

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

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MBA15:

Linking Mathematical Theories with Empirical Realities

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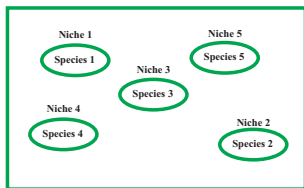
Outline

- 1 Introduction
- 2 Theory
- 3 Controversies
- 4 Conclusion

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

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- 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

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- 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.

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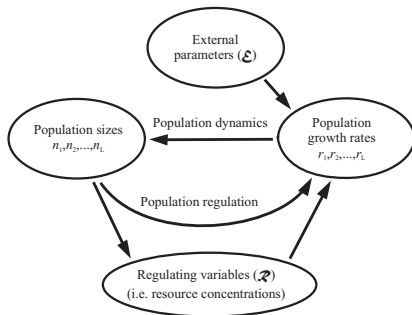
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Goal: Clarity to niche theory!

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



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Any model can be linearized!

Lotka-Volterra competition:

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

Generalized competition
coefficient:

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

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Classical niche theory (*ad hoc*):

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

Resource utilization

Proposed theory (derived):

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

Sensitivity of Species i

Impact of Species j

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Equilibrium:

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

Perturbation:

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

Robustness:

$$\det \mathbf{a} = \det(\mathbf{S}_i I_j)$$

must be large!

\Rightarrow Species should be different!

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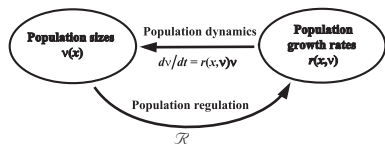
Larger similarity in
Impact or Sensitivity



Weaker robustness
of coexistence

[No absolute limit of similarity!]

Structural instability of continuous coexistence



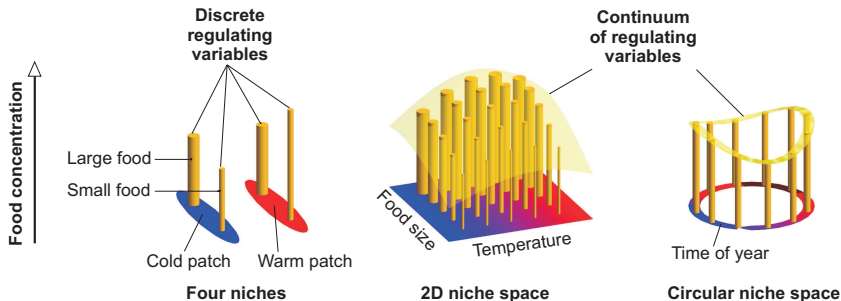
Theorems proven:

- 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

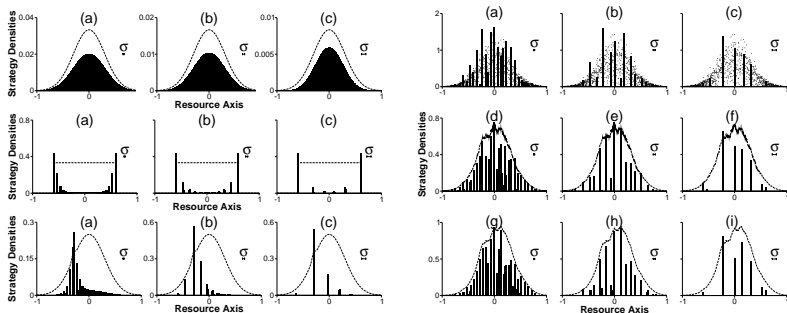
- population structure?
- spatial structure?
- temporal structure?
- facilitation?
- etc.

We have papers about them...

Structural instability of continuous coexistence

(Szabó & Meszén, *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:

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

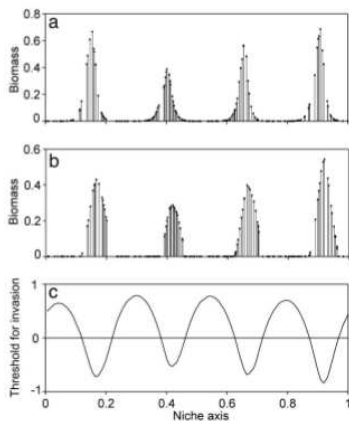
Degeneracies:

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

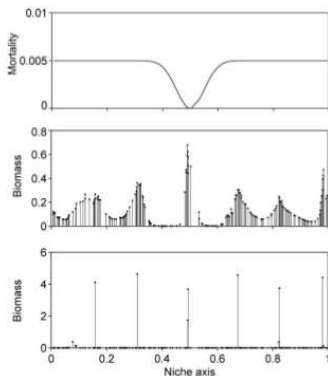
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Original model



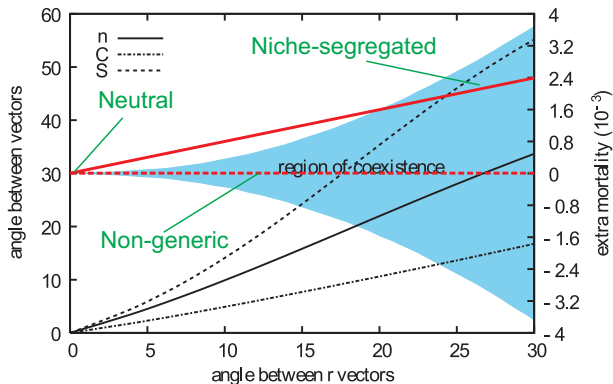
Degeneracies removed



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

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)
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- Péter Szabó (Szent István University)
- András Szilágyi (Eötvös University)

Thanks for your attention!