On the consequences of the interdependence of stabilizing and equalizing mechanisms

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January 7th, 2020
Modern Coexistence Theory in a nutshell
Modern Coexistence Theory in a nutshell:
Disentangling ecological differences

Differences in niche:
Which seeds to eat

Differences in fitness:
How good at eating a seed

Stabilizing mechanism
Equalizing mechanism
Modern Coexistence Theory in a nutshell:
Coexistence as a balance of niche overlap and fitness ratio

![Graph showing the relationship between niche overlap and fitness ratio, with regions for Coexistence, Exclusion, and Neutrality.](image)
Premise 1
Disentangle the relative roles of the stabilizing and equalizing mechanisms in shaping species coexistence

Premise 2
Provide a continuum of niche-neutrality continuum for species coexistence
Q1: What do we mean when we talk about stabilizing and equalizing mechanisms?
Two parallel sub-frameworks within Modern Coexistence Theory

**Two-species framework**

A niche for neutrality

Peter B. Adler, Janneke HilleRisLambers, Jonathan M. Levine

The importance of niches for the maintenance of species diversity

Jonathan M. Levine & Janneke HilleRisLambers

**Multi-species framework**

Chesson's coexistence theory

György Barabás, Rafael D'Andrea, Simon Maccracken Stump

Mean growth rate when rare is not a reliable metric for persistence of species

Jayant Pande, Tak Fung, Ryan Chisholm, Nadav M. Shnerb

Linking modern coexistence theory and contemporary niche theory

Andrew D. Letten, Po-Ju Ke, Tadashi Fukami

An expanded modern coexistence theory for empirical applications

Stephen P. Ellner, Robin E. Snyder, Peter B. Adler, Giles Hooker
The definitions of stabilizing and equalizing mechanisms in the two sub-frameworks

**Two-species framework**

Dynamics: \( \frac{1}{N_i} \frac{dN_i}{dt} = r_i \left( 1 - \sum_{j=1}^{2} a_{ij}N_j \right) \) \((i = 1, 2)\)

Stabilizing: \( 1 - \rho := 1 - \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}} \)

Equalizing: \( \frac{\kappa_1}{\kappa_2} := \sqrt{\frac{a_{21}a_{22}}{a_{12}a_{11}}} \)

**Multi-species framework**

Dynamics: \( \frac{1}{N_i} \frac{dN_i}{dt} = f_i(E_i, C_i) \) \((i = 1, \ldots, S)\)

Stabilizing: \( A := \frac{1}{S} \sum_{i=1}^{S} \frac{R_i}{\phi_i} \)

Equalizing: \( \begin{align*}
\frac{\xi_i}{\xi_j} &:= \frac{R_i}{\phi_i} - A \\
&= \frac{R_j}{\phi_j} - A
\end{align*} \)
Stabilizing and equalizing mechanisms are incompatible in the two-species and multispecies frameworks.

Fitness ratio in two-species framework

\[ \frac{\kappa_1}{\kappa_2} := \sqrt{\frac{a_{21}a_{22}}{a_{12}a_{11}}} \geq 0 \]

Fitness ratio in multispecies framework

\[ \frac{\xi_i}{\xi_j} := \frac{R_i/\phi_i - A}{R_j/\phi_j - A} = -1 \]

Scaled invasion rate of species 1

\[ \frac{\mathcal{R}_1}{\phi_1} \]

Scaled invasion rate of species 2

\[ \frac{\mathcal{R}_2}{\phi_2} \]

Fitness of species 1

\[ \xi_1 \]

Fitness of species 2

\[ \xi_2 \]

Scaled invasion rate

\[ \frac{1}{2} \left( \frac{\mathcal{R}_1}{\phi_1} + \frac{\mathcal{R}_2}{\phi_2} \right) \]
Q2: Can we disentangle the relative contributions of stabilizing and equalizing mechanisms?
MacArthur’s consumer-resource model as an example

Niche overlap

\[ \rho = \sqrt{\frac{a_{12}a_{21}}{a_{11}a_{22}}} = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}} \]

Fitness ratio

\[ \frac{\kappa_1}{\kappa_2} = \sqrt{\frac{a_{21}a_{22}}{a_{12}a_{11}}} = e^{-\frac{\mu_1^2 - \mu_2^2}{2(\sigma^2 + 1)}} \]
The effect of stabilizing/equalizing mechanism changes sensitively

\[ \frac{\kappa_1}{\kappa_2} = e^{-\frac{\mu_1^2 - \mu_2^2}{2(\sigma^2 + 1)}} \]

Niche overlap \( \rho = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}} \)
No simple or single pattern of the interdependence

\[
\frac{\kappa_1}{\kappa_2} = e^{-\frac{(\mu_1^2 - \mu_2^2)}{2(\sigma^2 + 1)}}
\]

\[
\rho = e^{-\frac{(\mu_1 - \mu_2)^2}{4\sigma^2}}
\]
Relative contribution of each mechanism is not necessarily indicative of how the two species coexist, unless we know the governing mechanistic model.
Q3: Do stabilizing and equalizing mechanisms provide a niche-neutrality continuum?
Breakdown of the niche-neutrality continuum

\[ \Delta \mu = |\mu_1 - \mu_2| > \frac{4|\mu_1|\sigma^2}{\sigma^2 + 1} \]
Interdependency leads to the breakdown of niche-neutrality continuum

phenomenologically **connected**
coexistence region

mechanistically **disconnected**
coexistence region

Cause: Interdependence
Proof of the generality of the breakdown

When trait change occurs in two originally identical species

\[
\frac{\kappa_1}{\kappa_2} \approx 1 + p \Delta \mu \\
\rho \approx 1 - q \Delta \mu^2 \quad \Rightarrow \quad \Delta \mu \gtrsim \frac{p}{q} \\
\rho < \frac{\kappa_1}{\kappa_2} < \frac{1}{\rho}
\]
Take-home message

• Q1: What do we mean when we talk about stabilizing and equalizing mechanisms?
• A1: Stabilizing mechanisms and equalizing mechanisms have two distinct sets of meanings within Modern Coexistence Theory
• Q2: Can we disentangle the relative contributions of stabilizing and equalizing mechanisms?
• A2: Complex interdependency makes it difficult unless we know the governing mechanistic model with parameters.
• Q3: Do stabilizing and equalizing mechanisms provide a niche-neutrality continuum?
• A3: Interdependency break this continuum under almost any biologically relevant circumstance.
Acknowledgement