Coherence of our field of study

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ETI seminar, 2022

Why don't we trust theory in ecology?

Why people 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.

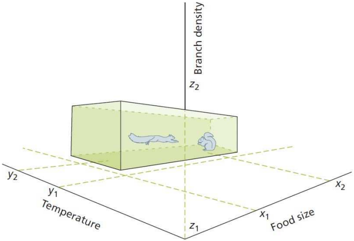
What is wrong with theory?

- Theoretical ecology is a zoo of independent models.
- Models are considered distinct. Their relationships are not asked.
- You don't know, 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.

Good Old Days – Hutchinson's niche in the '60s

Niche space

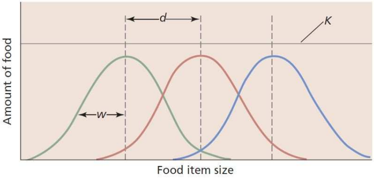


Species partition
an abstract space!

Niche axes:
scenopoetic & bionomic

Hutchinson (1957, 1978)

Resource utilization overlap



Competition
$\sim$ utilization overlap:

$$a_{ij} = \int u_i(R)u_j(R)dR$$

MacArthur & Levins (1967)

Age of Doubts – decline of Lotka-Volterra in the '80s

- What the heck 'niche' and 'niche axis' mean?
- Quality, or concentration on the axis?
- How can I measure *e.g.* niche width?
- Can I measure *anything* in this theory?
- Validity of Gause's principle?
- Is there a limit for similarity?
- Non-competitive interactions?
- Fluctuations?
- Disturbances?
- Isn't *Lotka-Volterra* too far from the real world?
- Aren't *all* models too far from the real world?
- Isn't ecology too complex for *any* theory?

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. More specific
3. Even more specific
4. ⋮
5. As specific, as you want.

Levels should be mathematically related!

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Competitve exclusion

Version 1: # species $\leq$ # resources (MacArthur & Levins, 1964)

Generally not true, zillions of counter-examples.

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

Mathematically 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.

The 2nd one is the correct high level theory.

Empty without the lower levels.

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Regulation and Adaptation

Regulating variable:
DEFINITION An environmental variable is called regulating, iff

- affects the population(s) AND
- affected by the population(s).

Single regulating variable -> Competitive exclusion, i.e., adaptation

- K-maximization (MacArthur, 1962)
- R^*-minimization (Tilman, 1980)
- Pessimization (Metz et al., 2008)

Multiple regulating variables -> Potential for coexistence
Diversity of regulation allows diversity of adaptation.

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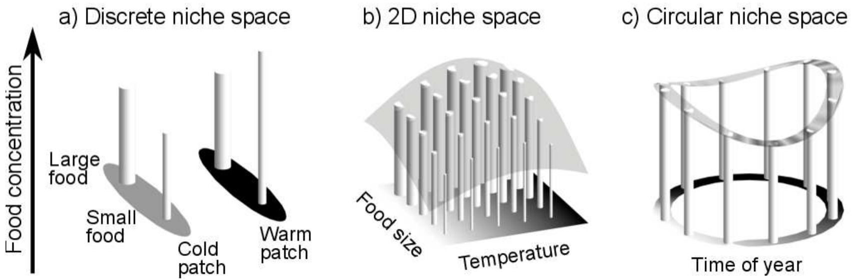
What is niche space



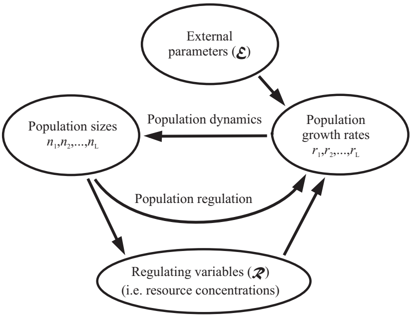
Big picture: species partition the niche space to avoid competition.

- Discrete and continuous.
- Resource and habitat segregation
- Temporal niche segregation.

(Similar with other regulating factors, instead of resources.)

Steps LV to genetral 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:

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

Steps LV to genetral theory

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Classical niche theory (*ad hoc*):

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

Resource utilization

Proposed theory (linearization):

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

Sensitivity of Species *i*

Impact of Species *j*

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Equilibrium:

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

Perturbation:

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

Robustness:

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

must be large!
⇒ Species should be different!

Steps LV to genetral theory

1. Resources ⇒
   Regulating variables
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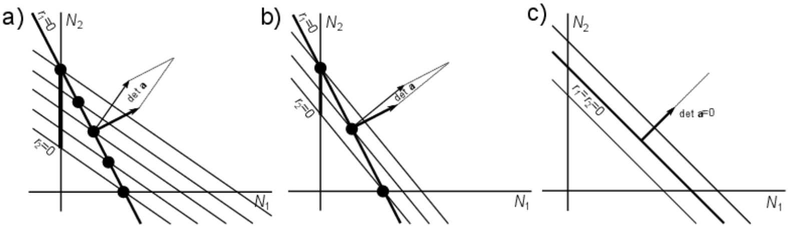
   Robustness of coexistence

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

[No absolute limit of similarity!]

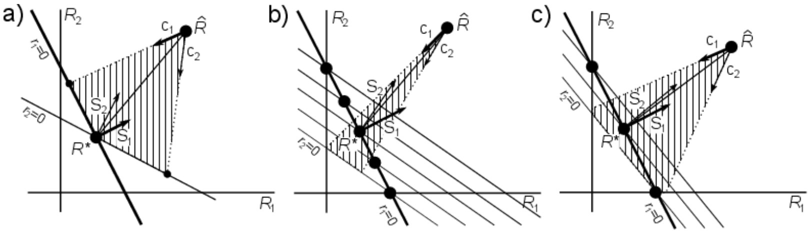
Robustness of coexistence, Lotka-Volterra



Robustness of coexistence is lost when $\det \boldsymbol{a} \to 0$, i.e. when the populations become similar in their interactions!

Conclusion of LV is model-independent!

Robustness of coexistence, Tilman/Leibod's model



Robustness of coexistence is lost when

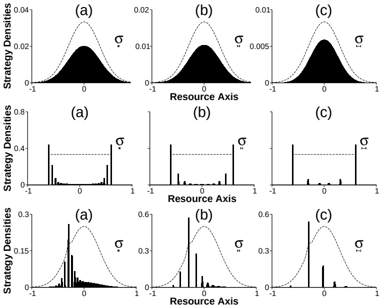
- either the population's impact on,
- or the their sensitivity towards,

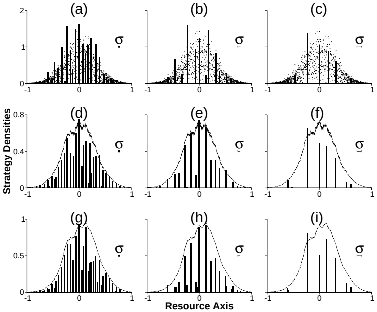
the regulating variables becomes similar!

See Thomas Koffel's lecture on non-competitve interactions!

Continuous coexistence or limiting similarity?

Lotka-Volterra competition *a la* MacArthur & Levins (1967)





Continuous coexistence:

with exactly Gaussian carrying capacity & competition kernel.

Except the immediate vicinity of continuous coexistence:

Discretization! Segregation by niche width!

Szabó & Meszéna (2006), Barabás & Meszéna (2009)

Continuous coexistence or limiting similarity?

Theorem

Coexistence of a continuum of species is structurally unstable.

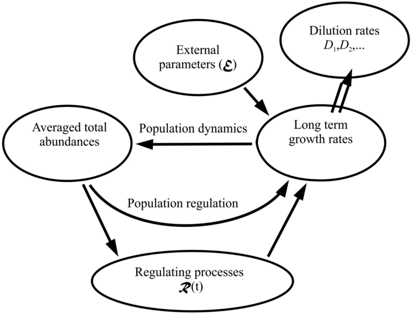
Sketch of Proof

- $\boldsymbol{a}$ is infinite dimensional
- continuity -> $\boldsymbol{a}$ is compact
- $\boldsymbol{a}^{-1}$ does not exist
- q.e.d.

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

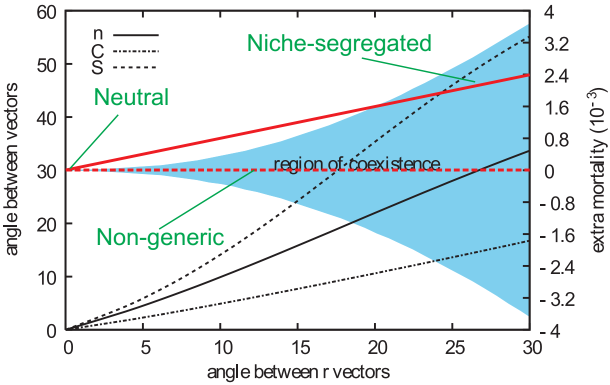
Structured population in an inhomogeneous and fluctuating environment?

Dimension reduction:
Pick up the "long-term growth rate" dimensions!



- Introduce a dilution rate for each population!
- Study the system, as a function of the dilution rates!
- Invert the functions to get a "density-dependent" description!
- q.e.d.

Spatial segregation between two patches



EITHER strictly neutral OR sufficiently niche-segregated!

Szilágyi & Meszéna (2009)

We need complicated formulas for a theory lecture

General scheme:

$$\sigma_i = -\sum_{j=1}^{S} a_{ij}^{-1} z_j,$$

Simple case:

$$\sigma_i = \frac{\partial N_i}{\partial \mathbb{E}}, \qquad a_{ij} = \sum_{\mu} \underbrace{\frac{\partial r_i}{\partial \mathcal{R}_\mu}}_{\mathcal{S}_{i,\mu}} \underbrace{\frac{\partial \mathcal{R}_\mu}{\partial N_j}}_{\mathcal{I}_{j,\mu}}, \qquad z_j = \frac{\partial r_j}{\partial \mathbb{E}}.$$

Periodic environment:

$$\sigma_i = \frac{1}{N_i(0)} \frac{\partial N_i(0)}{\partial \mathbb{E}}, \quad a_{ij} = -\delta_{ij} + \prod_{t=T-1}^{0} \left(\delta_{ij} + \sum_{\mu} \underbrace{\frac{\partial r_i(t)}{\partial \mathcal{R}_\mu(t)}}_{\mathcal{S}_{i,\mu}(t)} \underbrace{\frac{\partial \mathcal{R}_\mu(t)}{\partial N_j(t)} N_j(t)}_{\mathcal{I}_{j,\mu}(t)} \right), \quad z_j = \sum_{t=0}^{T-1} \frac{\partial r_j(t)}{\partial \mathbb{E}},$$

Barabás et al. (2014)

Even more

General structured populations

$$\sigma_i = \frac{\partial N_i}{\partial \mathbb{E}}, \quad a_{ij} = \sum_{\mu} \underbrace{\left(\sum_{a,b} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}_\mu} w_{i,b} \right)}_{\mathcal{S}_{i,\mu}} \underbrace{\sum_{\nu} \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \left(\sum_{c} \frac{\partial \mathcal{R}_\nu}{\partial N_{j,c}} w_{j,c} \right)}_{\mathcal{I}_{j,\nu}}$$

$$z_j = \sum_{a,b} v_{j,a} \frac{\partial A_{j,ab}}{\partial \mathbb{E}} w_{j,b} + \sum_{\mu,\nu} \left(\sum_{a,b} v_{i,a} \frac{\partial A_{i,ab}}{\partial \mathcal{R}_\mu} w_{i,b} \right) \left(\delta_{\mu\nu} - \frac{\partial \mathcal{G}_\mu}{\partial \mathcal{R}_\nu} \right)^{-1} \frac{\partial \mathcal{G}_\nu}{\partial \mathbb{E}}$$

$$\mathcal{G}_\mu \left(\mathcal{R}_\nu, \mathbb{E} \right) =$$

$$= \sum_{j} \sum_{a,b,c} \left(\frac{n_j}{\sum_d q_{j,d} w_{j,d}} \frac{\partial \mathcal{R}_\mu}{\partial n_{j,a}} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(w_{j,a}^k - \frac{\sum_e q_{j,e} w_{j,e}^k}{\sum_f q_{j,f} w_{j,f}} w_{j,a} \right) v_{j,b}^k \right) A_{j,bc} \left(\mathcal{R}_\nu, \mathbb{E} \right) w_{j,c}$$

Szilágyi & Meszéna (2009); Barabás et al. (2014)

ToDo list

- Trophic network: food types & predation pressures
- Stochastic environment: $\text{Cov}(\boldsymbol{S}_i(t), \boldsymbol{I}_j(t))$
- Dispersal limitation: pair approximation

Why speciate?

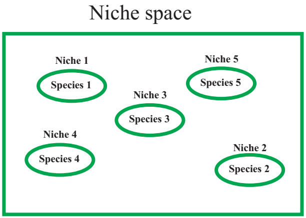
- Darwin:
  - Speciation is driven by the advantage of being different.
  - No clue on reproductive isolation.
- Allopatric (Mayr) speciation:
  - No way for divergent evolution in a panmictic population.
  - Populations must be geographically separated first!
- Ecological (competitive, adaptive, etc.)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

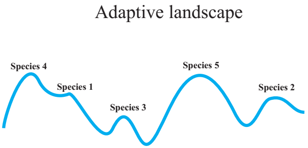
Nosil: Ecological Speciation. (2012)

Why are there so many kinds of animals?

Problem: different pictures in ecology and evolution:



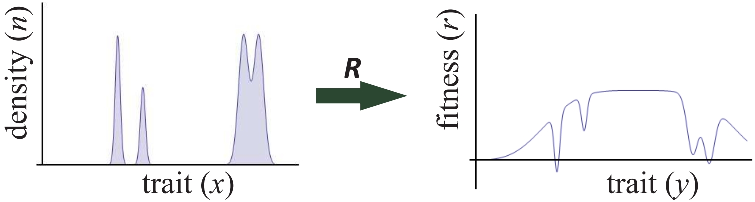
Species occupy different *niches*.



Species occupy different *peaks of landscape*.

Conceptual clarification is needed!

Regulated landscape



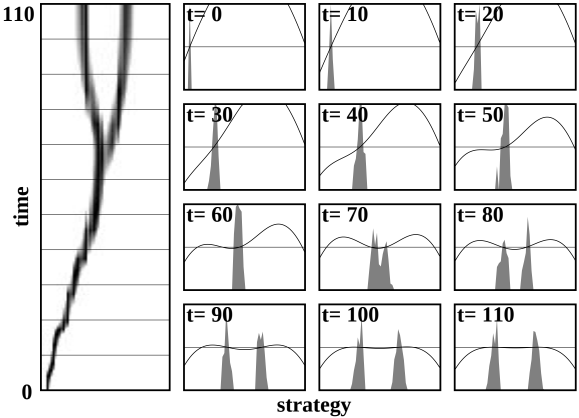
Competition: I eat your food and therefore reduce your fitness.

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

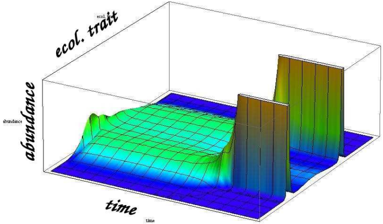
MacArthur & Levins ecology + mutation; clonal inheritance

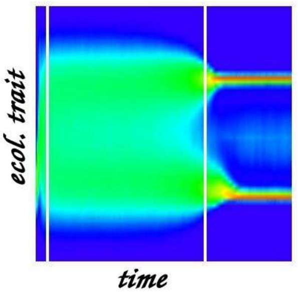


Branching, i.e. evolutionary discretization!

Gertitz, Metz, Kisd &, Meszéna (1997)

Three phase speciation process



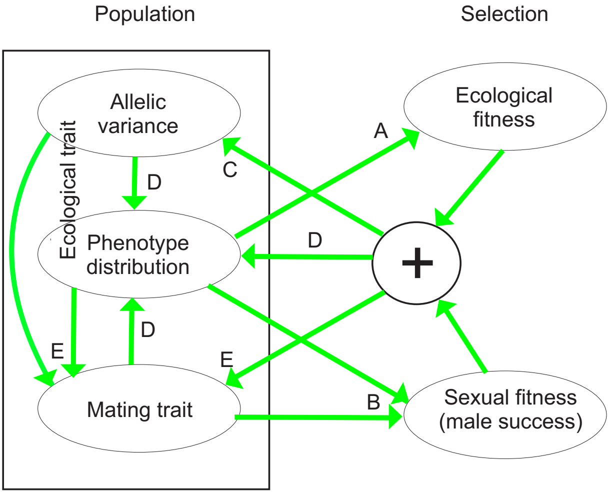


Three phases

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

Meszéna & Dieckmann, BioRxive

Feedback structure



Debate on diversity

- Niche theory?
- Nonequilibrium?
- Chesson?
- Neutrality?
- Niche-neutrality?
- Large random $\boldsymbol{a}$?

Only the first can be connected to adaptation, i.e. real biology.

Niche axes in rainforest

Empirical axes (Turner, 2001):

- Height at maturity
- Pioneer–climax

Model, Kohyama (1993):

- Size
- Gap dynamics

Why don't we say that forest diversity is understood, at least partially?

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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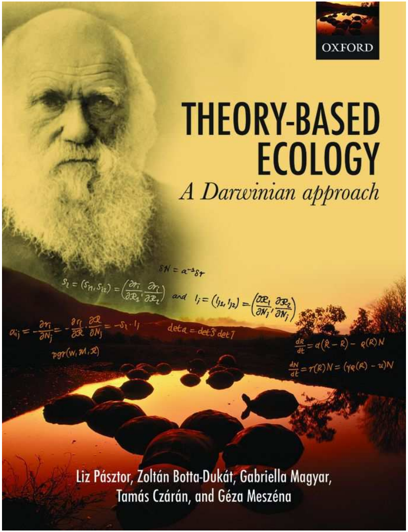
Closing

- Precise top level theory of niche segregation, which
  - integrate ecology and evolution
  - can be connected to detailed modeling precisely.
- No theory will spare you from studying the real thing:
  Figure out the niche structure of the different ecosystems!
- Macroecological patterns?

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
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(Former) students

- András Szilágyi
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Adaptive Dynamics

- Hans Metz
- Mats Gyllenberg
- Éva Kisdi
- Stefan Geritz
- Ulf Dieckmann

Questions?