Niche theory for a fluctuating world (Life in an uncertain word)

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Probability: From East to West
Monash@Prato, 2017

Outline

From East to West, my account

George Marx (1927–2002)

- Neutrino '72, Balatonfüred
- Zel'dovich meets West
- neutrino mass in cosmology
- birth of astroparticle physics

Adaptatation to a fluctuation?

Liz Pásztor

Éva Kisdi

- How to adapt to fluctuation?
- Well, it's averaged out, anyway!
- Well, but it's complicated!
- Frequency dependence!

Adaptative dynamics

Hans Metz

Stefan Geritz

- Directional evolution
- Singular points
- Evolutionary branching
- Speciation

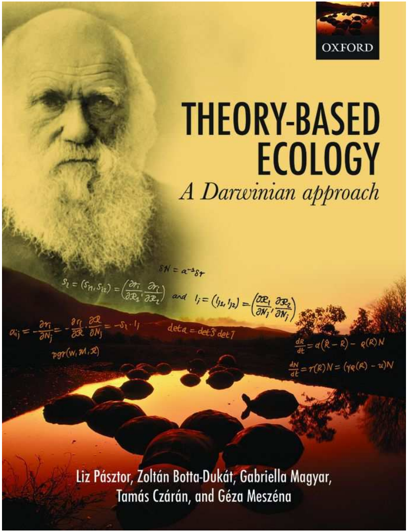
Ecological niche

Mats Gyllenberg

Gyuri Barabás

- Niche segregation with respect to regulation
- No continuous coexistence
- Temporal niche segregation
- Evolutionary branching is a process of niche segregation

Theory-Based Ecology: A Darwinian approach



Principles

1. Exponential growth
2. Growth regulation
3. Inherited variability
4. Finitness – stochasticity
5. Competitive exclusion
6. Coexistence
7. Constraints – trade-offs

Arbitrary, or adapted species?

There ara so many complications,
why don't consider species, as random?
Ideas in this vein:

- No competitive exclusion in a fluctuating world
- Neutral theory of biodiversity
- Random interaction matrix
- Allopatric/genetic theory of speciation

My take: Adapted species!

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My take: Adapted species!

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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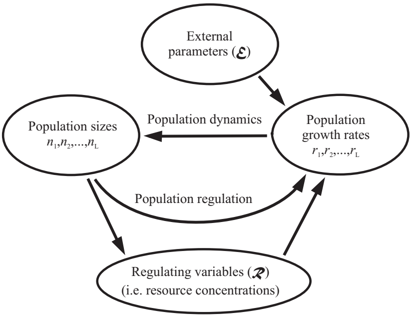
Steps from LV & classical niche to modern theory

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:

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

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!

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1. Resources ⇒ Regulating variables
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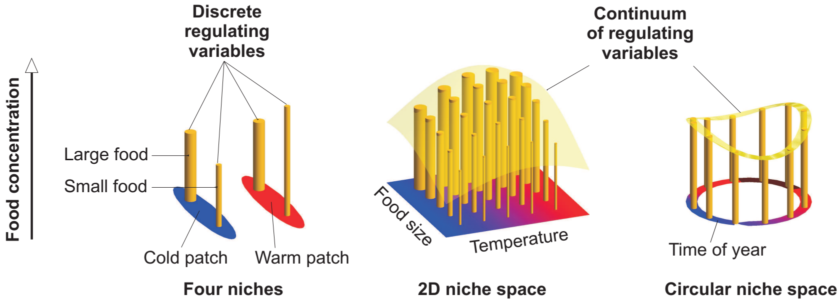
Larger similarity in
*I*mpact or *S*ensitivity
⇓
Weaker robustness
of coexistence

No absolute limit of similarity!

Coexistence of a continuum is
struturally unsable!

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.

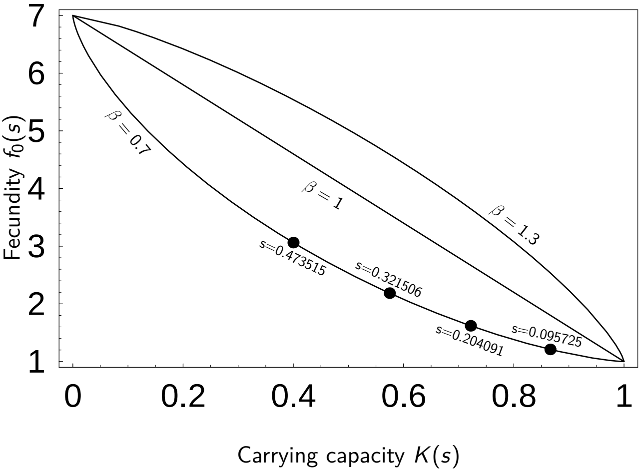
We have papers about them...

Disturbance-generated niche-segregation

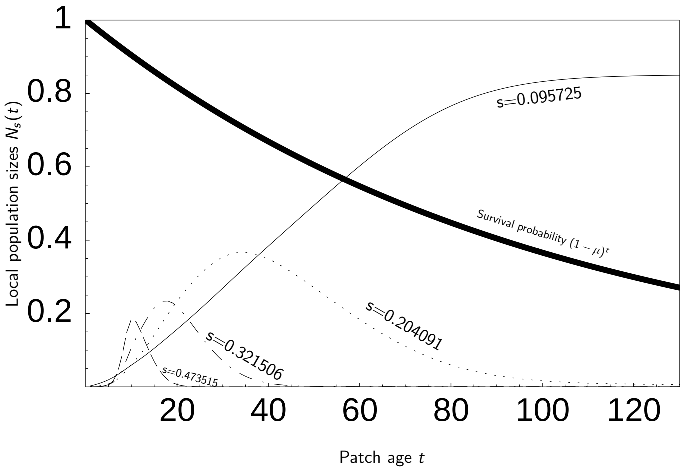
Kalle Parvinen

- Coexistence by disturbation?
- Metapopulation with local catastrophes.
- Explicit population dynamics in the patches.
- AD origin of successional types.

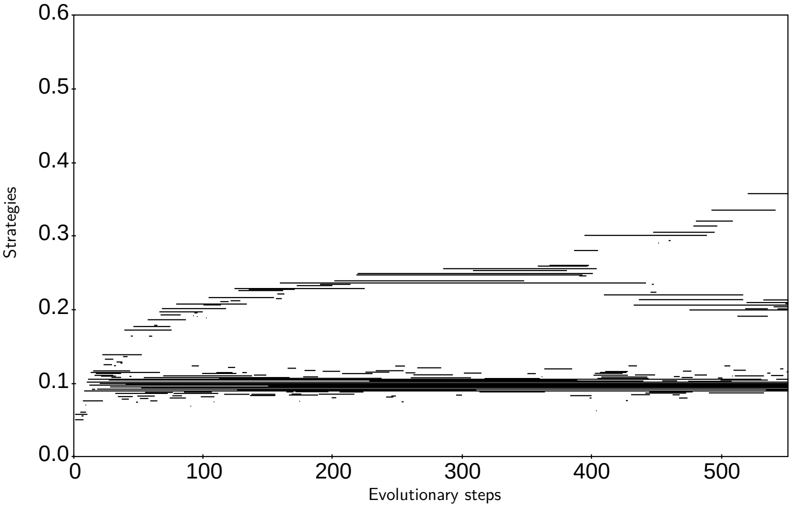
Trade-off between fecundity and local competitivity



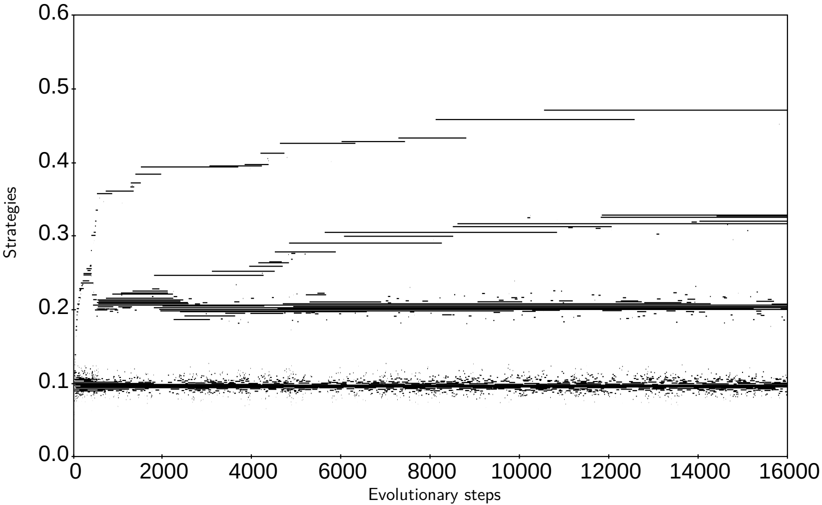
Species succession within a patch



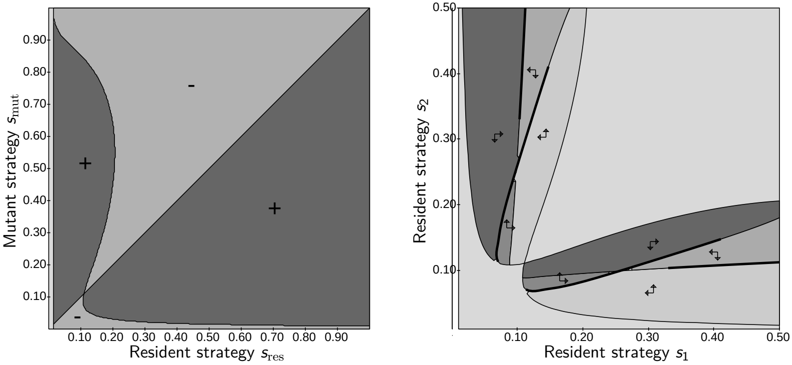
Evolutionary branchings



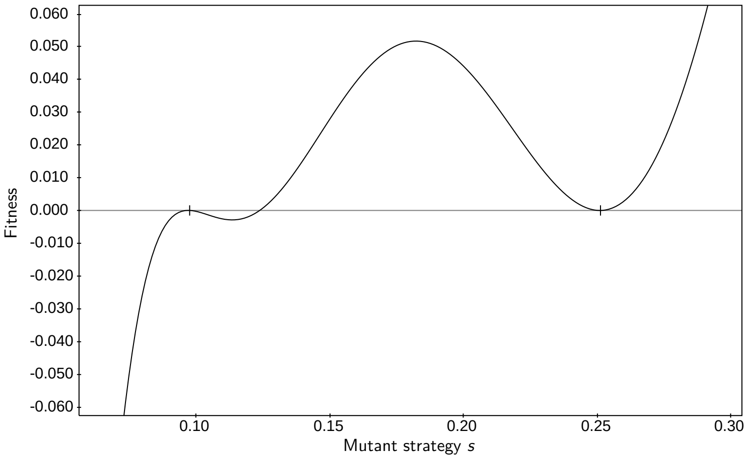
Evolution, longer time-scale



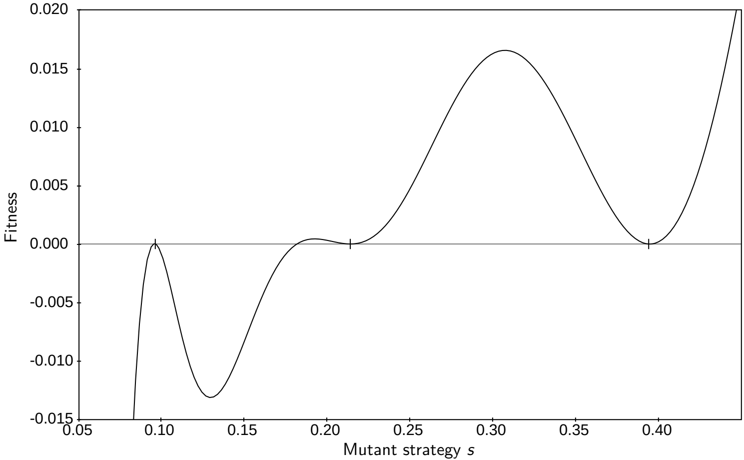
Pairwise invasibiliy



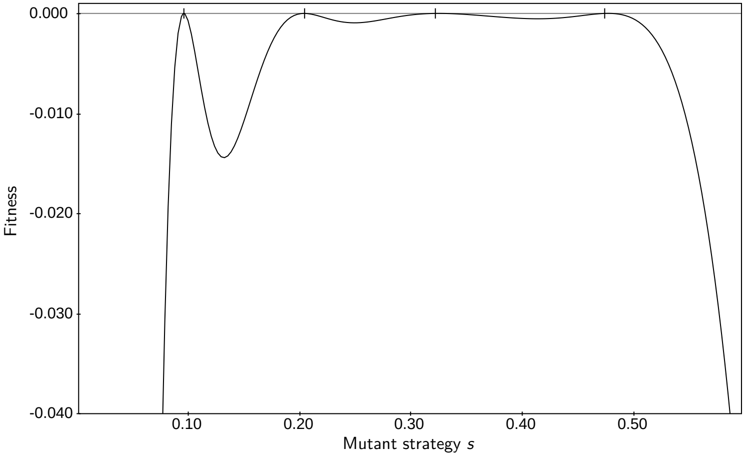
Fitness with dimporphic resident



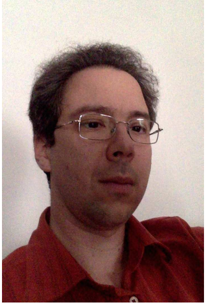
Trimporphic resident



Four residents



Effect of relative nonlinearity



András Szilágyi

- Minimal model for fluctuation-mediated coexistence!
- Linear models average out!
- Let us see a qudratic one!

Model

Population dynamics affected by a white noise $\xi(t)$:

$$\frac{\mathrm{d}}{\mathrm{d}t}n_i(t) = \overbrace{\left[\sigma_i\xi(t) - a_i(n(t) - K_i) - b_i(n(t) - K_i)^2\right]}^{r_i(t)} n_i(t),$$

$(n = \sum_i n_i)$

Averaged equation

Average it out!

$$\overline{r}_i = -a_i(\overline{n} - K_i) - b_i\overline{(n - K_i)^2} + \sigma_i\overline{\xi} = -a_i(\overline{n} - K_i) - b_i(\overline{n} - K_i)^2 - b_i V$$

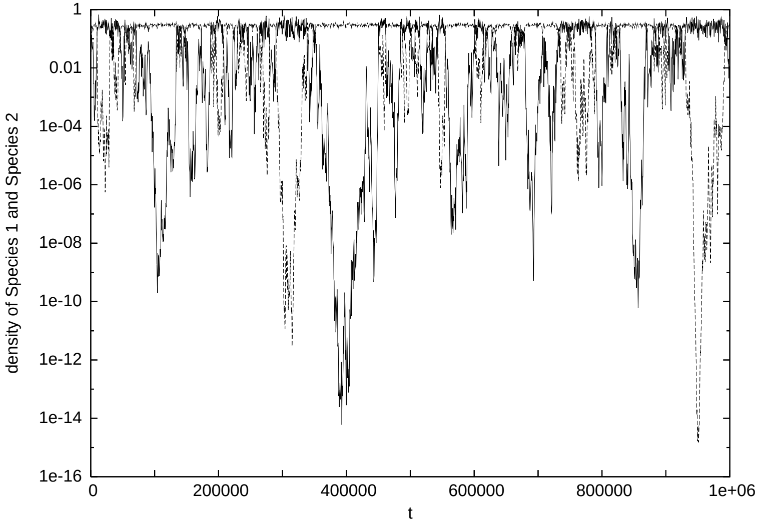
We have two regulating variables:

- average $\overline{n}$ of n
- variance V of n

At most two species can coexist!

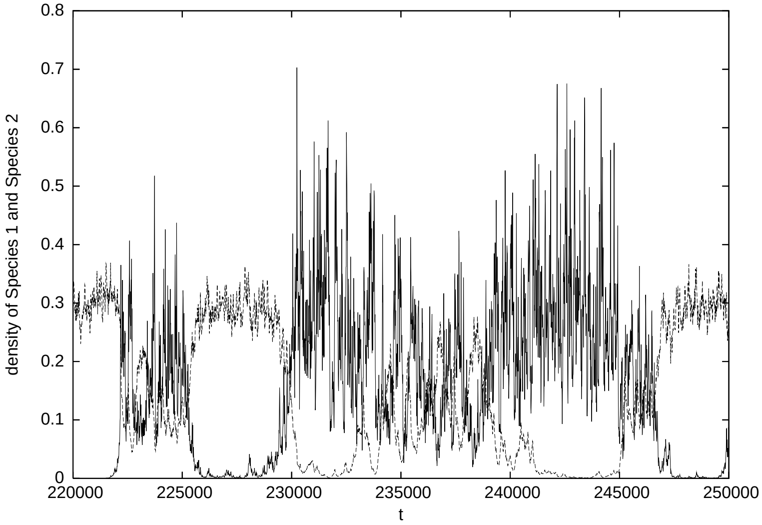
But it was extreemly hard to see it in simulation...

Time series



Non realistic population sizes!

Time series, different scale



The REAL danger for extinction

Mean time to extinction in constant environment:

$$\mathrm{MTE} = C_1 e^{bK} \sim \infty$$

(Hamza, Jagers & Klebaner, 2015); same for fluctuating environment:

$$\mathrm{MTE} = C_2 K^c \ll \infty.$$

(Ovaskainen & Meerson, 2010); exact theory?

Environmental & demographic stochasticity together is dangerous!

Take home

- Species have to adapt to *something*!
- They find their own constancy in the uncertain world.
- Coexisting species must differ in their way of regulation!
- There are no such things, as “equilibrium” vs. “fluctuating” ecology.
- Don’t forget the unsolved issues...

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Thanks for the coworkers!

- György Barabás (University of Linköping)
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- Éva Kisdi (University of Helsinki)
- Hans Metz (University of Leiden)
- Kalle Parvinen (University of Turku)
- Liz Pásztor (Eötvös University, Budapest)
- András Szilágyi (Eötvös University,Budapest)

Thanks for your attention!