Niche theory for a complicated world

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Outline

1. Intro: ecology vs. evolution
2. Niche theory
Population regulation – robust coexistence

Long-term equilibrium:

\[ r_i (\mathcal{E}, \mathcal{R}(n_1, n_2, \ldots, n_L)) = 0 \]

Effect of perturbation:

\[ \frac{dn}{d\mathcal{E}} = - \left( \frac{\partial r}{\partial n} \right)^{-1} \cdot \frac{\partial r}{\partial \mathcal{E}} = - \frac{M}{\det \left( \frac{\partial r_i}{\partial n_j} \right)} \cdot \frac{\partial r}{\partial \mathcal{E}} \]

Strength of regulation:

\[ J = \det \left( \frac{\partial r_i}{\partial n_j} \right) = \det \left( \frac{\partial r_i}{\partial \mathcal{R}} \cdot \frac{\partial \mathcal{R}}{\partial n_j} \right) \]

Strength of competition:

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Sensitivity niche vector:
Impact niche vector:

Strength of regulation expressed in terms of niches:

\[ |J| \leq \mathcal{V}_S \cdot \mathcal{V}_I \]

Volumes of parallelepipeds:

\[ \mathcal{V}_S = |S_1 \wedge S_2 \wedge \cdots \wedge S_L| \]
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Robust coexistence requires segregation in \( I \) and \( S \) – niche segregation.
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Similar \( I \) or \( S \) vectors
\[ \Rightarrow \text{small } V_I \text{ or } V_S \]
\[ \Rightarrow \text{small } |J| \]
\[ \Rightarrow \text{weak regulation} \]
\[ \Rightarrow \text{high sensitivity} \]
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What is niche space?

Niche space $\equiv$ set of regulating factors

Niche of a species $\equiv (I, S)$ (cf. resource utilisation function)

The niche space can be
- discrete
- continuous.

Niche segregation can be
- functional (local),
- habitat (spatial),
- temporal.

(Hutchinson, 1978)
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Ways of niche segregation

Niche space

Discrete

- warm patch
- cold patch

Continuous

- small food
- large food

4 elements ← Niche space → 2D continuum
Complications abound

What about

- population structure?
- spatial structure?
- environmental structure?
- individual locality? — Let us leave something for the future!
Chemostate principle

Controlled dilution (death) rate – everything relax to this rate!
Spatial niche segregation (Szilágyi & Meszéna, 2009)

Two regulating variables: total densities in the patches.
General structured population
(Szilágyi & Meszána, 2009; Barabás et al. in press)

\[
\frac{dn_i}{dE} = - \sum_{j=1}^{S} \left[ \sum_{\mu,\nu} \left(v_i \frac{\partial A_i}{\partial R_\mu} w_i\right) \left(\delta_{\mu\nu} - \frac{\partial G_\mu}{\partial R_\nu}\right)^{-1} \frac{\partial R_\nu}{\partial N_j} p_j \right]^{-1}
\]

\[
\times \left[ v_j \frac{\partial A_j}{\partial E} w_j + \sum_{\sigma,\varrho} \left(v_j \frac{\partial A_j}{\partial R_\sigma} w_j\right) \left(\delta_{\sigma\varrho} - \frac{\partial G_\sigma}{\partial R_\varrho}\right)^{-1} \frac{\partial G_\varrho}{\partial E}\right]
\]

where \( n_i = q_i \cdot N_i \) is total population size with weight vector \( q_i \) and

\[
G_\mu(R_\nu, E) = \sum_{j=1}^{S} \left[ \frac{n_j}{q_j w_j} \frac{\partial R_\mu}{\partial n_j} \sum_{k=2}^{s_j} \frac{1}{\lambda_j - \lambda_j^k} \left(w_j^k - \frac{q_j w_j^k}{q_j w_j} w_j\right) \otimes v_j^k \right]
\]

\[
\times A_j(R_\nu, E) w_j.
\]
Temporal niche segregation (Barabás & Meszéna, 2011)

Extension to cyclic (fluctuating) environment.

(Cyclic) time becomes niche axis.
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Periodic environment (Barabás et al., 2012)

\[
\frac{dn_i(0)}{d\mathcal{E}} = -n_i(0) \sum_{j=1}^{S} \left( \mathcal{T} \text{Exp} \left( \int_{0}^{T} \sum_{\mu} \frac{\partial r_i(\tau)}{\partial R_{\mu}(\tau)} \frac{\partial R_{\mu}(\tau)}{\partial n_j(\tau)} n_j(\tau) \, d\tau \right) - \delta_{ij} \right)^{-1} \\
\times \int_{0}^{T} \frac{\partial r_j(t)}{\partial \mathcal{E}} \, dt
\]

(\mathcal{T}: \text{time ordering})
Successional niche segregation

Structured metapopulation:
local population size has a dynamics also!
Random local catastrophes with rate $\mu$.

Strategy: $s$
Trade-off:
Competitivity: $K(s) = (1 - s)^{1/\beta}$
Fecundity: $f_0(s) = 1 + \gamma s^{1/\beta}$

Density dependent fecundity:

$$f \left( s, \sum N \right) = f_0(s) \exp \left( -\frac{\sum N}{K(s)} \ln f_0(s) \right)$$

Parvinen & Meszéna, EER 2009
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Local succession

Regulating variable: local density – for all patch ages.
Niche axis: patch age.
Gross (2008) model of facilitation (Barabás et al., submitted)

\[
\frac{1}{N_1} \frac{dN_1}{dt} = f_1(R_1) - m_1^0, \\
\frac{1}{N_i} \frac{dN_i}{dt} = f_i(R_1) - m_i^0 + d_i R_i \quad (i = 2 \ldots S), \\
\frac{dR_1}{dt} = g(R_1) - \sum_{i=1}^{S} c_i f_i(R_1) N_i, \\
R_\mu = 1 - \exp \left( -\theta \sum_{k<\mu} N_k \right) \quad (\mu = 2 \ldots S).
\]

With \( S \to \infty \), each new species contributes a new regulating variable!

Unlimited coexistence? NO!
After some work:

\[
\sqrt{S} V_S V_I \sim \exp \left( -\frac{\theta N}{2} S \right) \to 0 \quad \text{with } S \to \infty
\]
Continuous coexistence: Lotka-Volterra

Continuous niche variable: $x$

Population dynamics:

$$\frac{dn_i}{dt} = r_i n_i = \left[ r_0(x_i) - \sum_i a(x_i, x_j) n_j \right] n_i$$

$$r_0(x) = e^{-\frac{x^2}{2\omega^2}}$$

Gaussian carrying capacity

$$a(x_i, x_j) = e^{-\frac{(x_i - x_j)^2}{2\sigma^2}}$$

Gaussian competition kernel.

$$n(x) = \frac{\omega/\sigma}{\sqrt{2\pi(\omega^2 - \sigma^2)}} e^{-\frac{x^2}{2(\omega^2 - \sigma^2)}}$$

Continuous coexistence.
Structural instability of continuous coexistence

Lotka-Volterra:

(Szabó & Meszéna, Oikos, 2006)
Structural instability of continuous coexistence: General

Theorems by Mats:

- Compactness of the operator of regulation: coexistence of infinitely many fixed types is structurally unstable.
- + analicity in 1D: the possibility of a coexistence with limit point is structurally unstable

(Mészéna & Gyllenberg, JMB, 2005; Barabás et al., 2012, EER)
Neutral mutations are common, theory of neutral evolution is a success. Why don’t we just assume, that species coexistence is neutral?

Wait!

Neutral mutants are phenotypically inconsequential! There are serious biochemical reasons to have many inconsequential (neutral) mutants.

YES, species coexistence is neutral, if they are physiologically identical! Otherwise? It is extremely unlikely.

Neutrality by trade-offs? Requires a very specific, trade-off curve! (Purves & Turnbull, 2010)
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Niche-neutrality continuum?

No!

Non-generic niche-neutrality continuum at a singular point
⇒ evolutionary branching!
Niche-neutrality continuum?

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Non-generic niche-neutrality continuum at a singular point \( \Rightarrow \) evolutionary branching!
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Niche-neutrality continuum?

No!

Non-generic niche-neutrality continuum at a singular point => evolutionary branching!
Scheffer & Nes: Self-organized similarity (PNAS 2006)

No degeneracies $\Rightarrow$ No coexistence of similars at $t = \infty$!
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Niches within niches

Simulation by Gyuri Barabás.
Conclusion

- General mathematical theory of niche has been developed.
- Niche segregation is identified with the segregation in the ways of population regulation.
- Generalisations for structured populations and spatio-temporal heterogeneity are available.
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Deep & clean mathematics is the route for deep biological understanding.
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Thanks for your attention!