A mathematical perspective of community ecology

Priyanga Amarasekare
Department of Ecology and Evolutionary Biology
University of California Los Angeles
Mechanisms that maintain diversity

Diversity: Species coexistence

Coexistence: Non-linear * Environmental dynamics     heterogeneity
           (density-dependence)     (temporal, spatial)
Coexistence mechanisms

1. Non-linearity:
   negative feedback
   (negative density-dependence)

2. Heterogeneity
   (Jensen’s inequality)
Jensen’s Inequality

\[ f(\overline{x}) \neq \overline{f(x)} \]
Sources of non-linearity and heterogeneity

Non-linearity: resources, natural enemies
(Species interactions)

Heterogeneity: spatial/temporal variation in biotic/abiotic environment
Sources of non-linearity

Species interactions:

- Exploitative competition (-/-)
- Apparent competition (-/-)
- Mutualism (+/+)
- Consumer-resource (+/-)
Exploitative competition

Indirect interactions between individuals (of the same or different species) as the result of acquiring a resource that is in limiting supply.

Each individual affects others solely by reducing abundance of shared resource.
Exploitative competition

Consumer 1 → Resource → Consumer 2

Resource
Exploitative competition

\[
\frac{dR}{dt} = R \left( r \left( 1 - \frac{R}{K} \right) - a_1 C_1 - a_2 C_2 \right)
\]

\[
\frac{dC_1}{dt} = C_1 \left( e_1 a_1 R - d_1 \right)
\]

\[
\frac{dC_2}{dt} = C_2 \left( e_2 a_2 R - d_2 \right)
\]
Coexistence:

**Mutual invasibility:** each species must be able to increase when rare

**Stability:** coexistence equilibrium stable to perturbations
Exploitative competition

\[ R^*_C \frac{d_i}{e_ia_i} \quad (i, j = 1, 2; i \neq j) \]

Invasion criteria:

\[
\frac{d_1}{e_1a_1} < \frac{d_2}{e_2a_2} \\
\frac{d_2}{e_2a_2} < \frac{d_1}{e_1a_1}
\]

**R* rule**: consumer species that drives resource abundance to the lowest level will exclude others
Exploitative competition

In a constant environment, $R^*$ rule operates and the superior competitor excludes inferior competitors.

Coexistence not possible in the absence of other factors.
Sources of non-linearity

Species interactions:

Exploitative competition (-/-) ✓
Apparent competition (-/-)
Mutualism (+/+)
Resource-consumer (-/+)
Apparent competition

Indirect interactions between individuals that share a common natural enemy.

Each individual affects others solely by changing the abundance of shared enemy.
Apparent competition

Predator/parasite

Prey species 1

Prey species 2
Apparent competition

\[
\frac{dC_1}{dt} = C_1 \left( r_1 - a_1 P \right)
\]

\[
\frac{dC_2}{dt} = C_2 \left( r_2 - a_2 P \right)
\]

\[
\frac{dP}{dt} = P \left( e_1 a_1 C_1 - e_2 a_2 C_2 - d \right)
\]
Apparent competition

\[ P^* C_i = \frac{r_i}{a_i} \quad (i, j = 1, 2; i \neq j) \]

Invasion criteria:

\[ \frac{r_1}{a_1} > \frac{r_2}{a_2} \quad \text{Consumer 1} \]

\[ \frac{r_2}{a_2} > \frac{r_1}{a_1} \quad \text{Consumer 2} \]

**P* rule**: consumer species that can withstand the highest natural enemy pressure will exclude others
Apparent competition

In a constant environment, $P^*$ rule operates and the prey species that is least susceptible to predator excludes all others.

Coexistence not possible in the absence of other factors.
Exploitative and apparent competition

Per capita growth rate independent of species’ density (no negative feedback)

\[
\frac{dC_i}{dt} \frac{1}{C_i} = e_i a_i R - d_i
\]

No negative feedback \(\implies\) Loss of diversity
Coexistence:

Non-linearity
  (Negative feedback)

Heterogeneity
  (Jensen’s inequality)
Mechanisms of coexistence

Coexistence via non-linearity alone
(local niche partitioning)

Coexistence via interplay between non-linearity and heterogeneity
(spatial and temporal niche partitioning)
Coexistence via non-linearity alone

1. Inter-specific trade-offs ($R^*, P^*$)

2. Relative non-linearity (e.g., non-linear functional responses)

Negative feedback: local niche partitioning $\Rightarrow$

Intra-specific $>$ inter-specific
Coexistence via non-linearity: trade-offs

Predation/parasitism

Consumer 1 (IGPrey) → Consumer 2 (IGPredator)

Competition

Resource

Intraguild predation
Intraguild predation

\[ \frac{dR}{dt} = rR \left(1 - \frac{R}{K}\right) - a_1 RC_1 - a_2 RC_2 \]

\[ \frac{dC_1}{dt} = e_1 a_1 RC_1 - d_1 C_1 - \alpha C_1 C_2 \]

\[ \frac{dC_2}{dt} = e_2 a_2 RC_2 - d_2 C_2 + f \alpha C_1 C_2 \]
Intraguild predation

Non-dimensionalize model:

\[
\hat{R} = \frac{R}{K} \quad \hat{C}_i = \frac{C_i}{e_i K} \quad \hat{\alpha} = \frac{\alpha e_2 K}{r} \\
\hat{d}_i = \frac{d_i}{r} \quad (i, j = 1, 2, i \neq j) \\
\tau = r t \\
\hat{a}_i = \frac{a_i e_i K}{r} \\
\hat{f} = \frac{e_2 f}{e_1}
\]
Intraguild predation: non-dimensionalized model

\[
\frac{dR}{d\tau} = R(1 - R) - a_1 RC_1 - a_2 RC_2
\]

\[
\frac{dC_1}{d\tau} = a_1 RC_1 - d_1 C_1 - \alpha C_1 C_2
\]

\[
\frac{dC_2}{d\tau} = a_2 RC_2 - d_2 C_2 - f\alpha C_1 C_2
\]
Coexistence:

**Mutual invasibility**: each species must be able to increase when rare

**Stability**: coexistence equilibrium stable to perturbations
Mutual invasibility: invasion criteria

Invasion criteria: dominant eigenvalue of Jacobian matrix evaluated at boundary equilibrium
Computing invasion criteria

Jacobian matrix for the three species community:

\[
\begin{bmatrix}
1 - 2R^* - a_1 C_1^* - a_2 C_2^* & -a_1 R^* & -a_2 R^* \\
 a_1 C_1^* & a_1 R^* - d_1 - \alpha C_2^* & -C_1^* \alpha \\
 a_2 C_2^* & C_2^* f \alpha & a_2 R^* - d_2 + f \alpha C_1^*
\end{bmatrix}
\]

Evaluate Jacobian at boundary equilibrium
Boundary equilibria

Resource and Consumer 1 (IGPrey):

\[ R^* = \frac{d_1}{e_1}, \quad C_1^* = \frac{a_1 - d_1}{a_1^2}, \quad C_2^* = 0 \]

Resource and Consumer 2 (IGPredator):

\[ R^* = \frac{d_2}{e_2}, \quad C_1^* = 0, \quad C_2^* = \frac{a_2 - d_2}{a_2^2} \]
Computing invasion criteria

Jacobian evaluated at boundary equilibrium with Resource and Consumer 1:

\[
\begin{bmatrix}
-\frac{d_1}{a_1} & -d_1 & -a_2 \frac{d_1}{a_1} \\
1 - \frac{d_1}{a_1} & 0 & -\frac{(a_1-d_1)\alpha}{a_1^2} \\
0 & 0 & a_2 \frac{d_1}{a_1} - d_2 - \frac{(a_1-d_1)\alpha}{a_1^2}
\end{bmatrix}
\]

Dominant eigenvalue of Jacobian: invasion criterion for Consumer 2
Mutual invasibility criteria

Invasion criterion for IGPrey:

\[ a_2(a_1d_2 - a_2d_1) - (a_2 - d_2)\alpha > 0 \]

Invasion criterion for IGPredator:

\[ a_1(a_2d_1 - a_1d_2) + (a_1 - d_1)f\alpha > 0 \]
Mutual invasibility

Recall: \[ R_{C_1}^* = \frac{d_1}{a_1}, \quad R_{C_2}^* = \frac{d_2}{a_2} \]

Consider IGPrey to be the superior resource competitor.

Then,

\[ R_{C_1}^* < R_{C_2}^* < 1 \]

\[ \Rightarrow \frac{d_1}{a_1} < \frac{d_2}{a_2} < 1 \]

\[ \Rightarrow a_1 d_2 > a_2 d_2, \quad a_2 > d_2 \]
Mutual invasibility criteria

Invasion criterion for IGPrey:

\[ a_2(a_1 d_2 - a_2 d_1) - (a_2 - d_2)\alpha > 0 \]

Invasion criterion for IGPredator:

\[ a_1(a_2 d_1 - a_1 d_2) + (a_1 - d_1)f\alpha > 0 \]
Mutual invasibility

Then IGPrey can invade when rare if:

\[ a_2(a_1d_2 - a_2d_1) > (a_2 - d_2)\alpha \]

Resource competition  Intraguild predation

IGPredator can invade when rare if:

\[ (a_1 - d_1)f\alpha > a_1(a_2d_1 - a_1d_2) \]

Intraguild predation  Resource competition
Coexistence:

**Mutual invasibility**: each species must be able to increase when rare ✓

**Stability**: coexistence equilibrium stable to perturbations ?
Coexistence equilibrium

\[ R^* = \frac{fa_2d_1 - f\alpha - a_1d_2}{a_1a_2(f - 1) + f\alpha} \]

\[ C_1^* = \frac{a_2(a_1d_2 - a_2d_1) - \alpha(a_2 - d_2)}{\alpha(a_1a_2(f - 1) + f\alpha)} \]

\[ C_2^* = \frac{a_1(a_2d_1 - a_1d_2) + f\alpha(a_1 - d_1)}{\alpha(a_1a_2(f - 1) + f\alpha)} \]
Stability of coexistence equilibrium

Jacobian matrix for the three species community:

\[
\begin{bmatrix}
1 - 2R^* - a_1 C_1^* - a_2 C_2^* & -a_1 R^* & -a_2 R^* \\
a_1 C_1^* & 0 & -C_1^* \alpha \\
a_2 C_2^* & C_2^* f \alpha & 0
\end{bmatrix}
\]
Stability of coexistence equilibrium

Eigenvalues of the Jacobian are the roots of the characteristic equation:

\[ \lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0 \]

where

\[ A_1 = R^*, \]
\[ A_2 = R^*(a_1^2 C_1^* + a_2^2 C_2^*) + C_1^* C_2^* f \alpha^2, \]
\[ A_3 = -R^* C_1^* C_2^* \left( a_1 a_2 \alpha (1 - f) - f \alpha^2 \right). \]
Stability of coexistence equilibrium

Routh-Hurwitz criteria for the stability of the coexistence equilibrium:

\[ A_1 > 0, \ A_3 > 0 \text{ and } A_1 A_2 - A_3 > 0. \]

\[ A_1 = R^* > 0, \]

\[ A_3 > 0 \text{ if } a_1 a_2 \alpha(1 - f) - f \alpha^2 < 0 \]

\[ A_1 A_2 - A_3 > 0 \text{ if } \]

\[ R^* + \frac{a_1 a_2 C_1^* C_2^*}{a_1^2 C_1^* + a_2^2 C_2^*} \alpha(1 - f) > 0 \]
Stability of coexistence equilibrium

Consumer 1 (IGPrey) is superior at resource competition (high $a_1$, low $d_1$)

Consumer 2 (IGPredator) gains sufficient benefit from preying on Consumer 1 (high $\alpha$ and $f$)

Stability $\iff$ inter-specific trade-off
Coexistence via non-linearity: trade-offs

Intraguild predation

Consumer 1 (IGPrey) \[\longrightarrow\] Consumer 2 (IGPredator) \[\text{competition}\]

Resource

Intraguild predation

predation/parasitism
Coexistence via non-linearity: trade-offs

Interactions with competition and predation: intraguild predation

Coexistence: negative feedback via inter-specific trade-off

IGPrey is superior competitor for basal resource, IGPredator can consume IGPrey (local niche partitioning)
Coexistence via local non-linearity alone

1. Inter-specific trade-offs \((R^*, P^*)\)

2. Relative non-linearity (e.g., non-linear functional responses)
Coexistence via relative non-linearity

Consumer 1 ↔ Consumer 2

competition

Resource

Exploitative competition
Exploitative competition

\[
\frac{dR}{dt} = R \left( r \left( 1 - \frac{R}{K} \right) - a_1 C_1 - a_2 C_2 \right)
\]

\[
\frac{dC_1}{dt} = C_1 \left( e_1 a_1 R - d_1 \right)
\]

\[
\frac{dC_2}{dt} = C_2 \left( e_2 a_2 R - d_2 \right)
\]

Linear functional responses

**R* rule:** consumer species that drives resource abundance to the lowest level will exclude others
Exploitative competition with non-linear functional responses

\[
\frac{dR}{dt} = rR \left(1 - \frac{R}{K}\right) - \frac{a_1 RC_1}{1 + a_1 T_{h_1} R} - \frac{a_2 RC_2}{1 + a_2 T_{h_2} R}
\]

\[
\frac{dC_1}{dt} = e_1 \frac{a_1 RC_1}{1 + a_1 T_{h_1} R} - d_1 C_1
\]

\[
\frac{dC_2}{dt} = e_2 \frac{a_2 RC_2}{1 + a_2 T_{h_2} R} - d_2 C_2
\]
Non-linear functional responses

Higher attack rate and longer handling time

==> more non-linear functional response
Coexistence via non-linear functional responses

Consumer with more non-linear functional response generates fluctuations in resource abundance

Armstrong and McGehee 1980
Coexistence via relative non-linearity

Consumer with the more non-linear functional response generates fluctuations in resource abundance

If average resource abundance is greater than $R^*$ of the consumer with the less non-linear functional response, it can invade when rare

Coexistence: resource partitioning
Coexistence via non-linearity alone

1. Inter-specific trade-offs ✓
   (competition and predation)

2. Relative non-linearity in functional responses ✓
Mechanisms of coexistence

Coexistence via non-linearity alone ✓
(local niche partitioning)

Coexistence via interplay between non-linearity and heterogeneity
(spatial and temporal niche partitioning)