Non-linearity, variability and diversity: an integrative perspective

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Elucidate mechanisms from first principles

Generate predictions that can be tested with data
Non-linearity * Variability $\rightarrow$ Diversity
Non-linearity

Biotic factors --> density/frequency dependence in fitness (per capita growth rate)
Variability

Abiotic factors --> spatial/temporal variation in density/frequency dependent fitness
Non-linearity * Variability -->
Large-scale diversity patterns
Mechanistic underpinnings of interplay between non-linearity and variability
Mechanistic approach

Explain patterns

Predict changes due to perturbations
Conceptual underpinnings for environmental problems

Conservation

Invasive species

Climate warming
1. Non-linearity in the absence of variability
2. Interplay between non-linearity and variability
   - Spatial
   - Temporal
1. Non-linear dynamics in the absence of variability

Non-linearity: fundamental driver of dynamics and diversity
Non-linearity: negative/positive feedback

Feedback mechanisms: frequency-density-dependence
Negative density-dependence

Process underlying stable coexistence

Enables species to increase when rare and to decrease when they are abundant

Same principle as thermostat

Leads to attractors (coexistence equilibria)
Formal definition of density-dependence

Per capita growth rate is an increasing/decreasing function of density

\[ \frac{dN}{dt} = N f(N) \]

\[ \frac{dN}{dt} \frac{1}{N} = f(N) \]
Density-independent population growth
Consider the exponential model for population growth

\[
\frac{dN}{dt} = rN
\]

\[
\frac{dN}{dt} \frac{1}{N} = r
\]

Per capita growth rate is independent of density.
Now consider the logistic model for population growth

\[ \frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \]  \hspace{1cm} (1)

\[ \frac{dN}{dt} \frac{1}{N} = r \left(1 - \frac{N}{K}\right) \]  \hspace{1cm} (2)

Per capita growth rate is a decreasing function of density.
Negative density-dependence

Self-limitation (intra-specific competition for limiting resources)
Positive density-dependence

Per capita growth rate is an increasing function of density

Allee effects (single species, mutualistic interactions)

Type II (saturating) functional responses
Type II functional response

Handling time \((h)\) --> saturation of functional response
==> Resource underexploited when abundant
==> positive feedback in resource per capita growth rate

\[
f(R) = \frac{aR}{1 + ahR}
\]
Pairwise consumer-resource interaction

\[
\frac{dR}{dt} = rR\left(1 - qR\right) - \frac{aRC}{1 + ahR}
\]

\[
\frac{dC}{dt} = e\frac{aRC}{1 + ahR} - dC
\]

Self-limitation in resource \((q)\), saturating functional response in consumer \((h)\)
Consumer’s handling time ==> positive feedback in resource per capita growth rate

No self-limitation in resource

\[
\frac{dR}{dt} \frac{1}{R} = r - \frac{aC}{1 + ahR}
\]
Self-limitation in resource

\[ \frac{dR}{dt} \frac{1}{R} = r\left(1 - qR\right) - \frac{aC}{1 + ahR} \]

- \( R^* < R_c \Rightarrow \) limit cycle oscillations
- \( R^* > R_c \Rightarrow \) stable focus

Sustained oscillations: consumer handling time and resource self-limitation
Non-linearity

Negative density-dependence (self-limitation)

Positive density-dependence (saturating functional responses)
Mechanisms underlying non-linearity

Feedback processes arising from species interactions
Resources

Negative density-dependence (self-limitation)

Natural enemies

Positive density-dependence (saturating functional responses)
Goal

Elucidate mechanisms by which non-linearities in species interactions influence diversity
Diversity is an outcome and not a process, coexistence is the mechanism underlying diversity.
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 negatively affects others solely by reducing abundance of shared resource.
Exploitative competition

Consumer 1

Resource

Consumer 2
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 when the other species is at equilibrium with the resource

**Stability**: coexistence equilibrium stable to perturbations
Computing invasion criteria

Consumer species $i$ can invade when rare if it can maintain a positive per capita growth rate when consumer species $j$ is at equilibrium with the resource.

Consumer $j$ is at equilibrium with the resource when

$$\frac{dC_j}{dt} \frac{1}{C_i} = e_j a_j R - d_j = 0 \quad (j = 1, 2) \quad (1)$$

The resource level ($R$) at which consumer $j$’s per capita growth is zero is termed consumer $j$’s $R^*$ value, i.e., the resource value at which consumer $j$’s reproduction ($e_j a_j$) is balanced by its mortality ($d_j$).

This value is given by:

$$R^*_{C_j} = \frac{d_j}{e_j a_j}$$
Now we can write down consumer species $i$’s invasion criterion, i.e., its per capita growth rate when rare:

$$\frac{dC_i}{dt} \frac{1}{C_i} = e_i a_i R^*_C j - d_i \quad (i, j = 1, 2 \ i \neq j) \quad (1)$$

where $R^*_C j = \frac{d_j}{e_j a_j}$.

By substituting for $R^*_C j$ in Equation (1) we get,

$$\frac{dC_i}{dt} \frac{1}{C_i} e_i a_i \left(\frac{d_j}{e_j a_j}\right) - d_i \quad (2)$$

Consumer species $i$ can invade a community consisting of the resource and consumer $j$ when its per capita growth rate when rare is positive, i.e.,

$$\frac{dC_i}{dt} \frac{1}{C_i} e_i a_i \left(\frac{d_j}{e_j a_j}\right) - d_i > 0 \quad (3)$$
Mutual invasibility criteria

Consumer 1 can invade when rare if

\[ \frac{dC_1}{dt} \frac{1}{C_1} = e_1 a_1 R^*_C - d_1 > 0 \]

where \( R^*_C = \frac{d_2}{e_2 a_2} \). Consumer 2’s R* value

Consumer 2 can invade when rare if

\[ \frac{dC_2}{dt} \frac{1}{C_2} = e_2 a_2 R^*_C - d_2 > 0 \]

where \( R^*_C = \frac{d_1}{e_1 a_1} \). Consumer 1’s R* value
We can rewrite the invasion criteria as follows:

Consumer 1 can invade when rare if

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

Consumer 2 can invade when rare if

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

Invasion criteria are mutually exclusive. If one species can increase when rare, the other cannot.
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 ameliorating factors.
Species interactions

Exploitative competition (-/-) ✓

Apparent competition (-/-)

Mutualism (+/+)

Consumer-resource (+/-)
Apparent competition

Indirect interactions between individuals that share a common natural enemy.

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

Predator/parasite

Prey species 1

Prey species 2
Apparent competition

\[
\frac{dC_1}{dt} = C_1 \left( r_1 - a_1P \right)
\]
\[
\frac{dC_2}{dt} = C_2 \left( r_2 - a_2P \right)
\]
\[
\frac{dP}{dt} = P \left( e_1 a_1 C_1 - e_2 a_2 C_2 - d \right)
\]
Computing invasion criteria for apparent competition

Prey species $i$ can invade when rare if it can maintain a positive per capita growth rate when prey species $j$ is at equilibrium with the predator.

Prey species $j$ is at equilibrium with the predator when

$$\frac{dC_j}{dt} \frac{1}{C_j} = r_j - a_j P = 0 \quad (j = 1, 2) \quad (1)$$

Predator abundance ($P$) at which prey species $j$’s per capita growth is zero is termed prey species $j$’s $P^*$ value, i.e., the predator abundance at which prey species $j$’s reproduction ($r_j$) is balanced by mortality due to predation ($a_j$).

This value is given by:

$$P^* C_j = \frac{r_j}{a_j}$$
Now we can write down prey species $i$'s invasion criterion, i.e., its per capita growth rate when rare:

$$\frac{dC_i}{dt} \frac{1}{C_i} = r_i - a_i P^*_{C_j} \quad (i, j = 1, 2 \ i \neq j) \quad (1)$$

where $P^*_{C_j} = \frac{r_j}{a_j}$.

By substituting for $P^*_{C_j}$ in Equation (1) we get,

$$\frac{dC_i}{dt} \frac{1}{C_i} r_i - a_i \left( \frac{r_j}{a_j} \right) \quad (2)$$

Prey species $i$ can invade a community consisting of the prey species $i$ and the predator when its per capita growth rate when rare is positive, i.e.,

$$\frac{dC_i}{dt} \frac{1}{C_i} r_i - a_i \left( \frac{r_j}{a_j} \right) > 0 \quad (3)$$
Mutual invasibility criteria

Prey species 1 can invade when rare if

$$\frac{dC_1}{dt} \frac{1}{C_1} = r_1 - a_1 P^*_{C_2} > 0$$

where $P^*_{C_2} = \frac{r_2}{a_2}$. Prey species’ 2’s $P^*$ value

Prey species 2 can invade when rare if

$$\frac{dC_2}{dt} \frac{1}{C_2} = r_2 - a_2 P^*_{C_1} > 0$$

where $P^*_{C_1} = \frac{r_1}{a_1}$. Prey species’ 1’s $P^*$ value
We can rewrite the invasion criteria as follows:

Prey species 1 can invade when rare if

$$\frac{r_1}{a_1} > \frac{r_2}{a_2}$$

Prey species 2 can invade when rare if

$$\frac{r_2}{a_2} < \frac{r_1}{a_1}$$

Invasion criteria are mutually exclusive. If one species can increase when rare, the other cannot.
**P* rule**: prey 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 ameliorating factors.
Exploitative and apparent competition in constant environments

Mutual invasibility requires species be able to increase when rare.

This requires negative feedback, i.e., per capita growth rates have to be declining functions of species’ densities.
Exploitative competition

\[ \frac{dC_i}{dt} \frac{1}{C_i} = e_i a_i R - d_i \quad (i = 1, 2) \]

Apparent competition

\[ \frac{dC_i}{dt} \frac{1}{C_i} = r_i - a_i P \quad (i = 1, 2) \]

Species’ per capita growth rates are independent of density. No negative feedback.
Exploitative and apparent competition in constant environments

Exclusion due to insufficient non-linearity in local dynamics to allow for mutual invasibility.
Non-linearity * Variability $\rightarrow$ Diversity
Coexistence via non-linearity alone

Negative feedbacks arising from species interactions enable coexistence in the absence of spatial or temporal variation
Coexistence via non-linearity alone

1. Inter-specific trade-offs leading to partitioning of resources and/or natural enemies.

One species is a superior competitor for a common resource (lower $R^*$) but is more susceptible to a common natural enemy (higher $P^*$)
2. Relative non-linearity

Species have differential non-linear responses to a resource or natural enemy that give them an advantage when they are rare.
Coexistence via non-linearity alone

In both cases, negative feedback (density-dependence) such that species limit themselves more than they do others (i.e., stronger intra-specific competition than inter-specific competition).

This leads to local niche partitioning in the absence of environmental variation, and stable coexistence.
1. Coexistence via inter-specific trade-offs leading to resource partitioning
Intraguild predation

Species that compete for a common resource also engage in a trophic interaction.
Intraguild predation

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

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

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

Non-dimensionalize model:

\[
\begin{align*}
\hat{R} &= \frac{R}{K} \\
\hat{d}_i &= \frac{d_i}{r} \\
\tau &= rt
\end{align*}
\]

\[
\begin{align*}
\hat{C}_i &= \frac{C_i}{e_i K} \\
\hat{\alpha} &= \frac{\alpha e_2 K}{r} \\
\hat{a}_i &= \frac{a_i e_i K}{r} \\
\hat{f} &= \frac{e_2 f}{e_1}
\end{align*}
\]

\(i, j = 1, 2, i \neq j\)
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

1. Construct Jacobian matrix for the three species community:

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

2. Evaluate Jacobian matrix at the appropriate boundary equilibrium

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

Resource and Consumer 1 (IGPrey):

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

Resource and Consumer 2 (IGPredator):

\[ R^* = \frac{d_2}{a_2}, \quad C_1^* = 0, \quad C_2^* = \frac{a_2 - d_2}{a_2^2} \]
Compute invasion criterion for consumer 2 (IGPredator)

Evaluate Jacobian at boundary equilibrium with Resource and Consumer 1

Compute the eigenvalues of the Jacobian

 Dominant eigenvalue of Jacobian is the invasion criterion for Consumer 2 (IGPredator)
Invasion criterion for consumer 2 (IGPredator)

Jacobian evaluated at boundary equilibrium with Resource and Consumer 1:

\[
\begin{bmatrix}
- \frac{d_1}{a_1} & -d_1 & -a_2 \frac{d_1}{a_1} \\
1 - \frac{d_1}{a_1} & 0 & \frac{a_2}{a_1} \frac{d_1}{a_1} \\
0 & 0 & a_2 \frac{d_1}{a_1} - d_2 - \frac{(a_1 - d_1) \alpha}{a_1^2}
\end{bmatrix}
\]
The eigenvalues of the Jacobian are the roots of the characteristic equation

$$\lambda^3 + A_1 \lambda^2 + A_2 \lambda + A_3 = 0$$

The dominant eigenvalue is the eigenvalue that has the largest absolute value.
The dominant eigenvalue of the Jacobian evaluated at the boundary equilibrium with the resource and Consumer 1 (IGPrey) is the invasion criterion for consumer 2 (IGPredator)
Invasion criterion for consumer 2 (IGPredator)

IGPredator can invade when rare if:

\[ a_1(a_2 d_1 - a_1 d_2) + f \alpha(a_1 - d_1) > 0 \]
Compute invasion criterion for consumer 1 (IGPrey)

Evaluate Jacobian at boundary equilibrium with Resource and Consumer 2

Compute the eigenvalues of the Jacobian

Dominant eigenvalue of Jacobian is the invasion criterion for Consumer 1 (IGPrey)
Invasion criterion for consumer 1 (IGPrey)

IGPrey can invade when rare if:

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

Conditions under which each consumer (IGPrey and IGPredator) can increase from small numbers when the other consumer is at equilibrium with the resource
Invasion criterion for IGPrey:

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

Invasion criterion for IGPredator:

\[ a_1(a_2 d_1 - a_1 d_2) + f \alpha(a_1 - d_1) > 0 \]
Coexistence via non-linearity alone

1. Inter-specific trade-offs leading to partitioning of resources and/or natural enemies.

One species is a superior competitor for a common resource (lower $R^*$) but is more susceptible to a common natural enemy (higher $P^*$)
Trade-off mediated coexistence of consumers

Consumer 1 (IGPrey) is susceptible to predation from Consumer 2 (IGPredator)

Coexistence may be possible if IGPrey is a superior competitor for the basal resource
Recall:

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

If IGPrey is the superior resource competitor, it should have a lower \( R^* \), i.e.,

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

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

\[ \Rightarrow a_1 d_2 > a_2 d_1, \quad a_2 > d_2, \quad a_1 > d_1 \]
Invasion criterion for IGPrey:

IGPrey is the superior competitor

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

Positive

Invasion criterion for IGPredator:

IGPredator is the inferior competitor

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

Negative
Conditions for mutual invasibility

Then, the IGPrey can invade when rare if

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

Resource competition \hspace{2cm} \text{Intraguild predation}

The IGPredator can invade when rare if

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

\text{Intraguild predation} \hspace{2cm} \text{Resource competition}
Mutual invasibility via inter-specific trade-off between resource competition and intraguild predation

If both species are equal competitors, IGPredator has overall advantage and will exclude IGPrey.

If IGPrey is the inferior competitor, then it will be excluded very quickly.

Mutual invasibility only if IGPrey is superior resource competitor
Coexistence:

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

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

\[ R^* = \frac{f a_2 d_1 - f \alpha - a_1 d_2}{a_1 a_2 (f - 1) + f \alpha} \]

\[ C_1^* = \frac{a_2 (a_1 d_2 - a_2 d_1) - \alpha (a_2 - d_2)}{\alpha (a_1 a_2 (f - 1) + f \alpha)} \]

\[ C_2^* = \frac{a_1 (a_2 d_1 - a_1 d_2) + f \alpha (a_1 - d_1)}{\alpha (a_1 a_2 (f - 1) + f \alpha)} \]
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

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

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

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

\[ A_2 = R^* (a_1^2 C_1^* + a_2^2 C_2^*) + C_1^* C_2^* f \alpha^2 > 0. \]
Routh-Hurwitz criteria

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

\[ A_3 > 0 \text{ if } \]

\[ a_1 a_2 \alpha (1 - f) - f \alpha^2 < 0 \]

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

\[ R^* + \frac{a_1 a_2 C_1^* C_2^*}{a_1^2 C_1^* + a_2^2 C_2^*} \alpha (1 + f) > 0 \]
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 \( <==> \) inter-specific trade-off
Coexistence via non-linearity alone

1. Inter-specific trade-offs leading to partitioning of resources and/or natural enemies.

One species is a superior competitor for a common resource (lower $R^*$) but is more susceptible to a common natural enemy (higher $P^*$)
Coexistence via trade-offs

Intraguild predation

Consumer 1 (IGPrey) \rightarrow \text{Resource} \rightarrow \text{Predation/parasitism} \rightarrow \text{Consumers} \rightarrow \text{Competition} \rightarrow \text{Consumer 2 (IGPredator)}

Intraguild predation
Coexistence via non-linearity: trade-offs

Interactions with competition and predation: intraguild predation (IGP)

Coexistence: negative feedback via inter-specific trade-off

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

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

2. Relative non-linearity
What is a mechanism?
A mechanism is a system of causally interacting parts and processes that produce one or more effects.

Scientists explain phenomena by describing mechanisms that could produce the phenomena.
The question of why vs. how
Why does a particular pattern exist?
How does a particular pattern arise?
Why does a particular pattern exist?

How does a particular pattern arise?
The how question is part of the why question
Coexistence via non-linearity alone

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

2. Relative non-linearity
Coexistence via relative non-linearity

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

Non-linear functional responses

Coexistence via relative non-linearity
Type II functional response

Handling time ($h$) --> saturation of functional response

$\Rightarrow$ Resource underexploited when abundant

$\Rightarrow$ positive feedback in resource per capita growth rate

$$f(R) = \frac{aR}{1 + ahR}$$
Exploitative competition with non-linear functional responses

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

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

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

Higher attack rate and longer handling time ==> more non-linear functional response

Consumer 1: higher attack rate, longer handling time

Consumer 2: lower attack rate, shorter handling time
Longer the handling time, more non-linear the functional response, more likely to exhibit limit cycle oscillations.

\[ R^* < R_c \Rightarrow \text{limit cycle oscillations} \]

\[ R^* > R_c \Rightarrow \text{stable focus} \]
Coexistence via non-linear functional responses

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

Armstrong and McGehee 1980
Consumer 1 has the higher attack rate. If functional responses were linear, R* rule would operate and Consumer 1 could exclude consumer 2.
When consumers have non-linear functional responses, the species 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 occurs via a form of resource partitioning
Resource partitioning

Consumer with more non-linear functional response better at resource exploitation when resource abundance is low, consumer with less non-linear functional response better at resource exploitation when resource abundance is high.
Coexistence via relative non-linearity

Resource partitioning

The two consumers exploit different parts of the resource cycle

This separation increases the strength of intra-specific interactions relative to inter-specific interactions, and allows coexistence.
Coexistence via non-linearity alone

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

2. Relative non-linearity in functional responses ✓