instability of continuous coexistence

(Szabó & Meszéna, Oikos, 2006)

Lotka-Volterra competition for a resource continuum;
Gaussian competition kernel.



Except the immediate vicinity of continuous coexistence:
Segregation by niche width!

Self-organised similarity?

Scheffer & Nes, PNAS, 2006

Claim: coexistence of similars!!!!!

(Scheffer & Nes: Self-organized similarity, PNAS, 2006)

Model:

$$r(y) = r_0 \left(1 - \frac{\int \alpha(y,x) n(x) dx}{K(y)}\right) - g \frac{n(y)}{[n(y)]^2 + H^2} \quad (1)$$

apparent competition

Generalized competition:

$$\frac{\delta r(y)}{\delta n(x)} = -\frac{r_0}{K(y)} \alpha(y,x) - g\delta(y-x)... \quad (2)$$

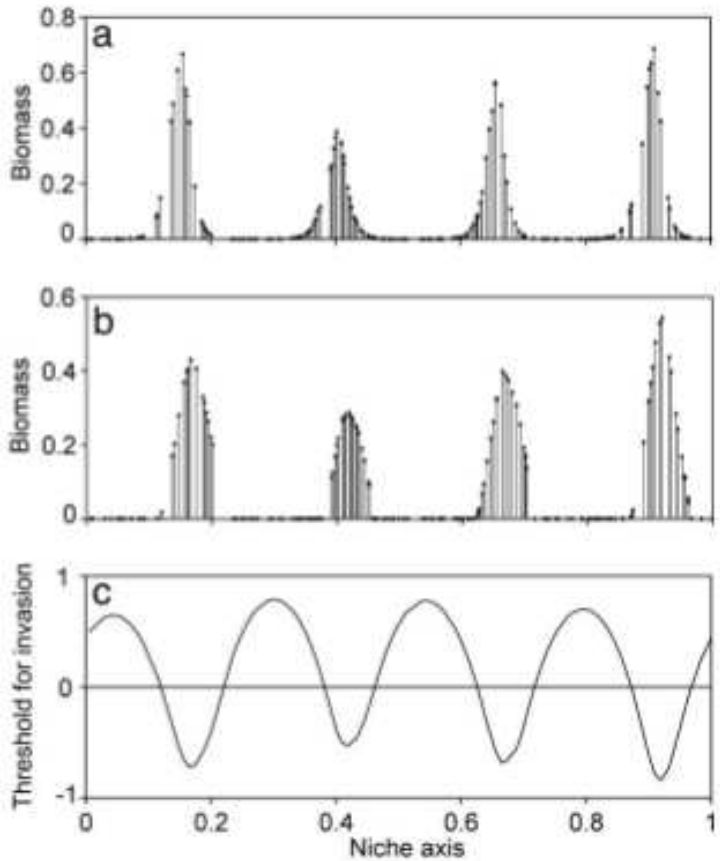
Degeneracies:

- They choose $K(y)$ =const.
- Delta function for apparent competition!

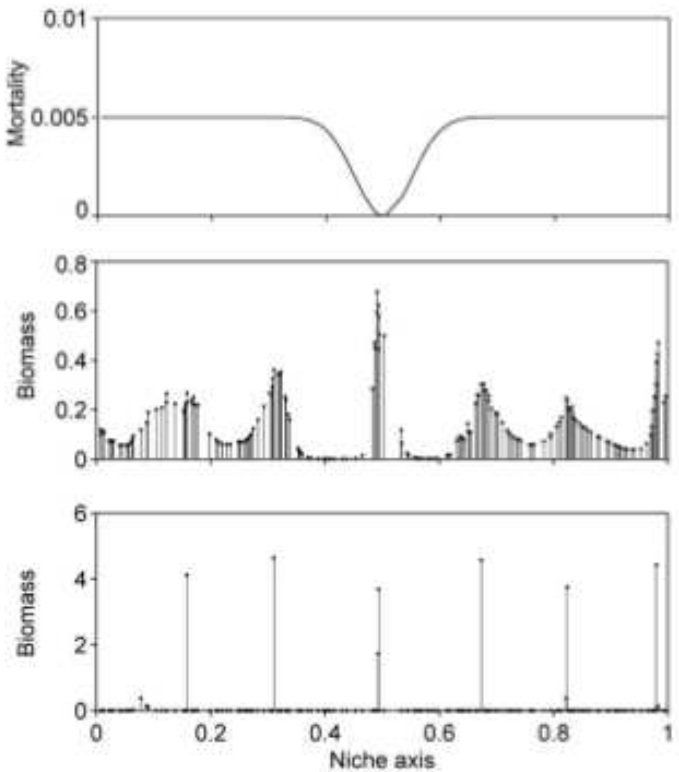
Self-organised similarity?

Scheffer & Nes, PNAS, 2006

Original model



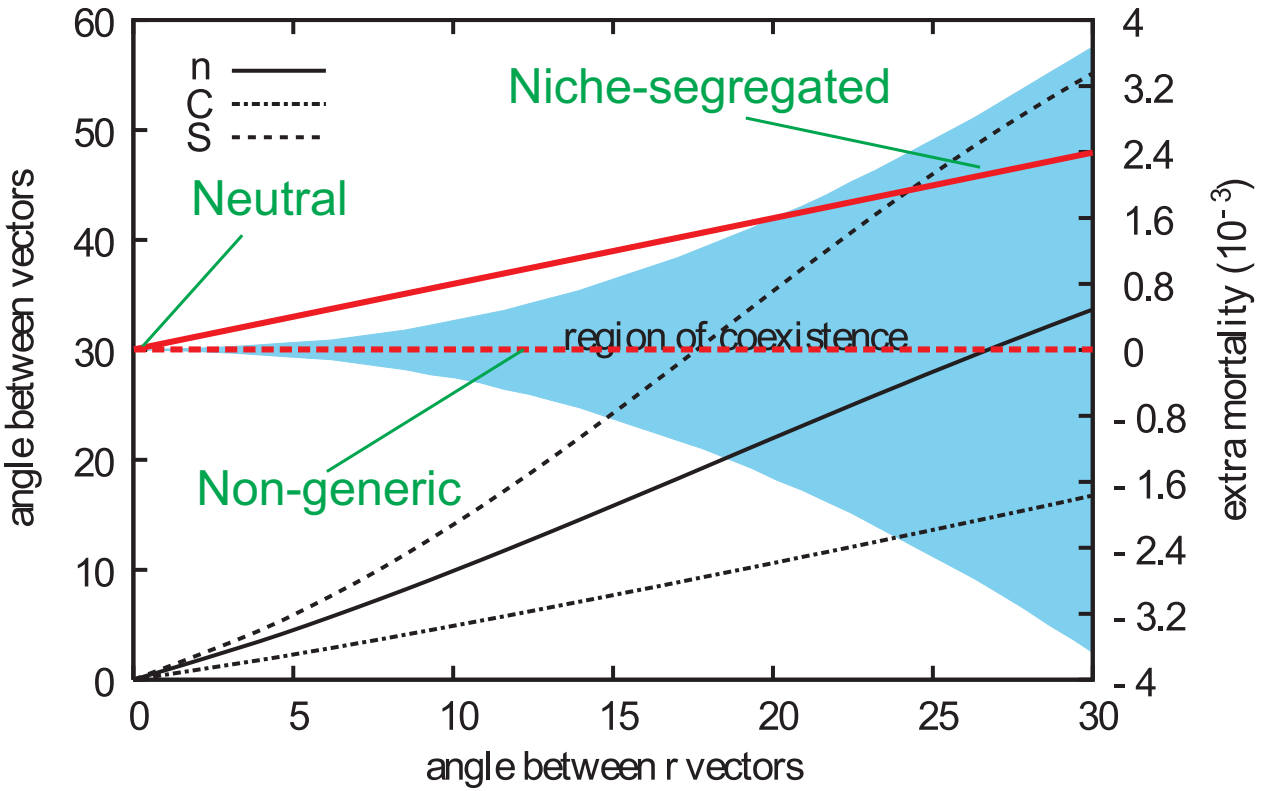
Degeneracies removed



No degeneracies $\Rightarrow$ No coexistence of similars at $t = \infty$!

Niche-neutrality continuum?

No!



EITHER strictly neutral OR sufficiently niche-segregated!

Conclusion: We have the theory

Coexisting species must differ
in their way of regulation!

- Niche space: set/list of regulating variables.
- Niche of a species: impact and sensitivity.
- Robustness of coexistence is lost when either the impact, or the sensitivity niches are too similar.
- Intuitive requirement for niche segregation by niche width prevails as a rule of thumb.
- Self-organized similarity and niche-neutrality are wrong concepts.

Thanks for the coworkers!

- György Barabás (University of Chicago)
- Mats Gyllenberg (University of Helsinki)
- Hans Metz (University of Leiden)
- Kalle Parvinen (University of Turku)
- Liz Pásztor (Eötvös University)
- Péter Szabó (Szent István University)
- András Szilágyi (Eötvös University)

Thanks for your attention!