Feasibilitiy and niche segregation

Géza Meszéna

Eötvös University

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Why don't we trust theory in ecology?

Why we don't trust theory in ecology?

- Theories oversimplify everything.
- You never know, whether the assumptions are justified.
- You could have many different models and they will give you many different results.
- You could have different models explaining the same outcome.
- You never will be sure, if parameter choices are correct.
- You can argue both ways citing models.
- Etc.

Something seems to be wrong here.

And what about empirical ecology?

Look for patterns and test hypotheses before doing theory!

- Coexistence of similars, or the different?
- Intermediate disturbance hypothesis?
- Productivity-diversity relationship?
- Stress dominance hypothesis?
- Etc.

Often: Yes and No or It depends

Something seems to be wrong here, too.

What is wrong with theory?

- Theoretical ecology is a zoo of independent models.
- Models are just considered different. Their relationships is not even asked.
- You cannot assess, if the conclusions are general, or highly dependent on the specific assumptions.
- Even when theory is well-developed in a subfield of ecology, it lacks connections outside the subfield.

Goal:

Consistent theory as a basis of ecology, as a discipline.
A coherence of the different levels of discussion.

Theory Ladder

Simple intuitive models? *or* Complex realistic models?

Neither of them connect the specific to the conceptual!

Instead: Theory Ladder

1. Conceptual level
2. Slightly more specific
3. Even more specific
4. ⋮
5. As specific, as you want.

Levels should be mathematically related!

- Specification of interactions/regulations
- Theory of structured populations
- Time-scale separation

Competitve exclusion?

Version 1: # species $\leq$ # resources

Generally not true, zillions of counter-examples.

Version 2: # species $\leq$ # regulating variables (Levins, 1970)

True, but not directly predictive.

What counts, as regulating variable?

Your choice:

- Read the zillions of papers, learn that Ver1 is unreliable and remain clueless about what is true.
- Rely on Ver2, and understand that the problem has a general structure. Use this understanding in studying your system.

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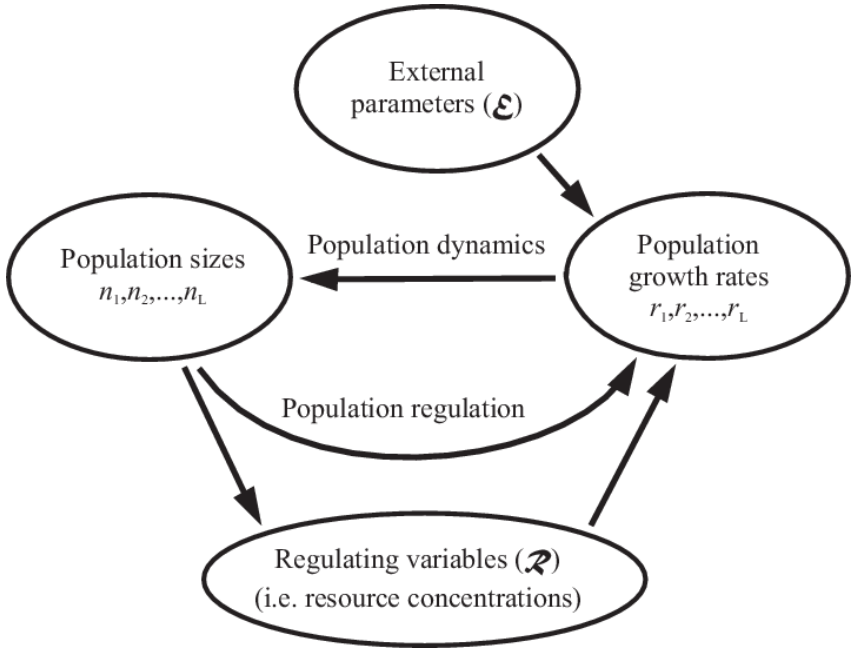
Steps from LV & classical niche to modern theory

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!

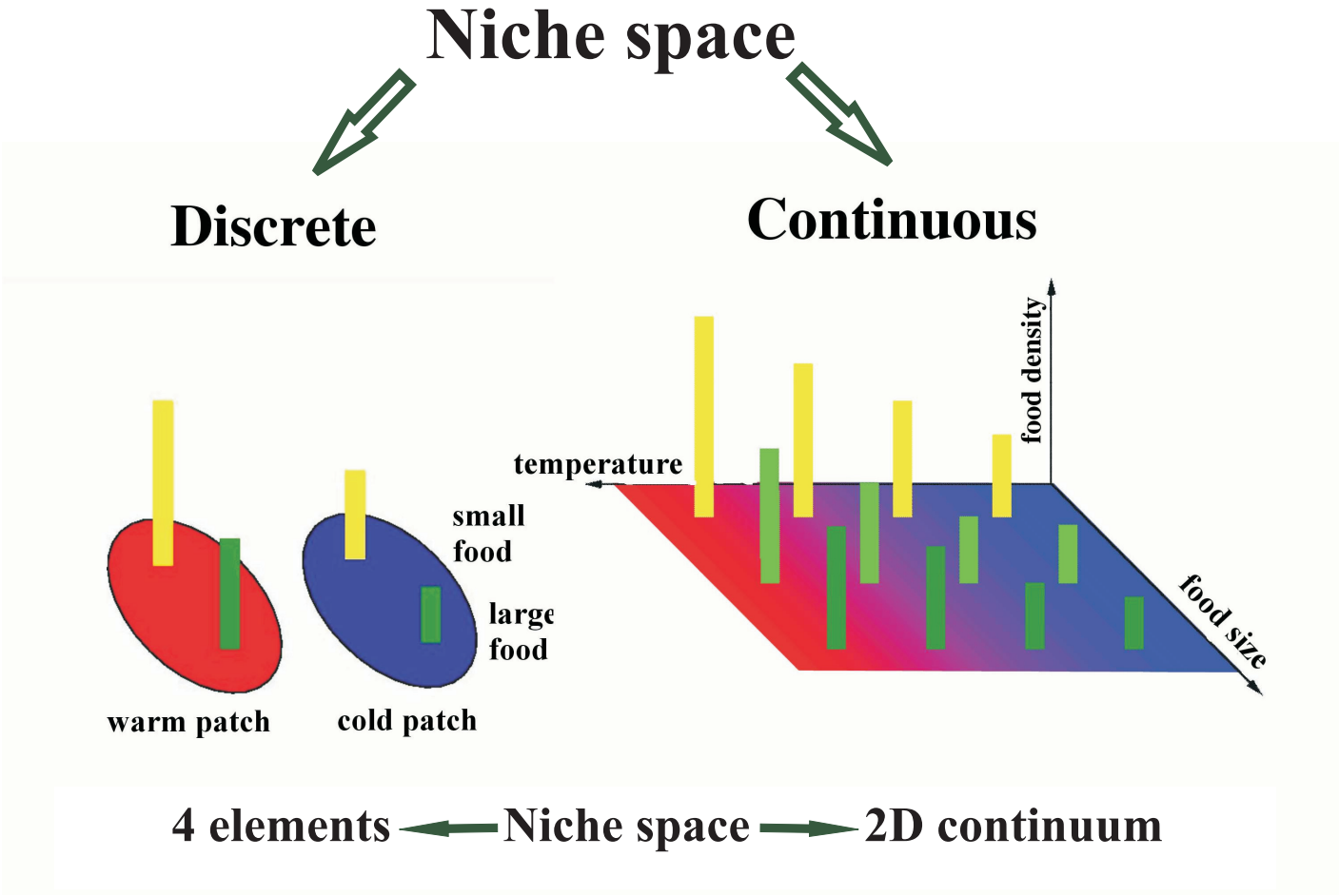
Steps from LV & classical niche to modern theory

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!]

Ecology of spatial structure: Ways of niche segregation



Discrete and continuous.

Parallelism between resource and habitat segregation!

Temporal niche segregation, instead of Chesson's unintuitive effects.

Feasibility

Feasibility: probability of existence of a positive equilibrium, when external parameters have a probability distribution.
(Grilli's feasibility: $p(\boldsymbol{\Delta})$ is uniform on a sphere in the $\boldsymbol{r}$ space.)

Modified equilibrium condition:

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

Environment is represented by the probability distribution $p(\boldsymbol{\Delta})$.
Probability of having an all-positive solution:

$$P(\boldsymbol{n} > 0) = \int_{\boldsymbol{n}>0} p[\boldsymbol{r}(\boldsymbol{n})] |\det \boldsymbol{a}| d\boldsymbol{n}$$

Scaled by $|\det \boldsymbol{a}|$!

Resource-consumer model

From Frederik's note:

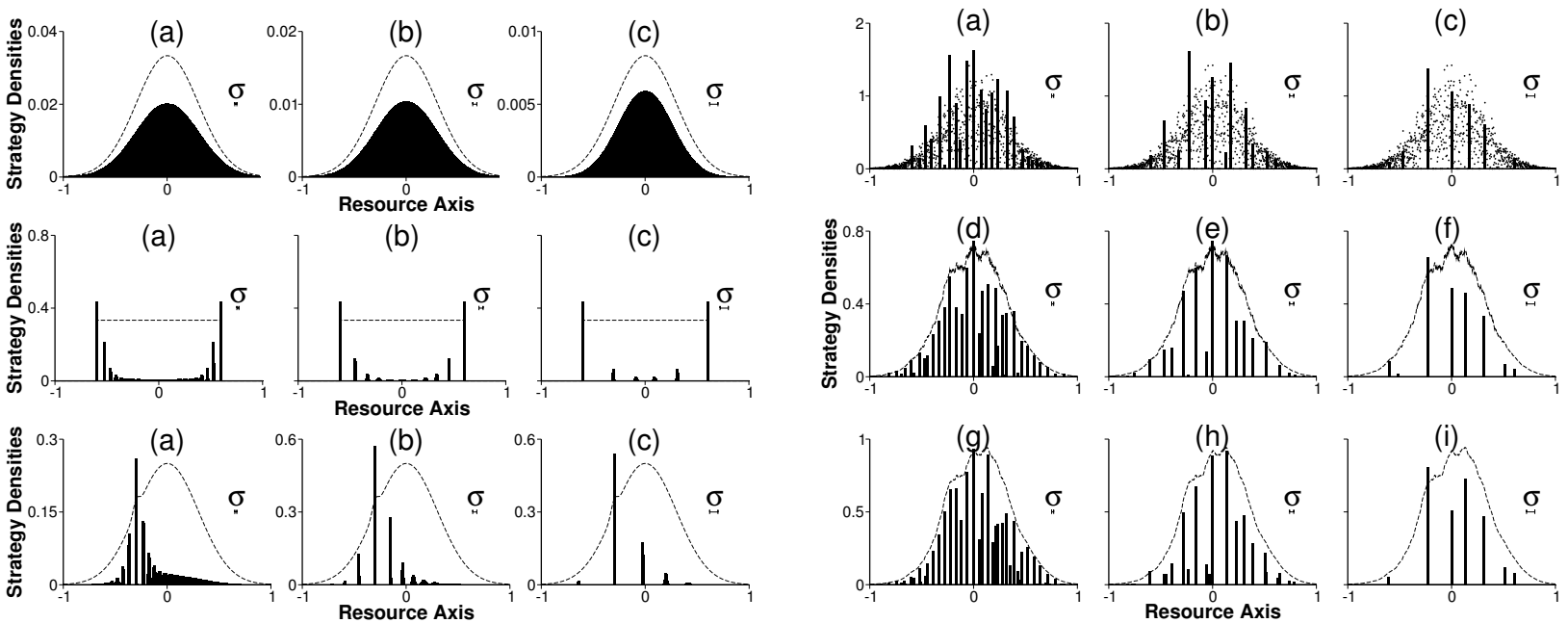
$$\boldsymbol{a} = \begin{pmatrix} \boldsymbol{I} & -\boldsymbol{B} \\ \boldsymbol{C} & \boldsymbol{0} \end{pmatrix}$$

$$\det \boldsymbol{a} = \det(\boldsymbol{B} \cdot \boldsymbol{C})$$

Feasibility: resources and consumers are mutually niche-segregated with respect to each others.

Continuous coexistence?

Lotka-Volterra competition *a la* MacArthur & Levins (1967)
Gaussian carrying capacity & competition kernel.



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

Gyllenberg & Meszéna (2005); Szabó & Meszéna (2006)

To discuss: What determines species diversity

Hypothesis: Emergence of species diversity requires:

Primary production
and
Niche segregation possibilities
and
Evolutionary time

- High primary production without niche segregation possibilities will not lead to diversification even on long run.
- Niche segregation structures are specific to the type of the ecosystem and is not always empirically understood.
- You will never test this hypothesis by statistical means.
- Instead you may want to understand the inner workings of the diverse ecosystems.

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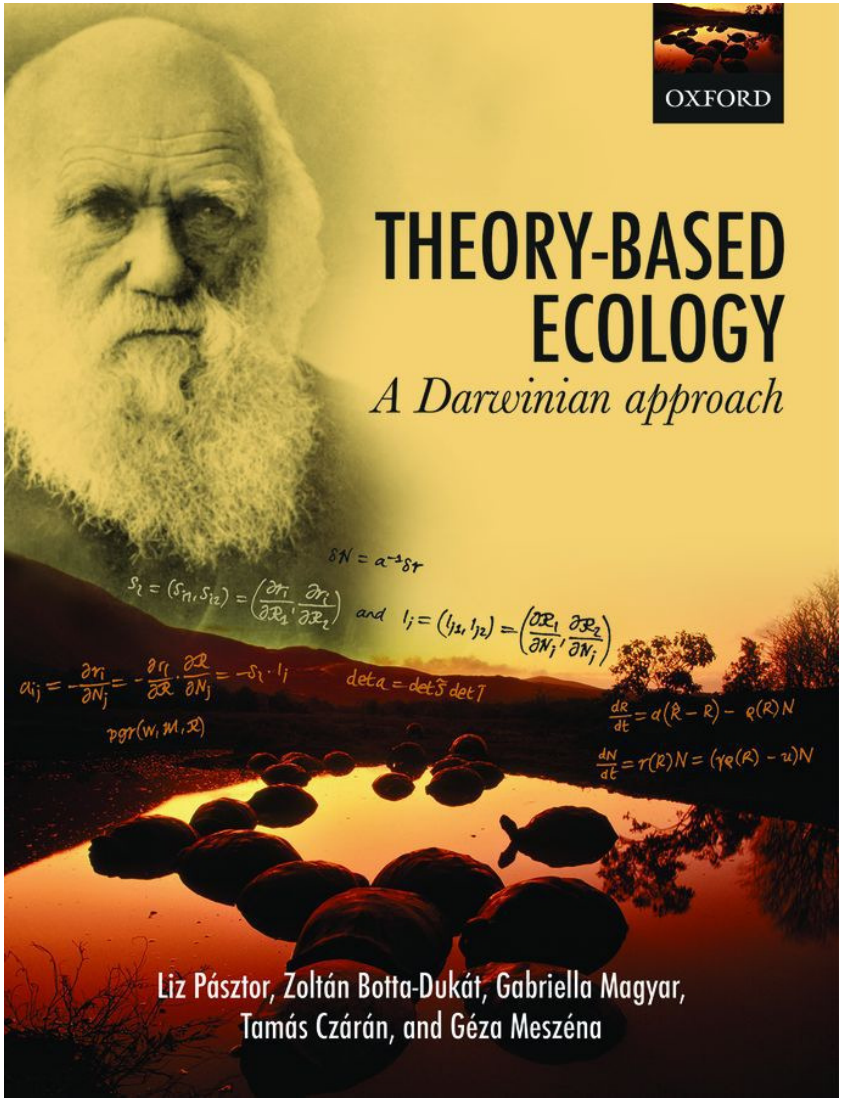
Conclusion

- Theory should go beyond the zoo of independent models.
- Sufficiently deep theory provides clarity on competitive exclusion, etc. It is a reliable framework studying diversity issues.
- No theory will spare you from studying the real thing.
- This is the real challenge.

Theory-Based Ecology: A Darwinian approach



Is there such thing, as theory-based ecology?

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

Enjoy!!!

Thanks

Theory Based Ecology

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- Zoltán Botta-Dukát
- Tamás Czárán
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Adaptive Dynamics

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Thanks for your attention!