Mathematical niche theory and the biodiversity problem

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Coexistence in complex ecological communities
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Outline

Diversity! Why???? Why are so many animals?

Diversity vs. Niche

Questions abound...

- Is it true that each species needs an own niche?
- If so, is it true that availabity of niches determines diversity?
- If so, what determines the number of available niches?
- ⋮
- By the way: Does "niche" mean *anything*?

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.
  - Attempts to interpret diversity via questioning competitition.
- Since, theoretical ecology has grown up:
  - Beyond the specific models (eg. Caswell).
  - Renewed interest in coexistence theory (eg. Chesson).
  - Niche has remained controversial.

Clear up this mess!

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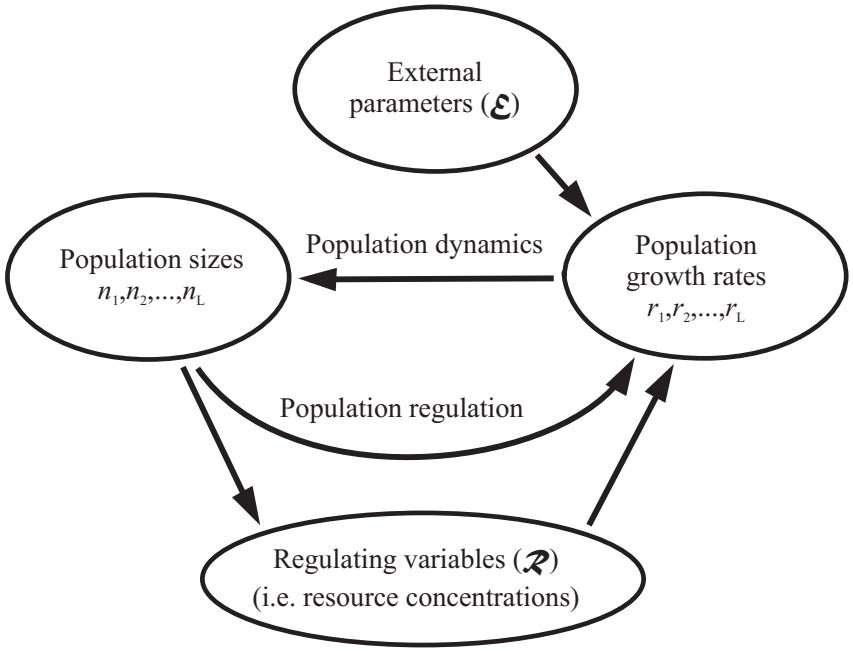
Steps from LV & classical niche to modern theory

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



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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):

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

Sensitivity of Species i

Impact of Species j

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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!

⇒ Species should be different!

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Larger similarity in
*I*mpact or *S*ensitivity
⇓
Weaker robustness
of coexistence

[No absolute limit of similarity!]

Complications abound

What about

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

We have papers about them...

Controversies abound

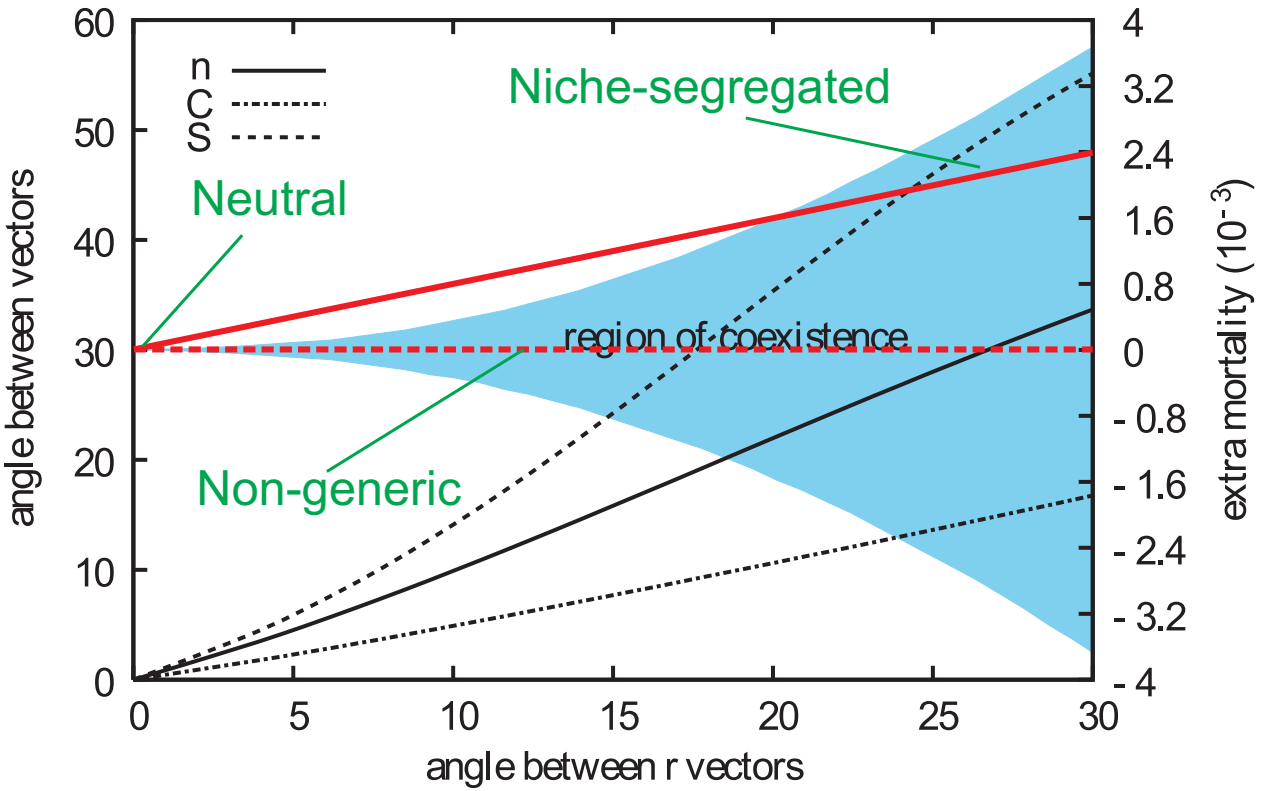
Ideas wishing to understand diversity via questioning competitive exclusion:

- Weakened competition?
- Neutral theory?
- Niche-neutrality continuum?
- Self-organised similarity?

They are all wrong...

Niche-neutrality continuum?

No!



EITHER strictly neutral OR sufficiently niche-segregated!

Trophic niche

Assume: Trophic network, no other interactions.
Question: Regulating variables?

Specify the food classes!
Regulating variables:

- concentration of all inorganic resources
- concentration of all organic food classes
- predation pressure on all food classes

Each species has an impact and sensitivity on these.

Key: the food classification $\sim$ consumer specifcity.
Warning: potentially unlimited and empty...

How many niches are out there?

Is it a well-defined number?

- Yes, e.g. a finite number of well-defined resources.
- No, species partition a niche continuum, depending on their niche width.
- No, any new species extend the niche space, allowing further species.

Productivity-diversity: The controversy

Nontrivial empirical relationship:

- High diversity seems to require high primary production.
- High producton does not necessarily lead to high diversity – sometimes the opposite.

Suggestion for non-monotonicity ("humpback"):
Too much productivity increases competition and decreases diversity.

- wrong theoretical concept for competition
- empirical sitution is confused

Productivity-diversity: Niche connection

NO amount of productivity leads diversity without the possibility of niche segregation!

Increasing productivity may increase the number of available niches:

- Allows finer specialisation and more species along the niche continuum.
- Allows e.g. more trophic leves.

Conclusion A: we have the theory of niche

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.

Conclusion B: what determines diversity?

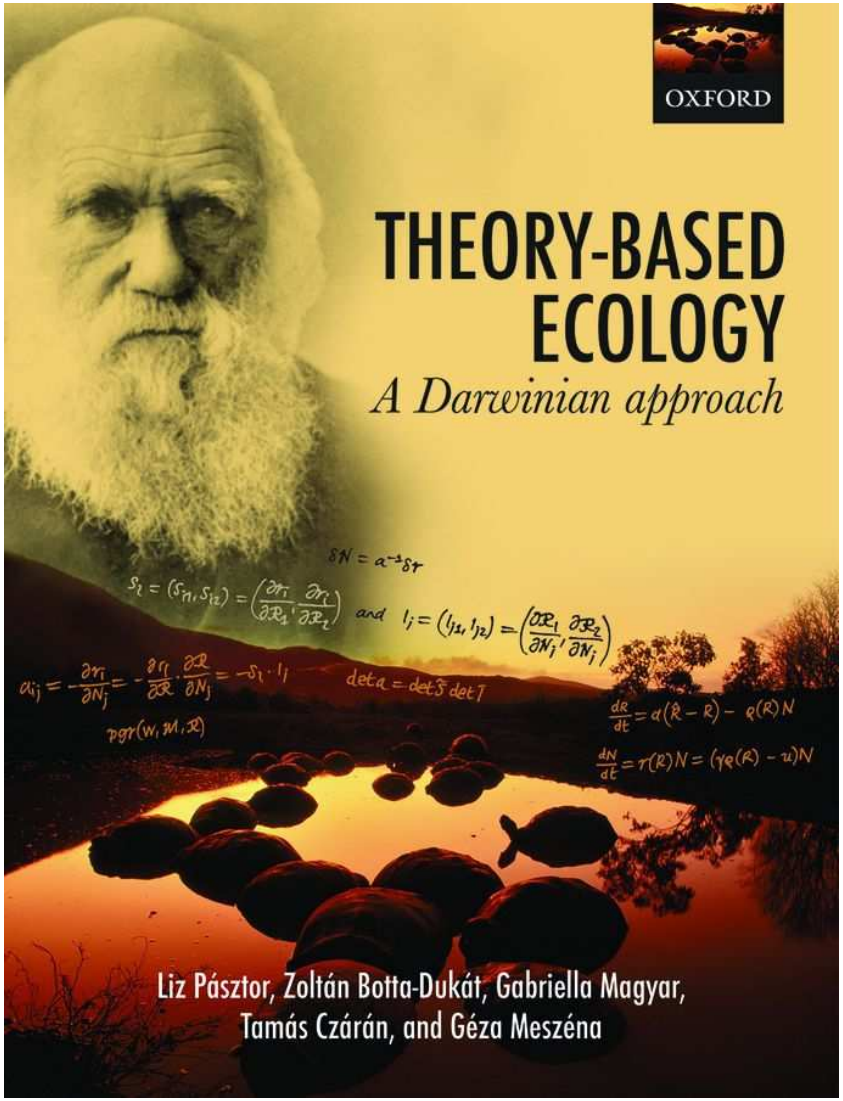
Large diversity requires:

- Possibility for niche differentiation. AND
- Large productivty. AND
- Sufficient time for evolution.

You cannot escape the job to understand your system!

Hope: It should not be *that* hard.
Needed: Theory-motivated empirical interest.

Theory-Based Ecology: A Darwinian approach



Is there such thing, as theory-based ecology?

At least, we have a book on it...

Enjoy!!!

(And buy it cheaper: ACFLYP8)

Thanks for the coworkers!

- TBE coauthors, esp. Liz Pásztor
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Thanks for your attention!