

On the role of theory in ecology

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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?

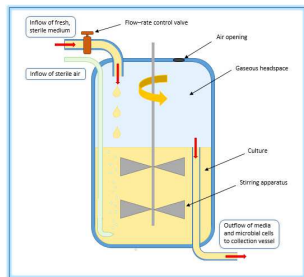
- Theoretical ecology is a zoo of independent models.
- Models are just considered different. Their relationships is not even asked.
- You cannot assess, if the conclusions are general, or highly dependent on the specific assumptions.
- Even when theory is well-developed in a subfield of ecology, it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

Goal:

Consistent theory as a basis of ecology, as a discipline.

A coherence of the different levels of discussion.

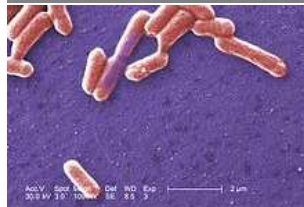
Example 1: prey-predator in equilibrium



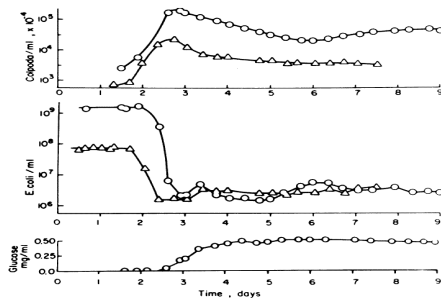
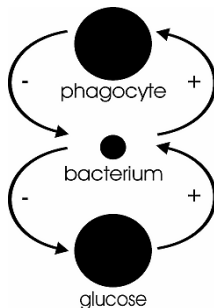
E. Coli eats sugar.

Colpoda eats *E. Coli*.

Who will benefit from
increased sugar concentration?



Who will benefit from more sugar?



The *E. coli* remains unaffected! Why?

Because it is determined by the equilibrium condition of the *Colpoda*!

Could you guess this without understanding theory?

Example 2: Competitive exclusion

Version 1: $\# \text{ species} \leq \# \text{ resources}$

Generally not true, zillions of counter-examples.

Version 2: $\# \text{ species} \leq \# \text{ regulating variables}$ (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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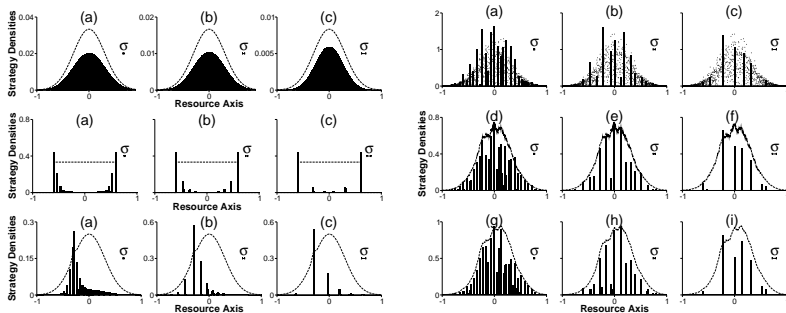
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Is there a limit for similarity?

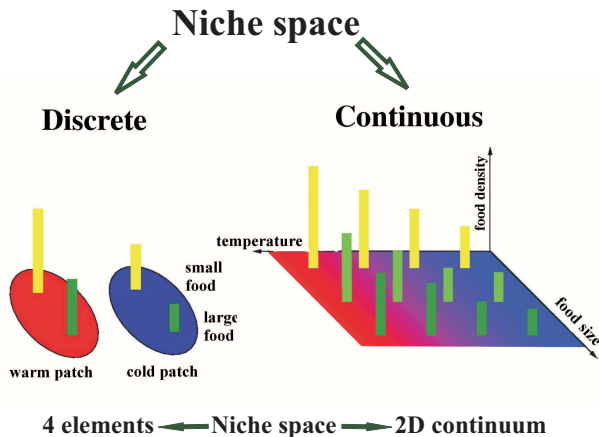
Lotka-Volterra competition *a la* MacArthur & Levins (1967)
Gaussian carrying capacity & competition kernel.



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

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

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

Example 3: Why speciate?

- Darwin:
 - Speciation is driven by the advantage of being different.
 - No clue on reproductive isolation.
- Allopatric (Mayr) speciation:
 - No way for divergent evolution in a panmictic population.
 - Populations must be geographically separated first!
- Ecological (competitive, adaptive, etc.) speciation:
 - Reproductive isolation is a consequence of divergent selection.
 - Parsimony: ecological possibility for diversification drives diversification.

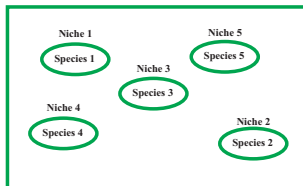
Mallet: Mayr's view of Darwin: was Darwin wrong about speciation? (2008)

Nosil: Ecological Speciation. (2012)

Why are there so many kinds of animals?

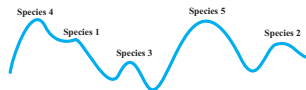
Background: different pictures in ecology and evolution:

Niche space



Species occupy different
niches.

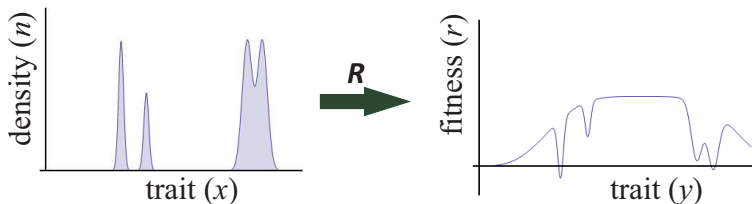
Adaptive landscape



Species occupy different
peaks of landscape.

Conceptual clarification is needed!

Regulated landscape



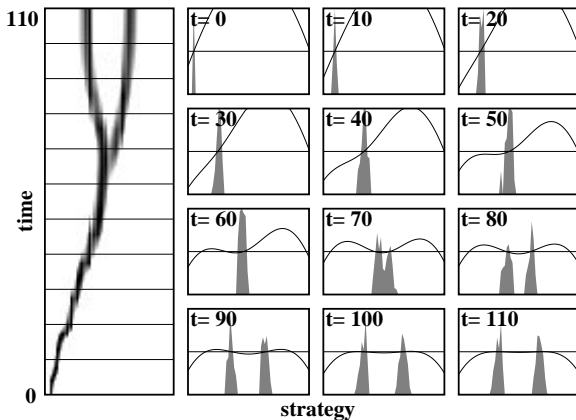
Competition: I eat your food and therefore reduce your fitness.

Competition and evolution to avoid competition are meaningless on a landscape which do not take into account the biotic feedback.

Meszéna (2005); Meszéna, Gyllenberg, Jacobs & Metz et al. (2005)

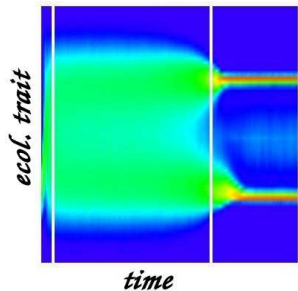
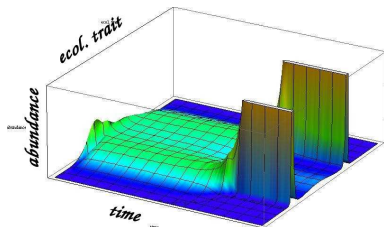
Evolutionary branching for clonal organism

MacArthur & Levins ecology + mutation; clonal inheritance



Branching, i.e. evolutionary discretization!

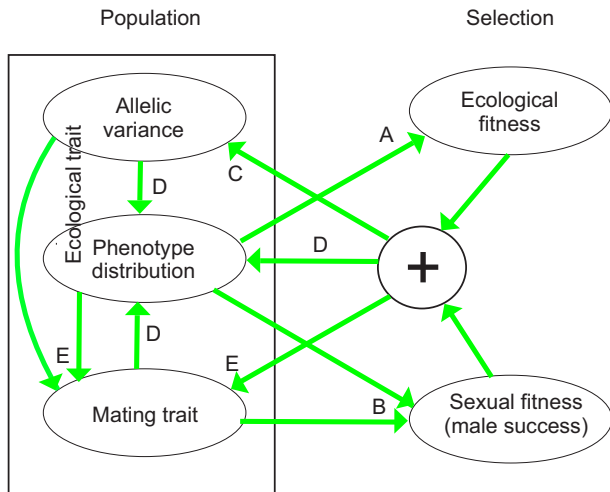
Three phase speciation process



Three phases

- First: fast to the middle, widened trait distribution
- Second: slow, gradual transition to bimodality
- Third: fast completion of segregation

Feedback structure



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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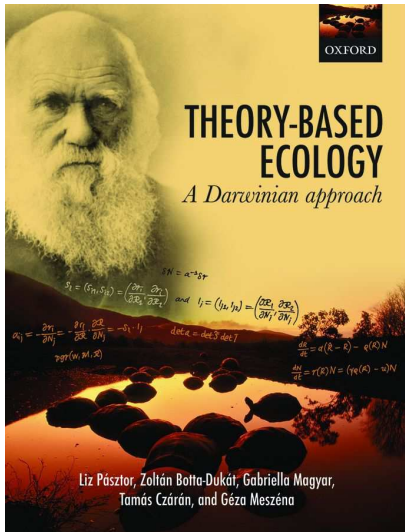
Conclusion

- It is often impossible to understand even the simplest ecological situations without theory.
- 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.
- Consistent ecological theory has clean connection to evolutionary theory.
- Speciation is a natural phenomenon in an evolutionary theory based on ecology.

Take home

- No theory will spare you from studying the real thing.
- This is the real challenge.
- Please go beyond statistical testing of hypotheses!

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

- Liz Pásztor
- Zoltán Botta-Dukát
- Tamás Czárán
- Gabriella Magyar

Adaptive Dynamics

- Hans Metz
- Mats Gyllenberg
- Éva Kisdi

(Former) students

- István Czibula
- András Szilágyi
- Gyuri Barabás
- Benjamin Márkus

- Stefan Geritz
- Ulf Dieckmann

Thanks for your attention!