Non-linearity, variability and diversity: an integrative perspective

Priyanga Amarasekare

Department of Ecology and Evolutionary Biology

University of California Los Angeles

Elucidate mechanisms from first principles

Generate predictions that can be tested with data

Non-linearity * Variability $\Longrightarrow$ 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

$$\frac{dN}{dt} = Nf(N)$$

$$\frac{dN}{dt}\frac{1}{N} = f(N)$$

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

$$\frac{dN}{dt} = rN(1 - \frac{N}{K}) \tag{1}$$

$$\frac{dN}{dt}\frac{1}{N} = r(1 - \frac{N}{K}) \tag{2}$$

Per capita growth rate is a decreasing function of density.

Negative density-dependence

Self-limitation (intra-specific competition for limiting resources)

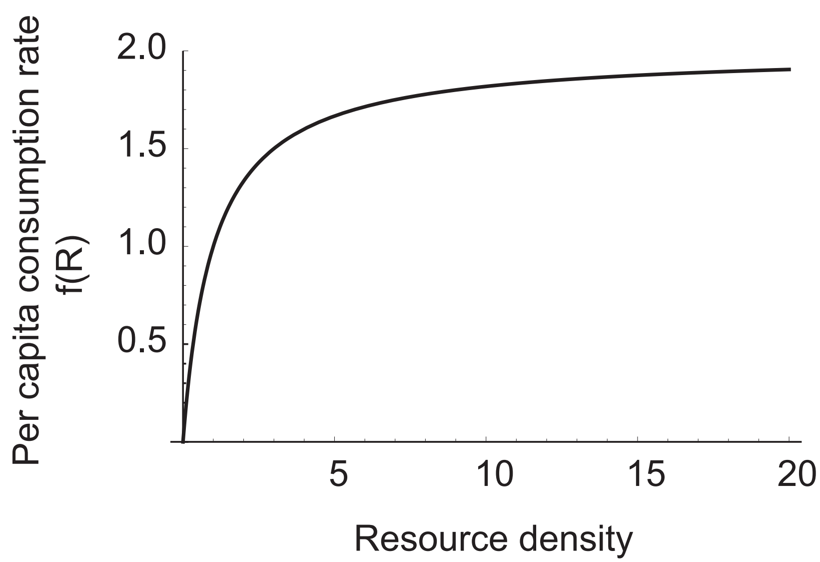
Positive density-dependence

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



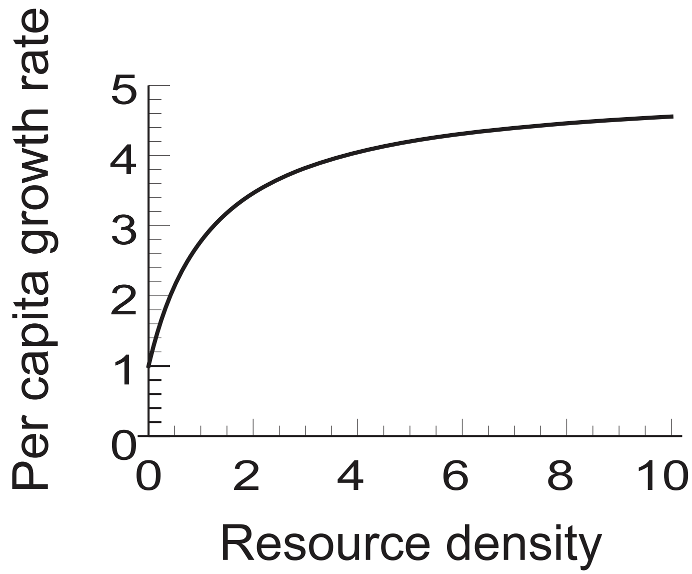
$$f(R) = \frac{aR}{1 + a\mathbf{h}R}$$

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

Pairwise consumer-resource interaction

$$\frac{dR}{dt} = rR\left(1 - \mathbf{q}R\right) - \frac{aRC}{1 + a\mathbf{h}R}$$
$$\frac{dC}{dt} = e\frac{aRC}{1 + a\mathbf{h}R} - dC$$

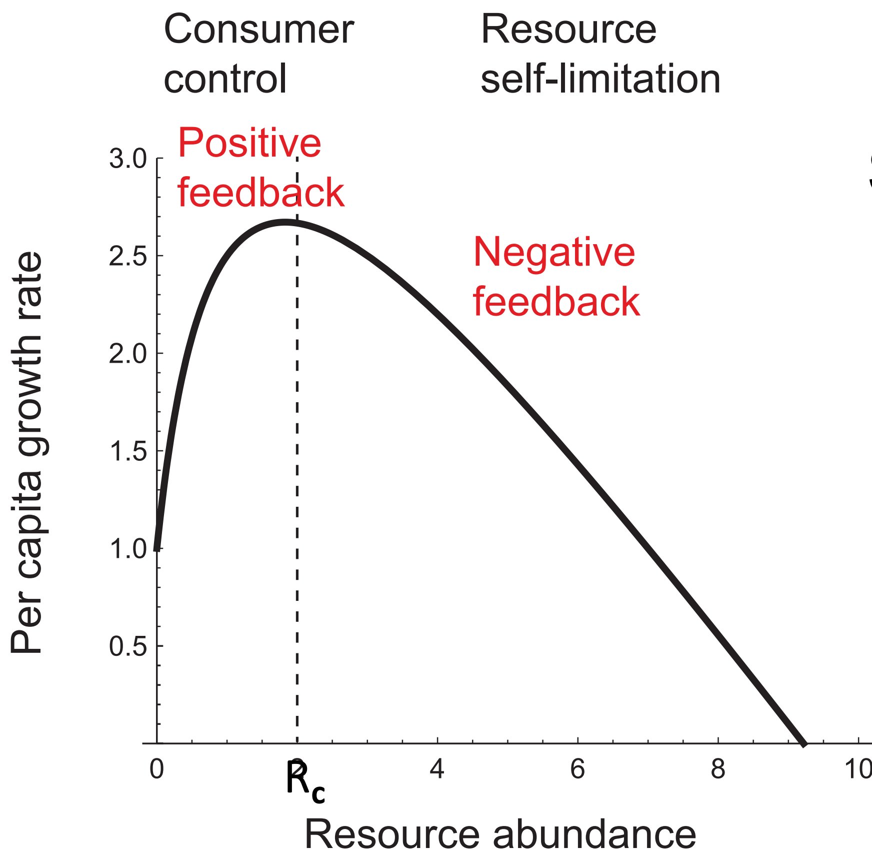
Self-limitation in resource (**q**),
saturating functional response in consumer (**h**)



No self-limitation in resource

$$\frac{dR}{dt}\frac{1}{R} = r - \frac{aC}{1 + a\mathbf{h}R}$$

Consumer's handling time ==> positive feedback in resource per capita growth rate



Self-limitation in resource

$$\frac{dR}{dt}\frac{1}{R} = r\Big(1 - \mathbf{q}R\Big) - \frac{aC}{1 + a\mathbf{h}R}$$

$$R^{\star} < R_c \Rightarrow \text{limit cycle oscillations}$$

$$R^{\star} > R_c \Rightarrow \text{stable focus}$$

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 (+/+)

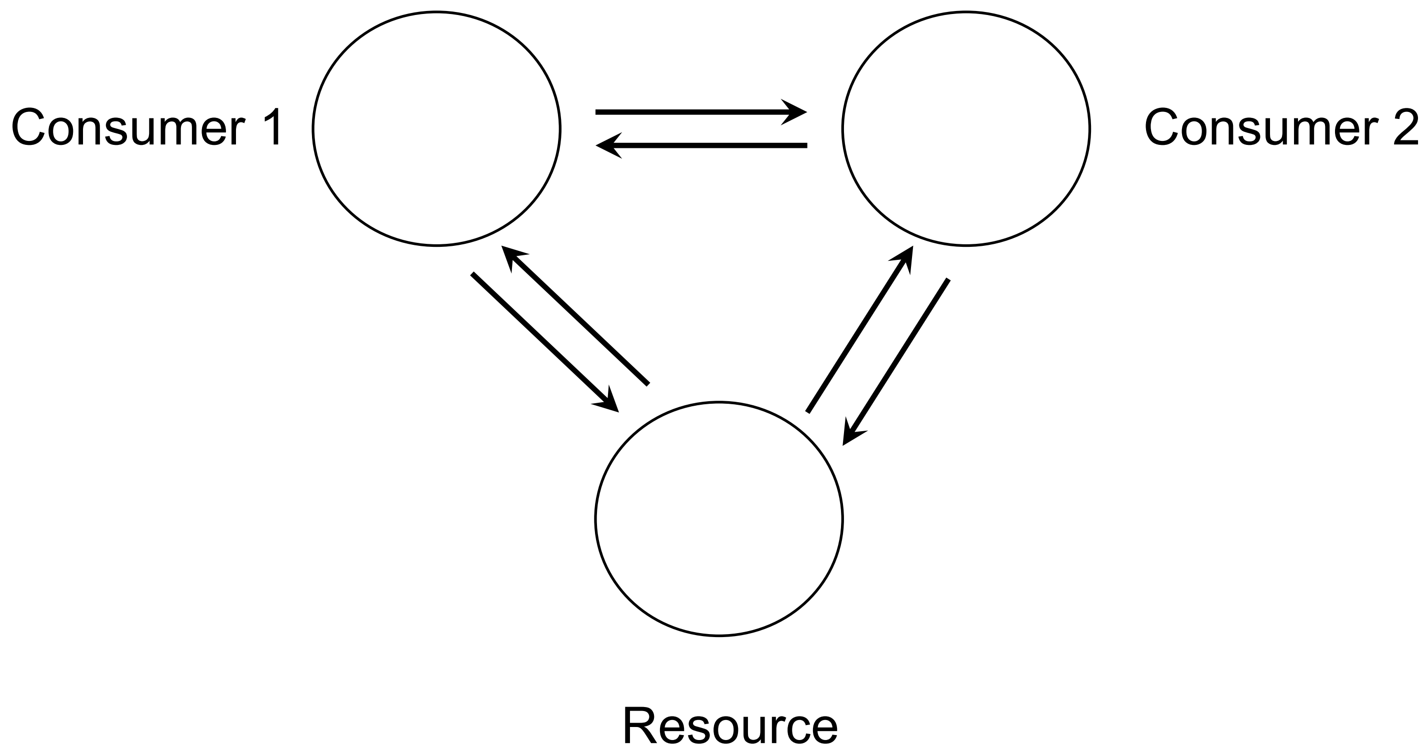
Consumer-resource (+/-)

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



Exploitative competition

$$\frac{dR}{dt} = R\left(r(1-\frac{R}{K}) - a_1C_1 - a_2C_2\right)$$ Resource

$$\frac{dC_1}{dt} = C_1\left(e_1a_1R - d_1\right)$$ Consumer 1

$$\frac{dC_2}{dt} = C_2\left(e_2a_2R - d_2\right)$$ Consumer 2

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

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

The resource level (R) at which consumer j's per capita growth is zero is termed consumer j's $R^\star$ 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:

$R^\star{}_{C_j} = \frac{d_j}{e_j a_j}$

Now we can write down consumer species i's invasion criterion, i.e., its per capita growth rate when rare:

$$\frac{dC_i}{dt}\frac{1}{C_i} = e_i a_i {R^\star}_{C_j} - d_i \quad (i, j = 1, 2 \; i \neq j) \tag{1}$$

where ${R^\star}_{C_j} = \frac{d_j}{e_j a_j}$.

By substituting for ${R^\star}_{C_j}$ in Equation (1) we get,

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

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.,

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

Mutual invasibility criteria

Consumer 1 can invade when rare if

$$\frac{dC_1}{dt}\frac{1}{C_1} = e_1 a_1 R^{\star}{}_{C_2} - d_1 > 0$$

where $R^{\star}{}_{C_2} = \frac{d_2}{e_2 a_2}$.

Consumer 2's R* value

Consumer 2 can invade when rare if

$$\frac{dC_2}{dt}\frac{1}{C_2} = e_2 a_2 R^{\star}{}_{C_i} - d_2 > 0$$

where $R^{\star}{}_{C_1} = \frac{d_1}{e_1 a_1}$.

Consumer 1's R* value

We can rewrite the invasion criteria as follows:

Consumer 1 can invade when rare if

$$\frac{d_1}{e_1 a_1} < \frac{d_2}{e_2 a_2}$$

Consumer 2 can invade when rare if

$$\frac{d_2}{e_2 a_2} < \frac{d_1}{e_1 a_1}$$

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 (+/+)

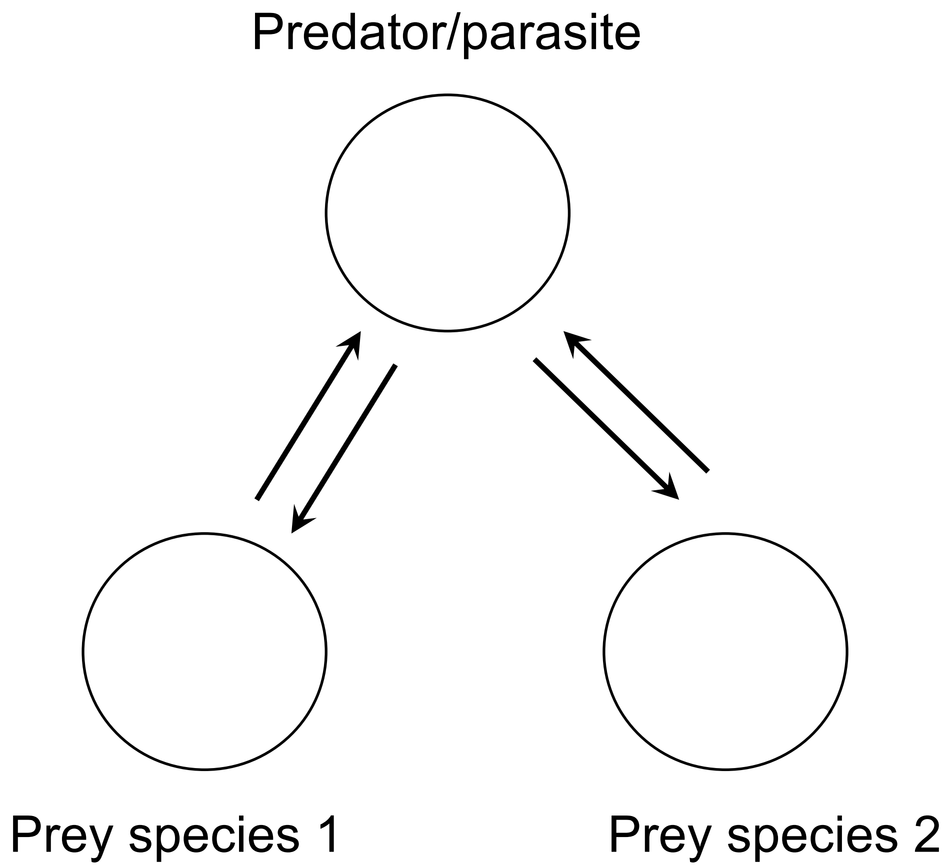
Consumer-resource (+/-)

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



Apparent competition

$$\frac{dC_1}{dt} = C_1\left(r_1 - a_1 P\right)$$ Prey species 1

$$\frac{dC_2}{dt} = C_2\left(r_2 - a_2 P\right)$$ Prey species 2

$$\frac{dP}{dt} = P\left(e_1 a_1 C_1 - e_2 a_2 C_2 - d\right)$$ Predator

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

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

Predator abundance (P) at which prey species j's per capita growth is zero is termed prey species j's $P^\star$ 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:

$P^\star{}_{C_j} = \frac{r_j}{a_j}$

Now we can write down prey species i's invasion criterion, i.e., its per capita growth rate when rare:

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

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

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

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

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.,

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

Mutual invasibility criteria

Prey species 1 can invade when rare if

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

where $P^\star{}_{C_2} = \frac{r_2}{a_2}$.

Prey species' 2's P* value

Prey species 2 can invade when rare if

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

where $P^\star{}_{C_1} = \frac{r_1}{a_1}$.

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 $\Longrightarrow$ 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^*)

Coexistence via non-linearity alone

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.

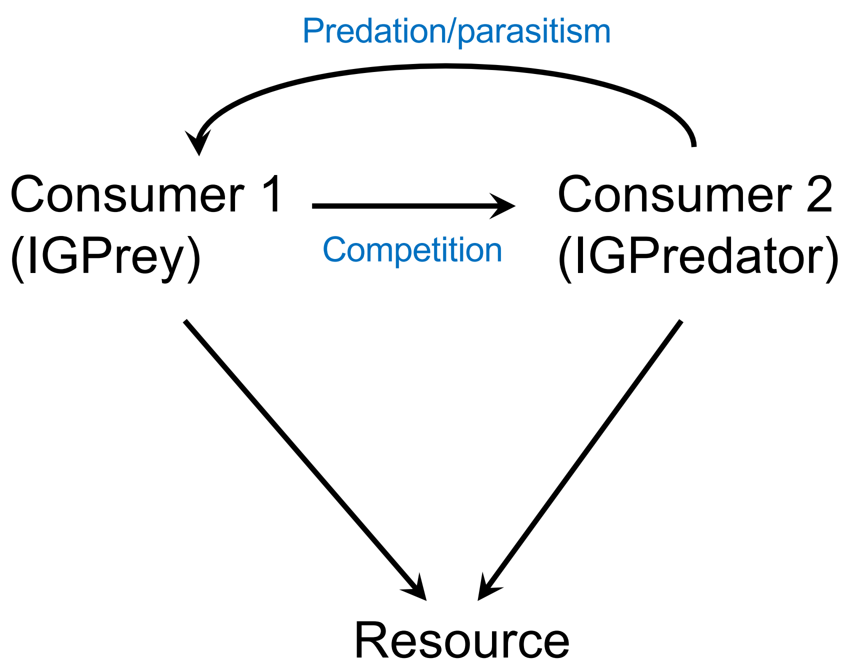
Coexistence via non-linearity alone

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

$$\frac{dR}{dt} = rR(1 - \frac{R}{K}) - a_1RC_1 - a_2RC_2$$ Resource

$$\frac{dC_1}{dt} = e_1a_1RC_1 - d_1C_1 - \alpha C_1C_2$$ IGPrey

Competition

Predation

$$\frac{dC_2}{dt} = e_2a_2RC_2 - d_2C_2 + f\alpha C_1C_2$$ IGPredator

Intraguild predation

Non-dimensionalize model:

$$\hat{R} = \frac{R}{K} \qquad \hat{C}_i = \frac{C_i}{e_i K} \qquad \hat{a}_i = \frac{a_i e_i K}{r}$$

$$\hat{d}_i = \frac{d_i}{r} \qquad \hat{\alpha} = \frac{\alpha e_2 K}{r} \qquad \hat{f} = \frac{e_2 f}{e_1}$$

$$\tau = rt \qquad (i, j = 1, 2, i \neq j)$$

Intraguild predation: non-dimensionalized model

$$\frac{dR}{d\tau} = R(1 - R) - a_1 R C_1 - a_2 R C_2$$

$$\frac{dC_1}{d\tau} = a_1 R C_1 - d_1 C_1 - \alpha C_1 C_2$$

$$\frac{dC_2}{d\tau} = a_2 R C_2 - d_2 C_2 - f \alpha C_1 C_2$$

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:

$$\begin{bmatrix} 1-2R^\star - a_1{C_1}^\star - a_2{C_2}^\star & -a_1R^\star & -a_2R^\star \\ a_1{C_1}^\star & a_1R^\star - d_1 - \alpha{C_2}^\star & -{C_1}^\star\alpha \\ a_2{C_2}^\star & {C_2}^\star f\alpha & a_2R^\star - d2 + f\alpha{C_1}^\star \end{bmatrix}$$

Computing invasion criteria

2. Evaluate Jacobian matrix at the appropriate boundary equilibrium

$$\begin{bmatrix} 1 - 2R^\star - a_1{C_1}^\star - a_2{C_2}^\star & -a_1R^\star & -a_2R^\star \\ a_1{C_1}^\star & a_1R^\star - d_1 - \alpha{C_2}^\star & -{C_1}^\star\alpha \\ a_2{C_2}^\star & {C_2}^\star f\alpha & a_2R^\star - d2 + f\alpha{C_1}^\star \end{bmatrix}$$

Boundary equilibria

Resource and Consumer 1 (IGPrey):

$$R^\star = \frac{d_1}{a_1}, {C_1}^\star = \frac{a_1 - d_1}{a_1^2}, {C_2}^\star = 0$$

Resource and Consumer 2 (IGPredator):

$$R^\star = \frac{d_2}{a_2}, {C_1}^\star = 0, {C_2}^\star = \frac{a_2 - d_2}{a_2^2}$$

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:

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

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:

$$a_2(a_1 d_2 - a_2 d_1) - \alpha(a_2 - d_2) > 0$$

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:

$R_{C_1}{}^{\star} = \frac{d_1}{a_1}, R_{C_2}{}^{\star} = \frac{d_2}{a_2}$

If IGPrey is the superior resource competitor, it should have a lower $R^{\star}$, i.e.,

$R_{C_1}{}^{\star} < R_{C_2}{}^{\star} < 1$

$\Rightarrow \frac{d1}{a1} < \frac{d2}{a2} < 1$

$\Rightarrow a_1 d_2 > a_2 d_1, a_2 > d_2, a_1 > d_1$

Invasion criterion for IGPrey:

IGPrey is the superior competitor

$$a_2(\underbrace{a_1 d_2 - a_2 d_1}_{\text{Positive}}) - \alpha(a_2 - d_2) > 0$$

Invasion criterion for IGPredator:

IGPredator is the inferior competitor

$$a_1(\underbrace{a_2 d_1 - a_1 d_2}_{\text{Negative}}) + f\alpha(a_1 - d_1) > 0$$

Conditions for mutual invasibility

Then, the IGPrey can invade when rare if

$$a_2(a_1 d_2 - a_2 d_1) > (a_2 - d_2)\alpha$$

Resource competition Intraguild predation

The IGPredator can invade when rare if

$$(a_1 - d_1) f\alpha > a_1(a_2 d_1 - a_1 d_2)$$

Intraguild predation 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

$$R^\star = \frac{fa_2d1 - f\alpha - a_1d_2}{a_1a_2(f-1) + f\alpha}$$

$$C_1{}^\star = \frac{a_2(a_1d_2 - a_2d_1) - \alpha(a_2 - d_2)}{\alpha(a_1a_2(f-1) + f\alpha)}$$

$$C_2{}^\star = \frac{a_1(a_2d_1 - a_1d_2) + f\alpha(a_1 - d_1)}{\alpha(a_1a_2(f-1) + f\alpha)}$$

Stability of coexistence equilibrium

Jacobian matrix for the three species community:

$$\begin{bmatrix} 1 - 2R^\star - a_1{C_1}^\star - a_2{C_2}^\star & -a_1R^\star & -a_2R^\star \\ a_1{C_1}^\star & 0 & -{C_1}^\star\alpha \\ a_2{C_2}^\star & {C_2}^\star f\alpha & 0 \end{bmatrix}$$

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

$$A_1 = R^\star,$$

$$A_2 = R^\star(a_1^2 C_1{}^\star + a_2^2 C_2{}^\star) + C_1{}^\star C_2{}^\star f\alpha^2,$$

$$A_3 = -R^\star C_1{}^\star C_2{}^\star\Big(a_1 a_2 \alpha(1-f) - f\alpha^2\Big).$$

Routh-Hurwitz criteria for stability of coexistence equilibrium

$A_1 > 0, A_3 > 0$ and $A_1 A_2 - A_3 > 0.$

$A_1 = R^\star > 0,$

$A_2 = R^\star(a_1^2 {C_1}^\star + a_2^2 {C_2}^\star) + {C_1}^\star {C_2}^\star f \alpha^2 > 0.$

Routh-Hurwitz criteria

$A_1 > 0, A_3 > 0$ and $A_1 A_2 - A_3 > 0.$

$A_3 > 0$ if

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

$A_1 A_2 - A_3 > 0$ if

$$R^\star + \frac{a_1 a_2 C_1{}^\star C_2{}^\star}{a_1^2 C_1{}^\star + a_2^2 C_2{}^\star} \alpha(1 + f) > 0$$

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 α and f)

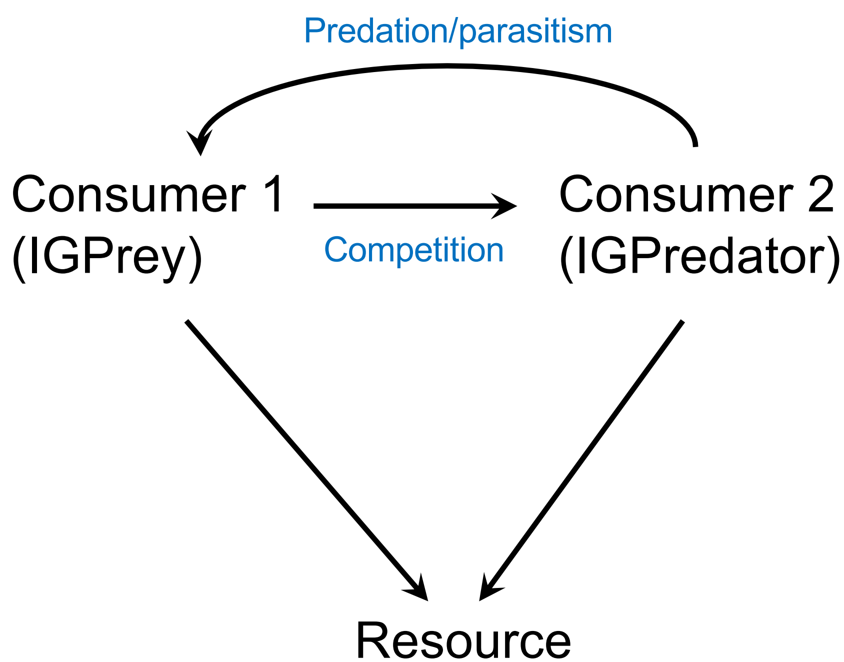
Stability <==> inter-specific trade-off

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

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, IGPredator 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?**

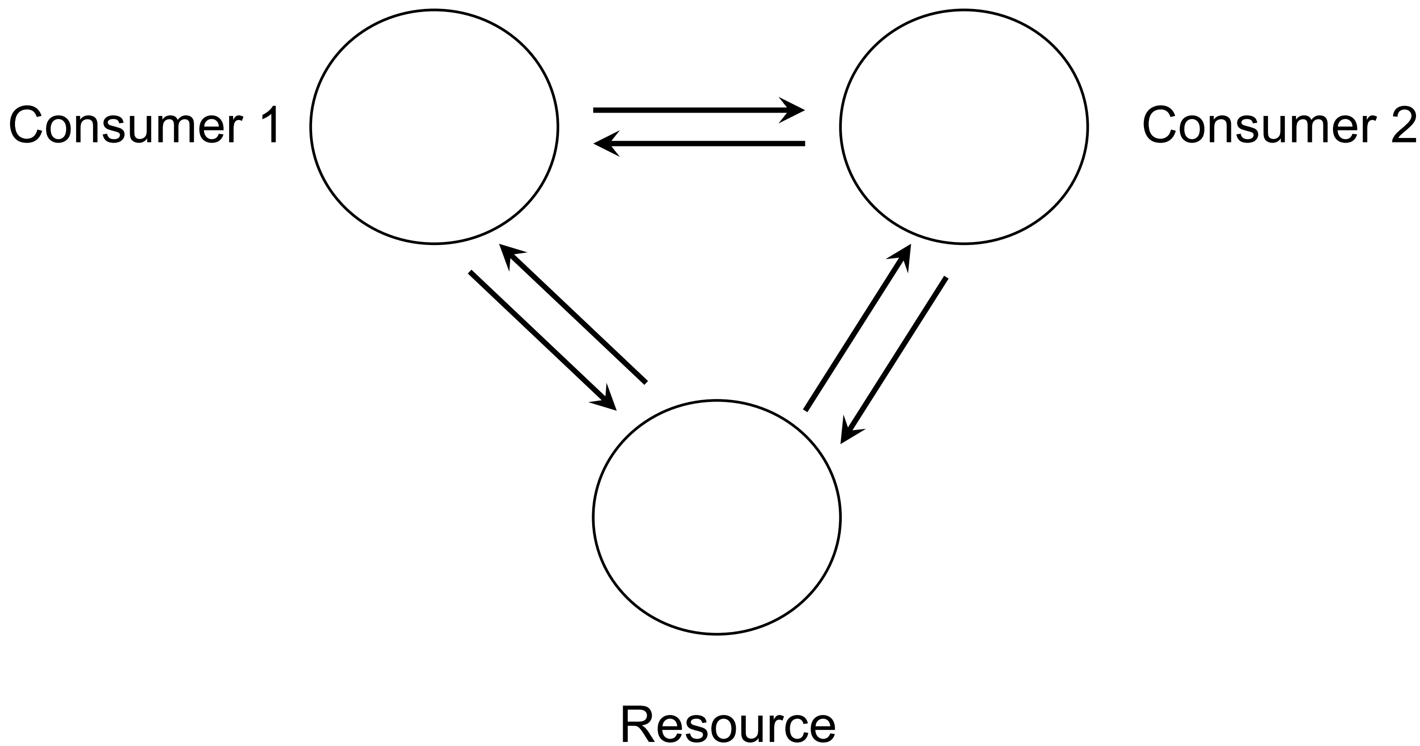
The how question is part of the why question

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

$$\frac{dR}{dt} = R\left(r(1-\frac{R}{K}) - a_1C_1 - a_2C_2\right)$$

$$\frac{dC_1}{dt} = C_1\left(e_1a_1R - d_1\right)$$

$$\frac{dC_2}{dt} = C_2\left(e_2a_2R - d_2\right)$$

Linear functional responses

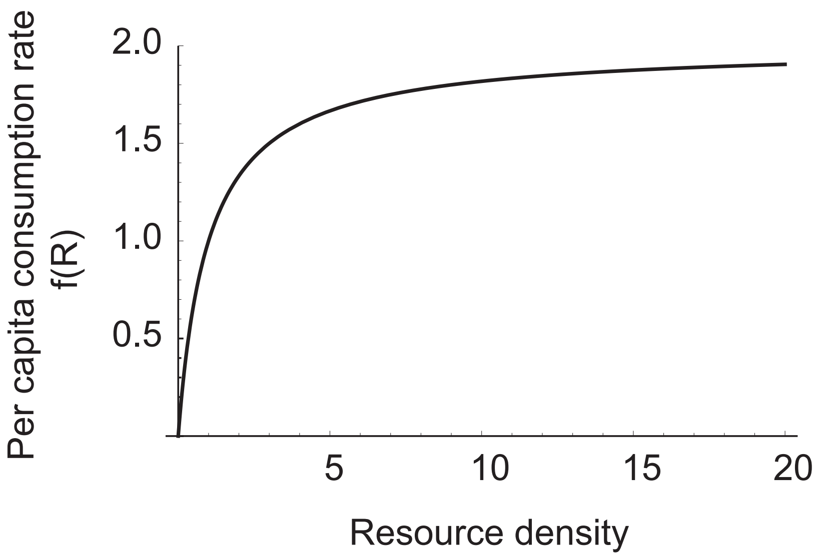
R^* rule: consumer species that drives resource abundance to the lowest level will exclude others

Exploitative competition

Non-linear functional responses

Coexistence via **relative non-linearity**

Type II functional response



$$f(R) = \frac{aR}{1 + a\mathbf{h}R}$$

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

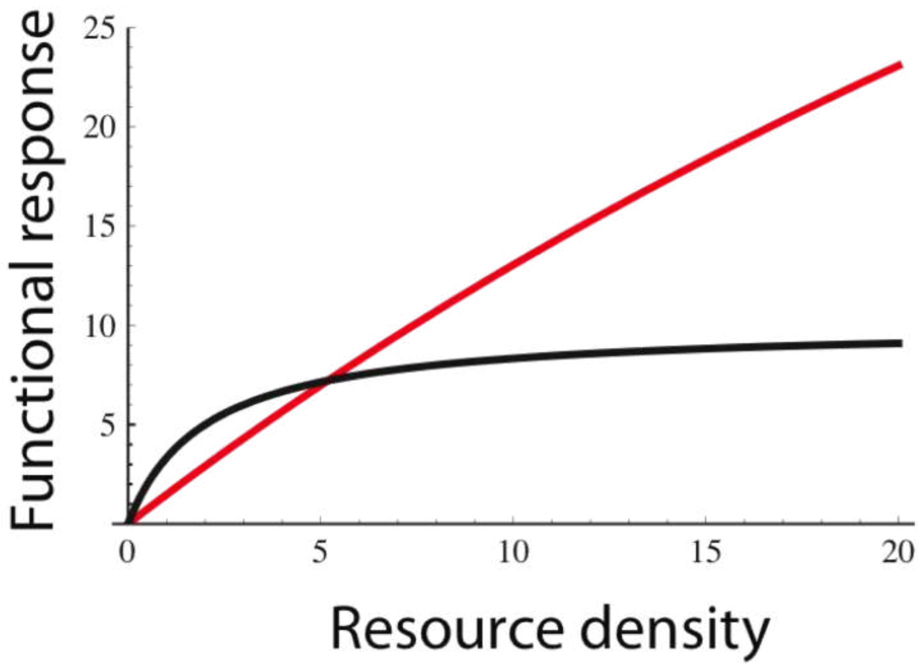
Exploitative competition with non-linear functional responses

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{a_1 R C_1}{1 + a_1 h_1 R} - \frac{a_2 R C_2}{1 + a_2 h_2 R}$$

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

$$\frac{dC_2}{dt} = e_2 \frac{a_2 R C_2}{1 + a_2 h_2 R} - d_2 C_2$$

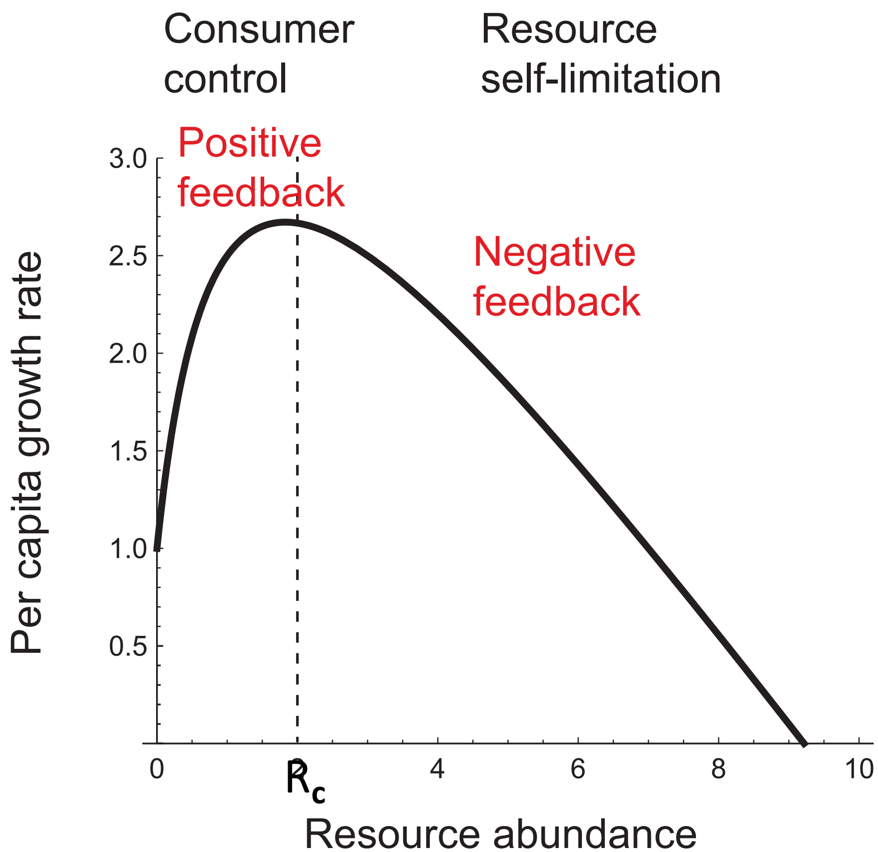
Non-linear functional responses



Consumer 2: lower attack rate, shorter handling time

Consumer 1: higher attack rate, longer handling time

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

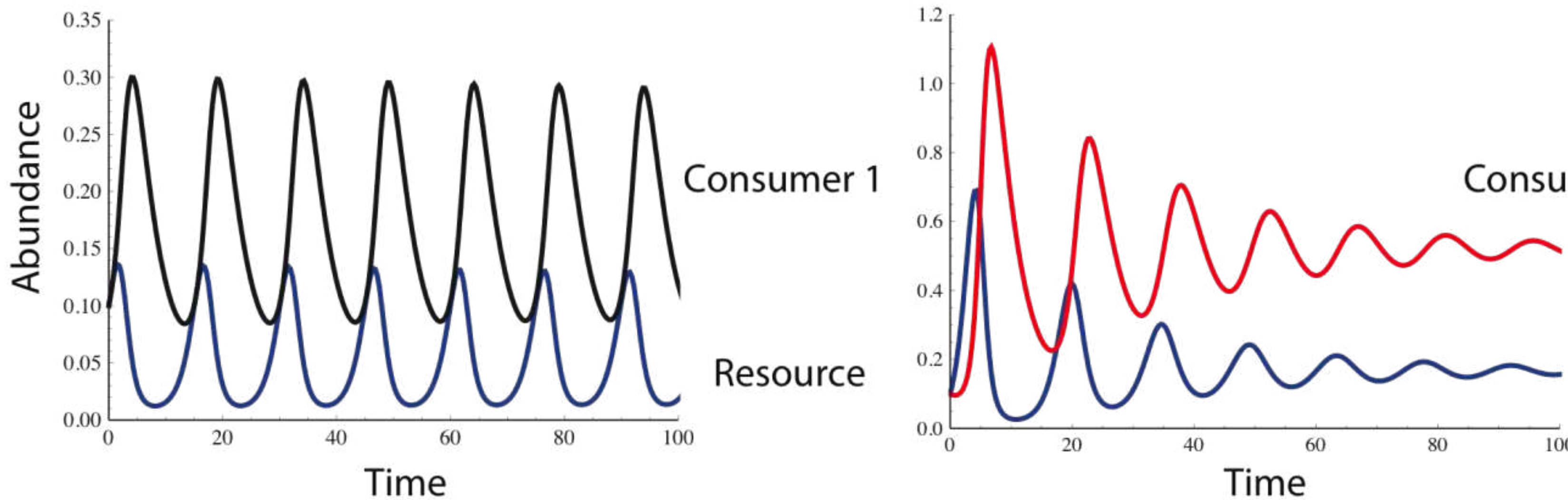


$R^{\star} < R_c \Rightarrow$ limit cycle oscillations

$R^{\star} > R_c \Rightarrow$ stable focus

Longer the handling time, more non-linear the functional response, more likely to exhibit limit cycle oscillations

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 ✓