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 $\Longrightarrow$ 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

Use mathematical models to understand mechanistic underpinnings of interplay between non-linearity and variability

Mechanistic understanding

Explain patterns

Predict changes due to perturbations

Mechanistic theory provides 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

Density-dependent feedback processes

Negative density-dependence

Positive 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)

Density-dependent feedback processes

Negative density-dependence ✓

Positive density-dependence

Positive density-dependence

Per capita growth rate is an increasing function of density

Allee effects (single species, mutualistic interactions

Type II (saturating) functional responses

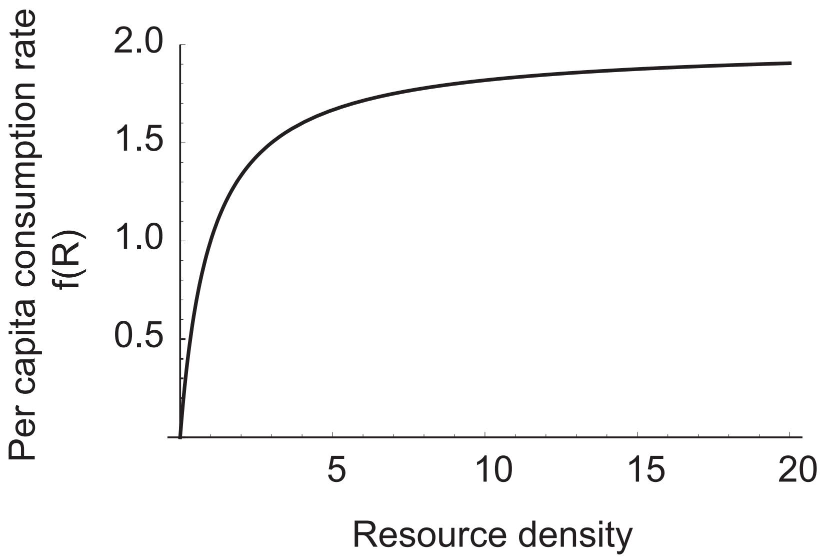
Saturating functional response

Positive feedback generates consumer-resource oscillations

Functional response

Per capita consumption rate, number of prey consumed by a single predator per unit time

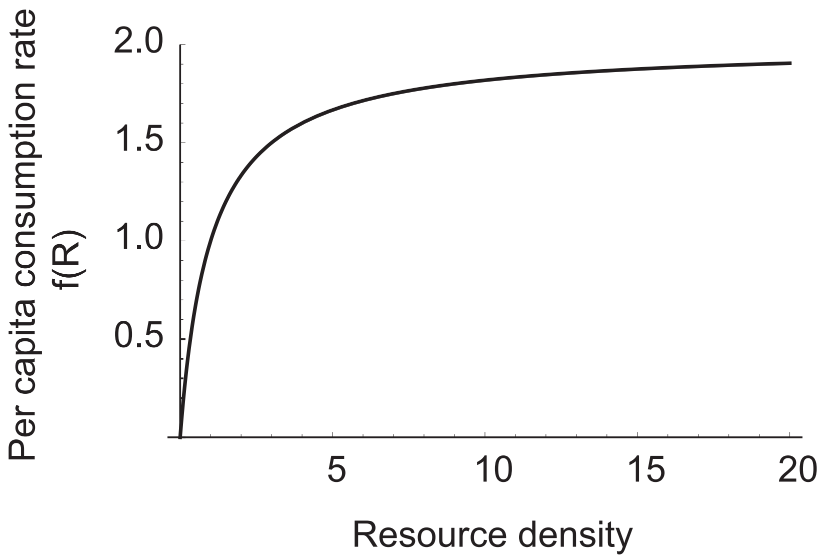
Type II functional response



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

Per capita consumption rates saturates at high resource densities

Type II functional response



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

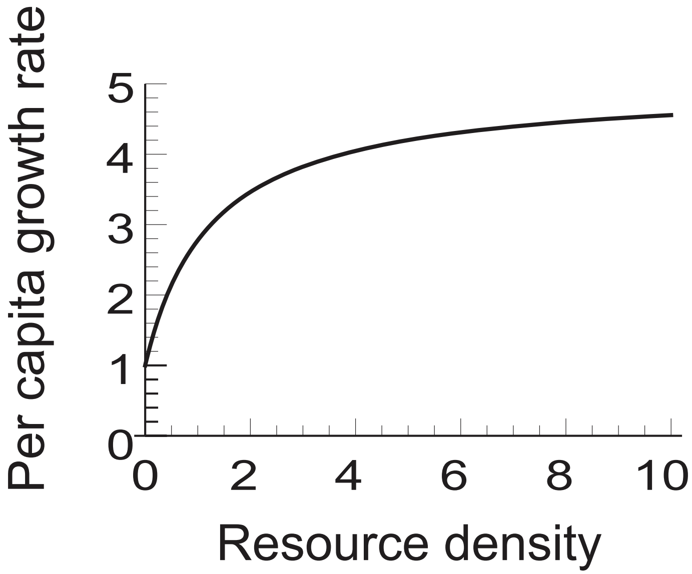
Handling time (***h***) --> saturation of functional response
==> Resource underexploited when abundant
==> positive feedback in resource per capita growth rate

Pairwise consumer-resource interaction

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

$$\frac{dC}{dt} = e\frac{aRC}{1 + a\mathbf{h}R} - dC$$

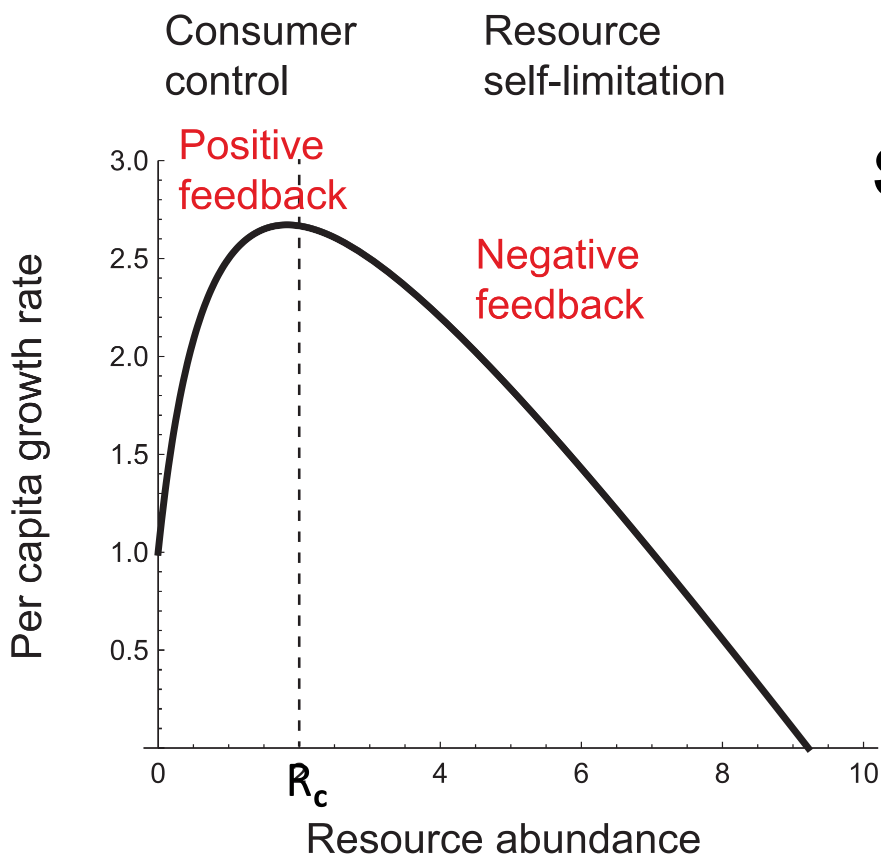
Self-limitation in resource (**q**),
saturating functional response in consumer (**h**)



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

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

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

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

Sustained oscillations: consumer handling time and resource self-limitation

Non-linearity

Negative density-dependence (self-limitation)

Positive density-dependence (saturating functional responses)

Non-linearities arise from feedback processes (negative or positive)

Feedback processes arise from interactions within or between species

Resources

Negative density-dependence (self-limitation)

Natural enemies

Positive density-dependence (saturating functional responses)

Goal

Understand 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 (+/+)

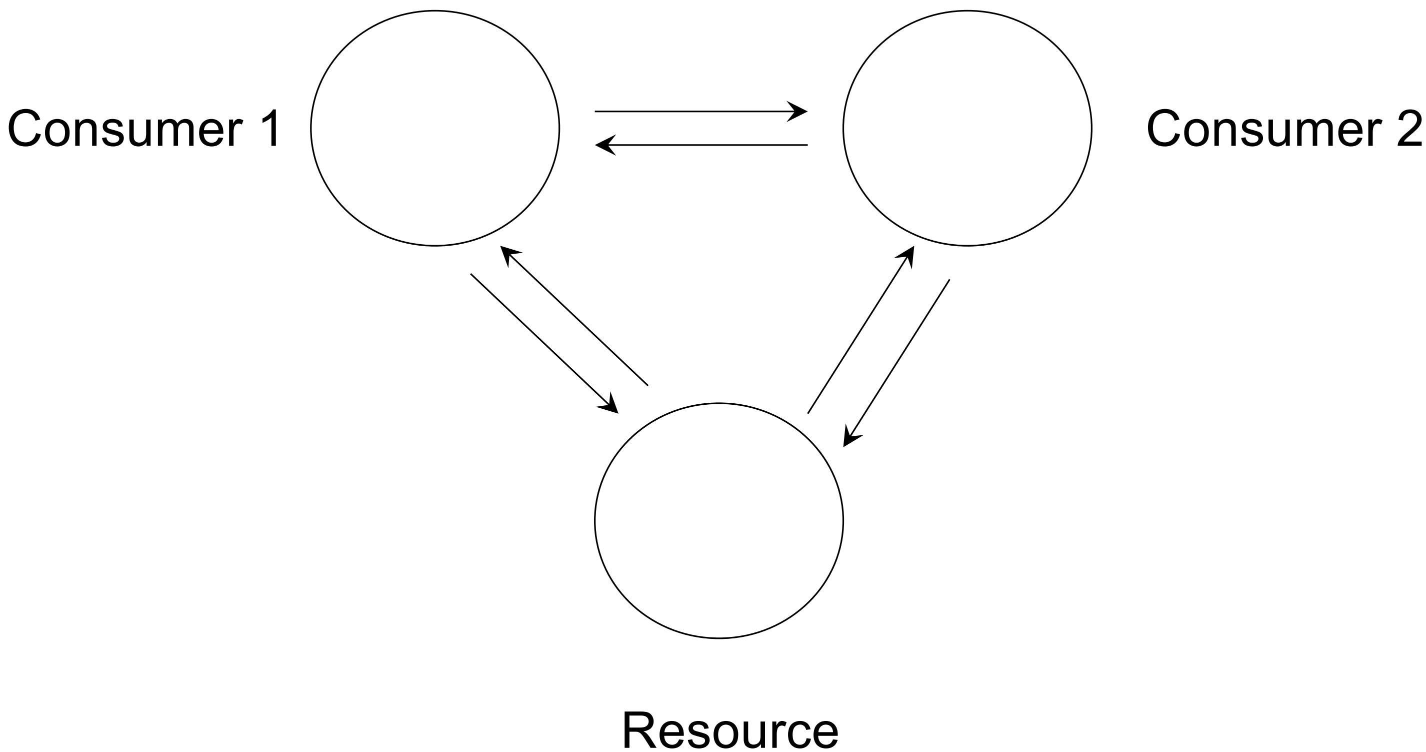
Consumer-resource (+/-)

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

Criteria for coexistence

Mutual invasibility: each species must be able to increase when rare when its competitor is at equilibrium with the resource (necessary condition)

Stability: coexistence equilibrium stable to perturbations (sufficient condition)

Mutual invasibility

Compute invasion criteria

Consumer *i* can invade when rare if it can maintain a *positive per capita growth rate* when its competitor (consumer *j, i*, *j=1, 2*) is at equilibrium with the resource

Mutual invasibility

Compute invasion criteria

R*, resource level required for a consumer species to just maintain itself, i.e., to balance consumption and mortality

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

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

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

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).

Consumer j is at equilibrium with the resource when

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

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

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.

Superior competitor: higher attack rate and conversion efficiency and/or lower death rate

Coexistence not possible in the absence of environmental variability.

Conclusion

Exploitative competition in a homogeneous environment leads to competitive exclusion and loss of diversity

Species interactions

Exploitative competition (-/-) ✓

Apparent competition (-/-)

Mutualism (+/+)

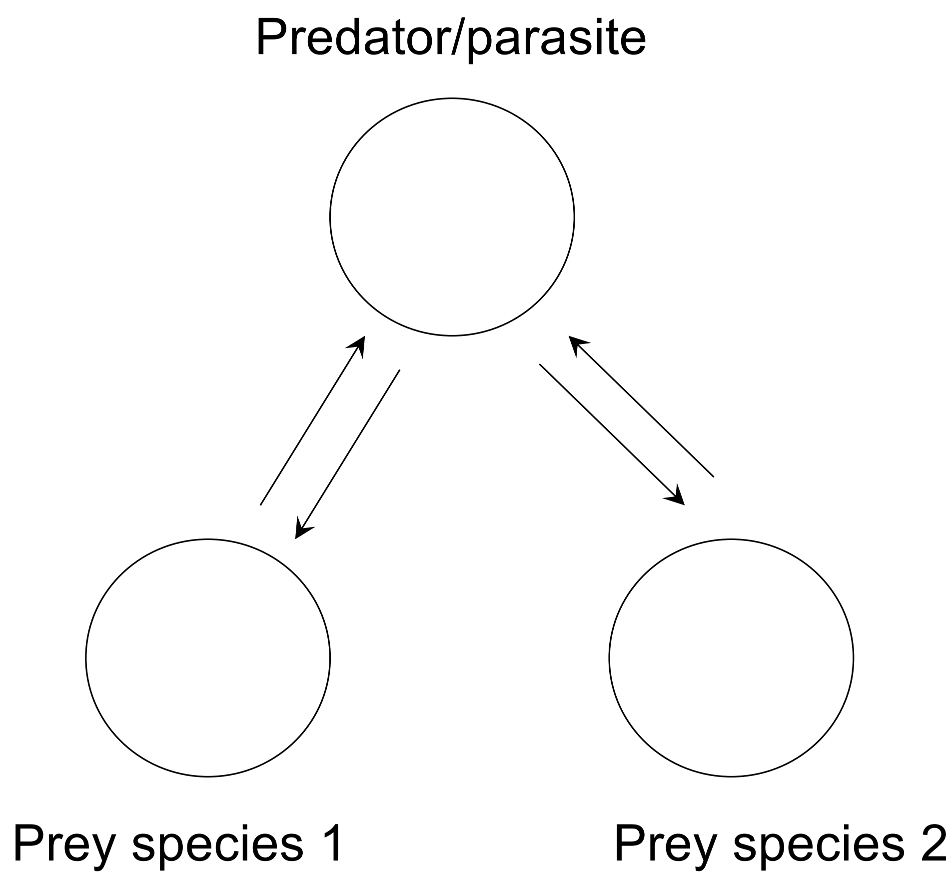
Consumer-resource (+/-)

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).

Prey species j is at equilibrium with the predator when

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

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

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 environmental variability.

Why is coexistence not possible with pure exploitative and apparent competition in constant environments?

Exploitative and apparent competition in constant environments

Stable coexistence 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 ⟹ Diversity

Coexistence via non-linearity alone

Negative feedbacks arising from species interactions enable coexistence in the absence of spatial or temporal variation

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.

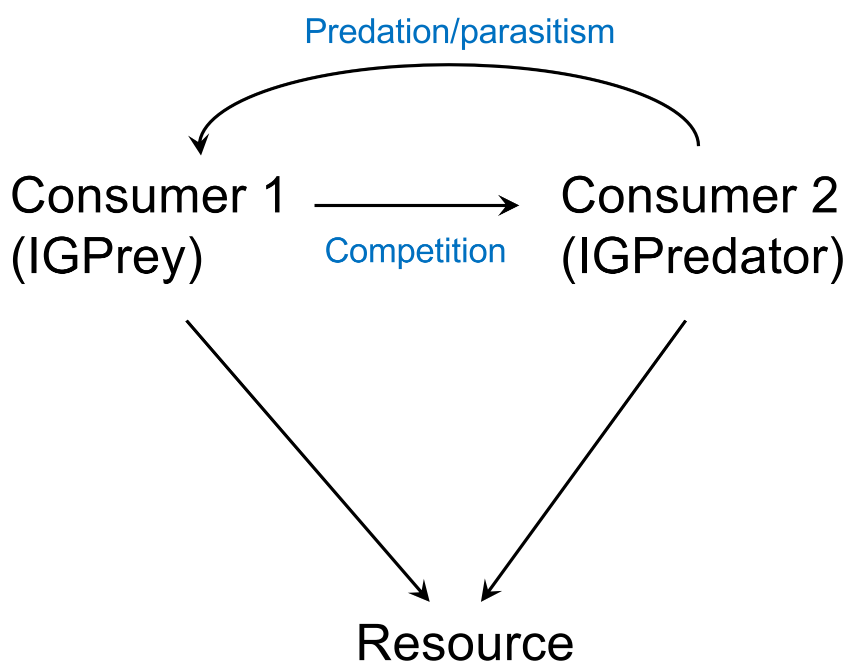
Coexistence via non-linearity alone

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

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

$$\frac{dC_1}{dt} = e_1 a_1 RC_1 - d_1 C_1 - \alpha C_1 C_2$$ IGPrey

Competition

Predation

$$\frac{dC_2}{dt} = e_2 a_2 RC_2 - d_2 C_2 + f \alpha C_1 C_2$$ IGPredator

Intraguild predation

Non-dimensionalize model

Reduces number of parameters and highlights natural scaling relationships between parameters

Scale species' abundances by carrying capacity

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

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

Scale background mortality by resource growth rate

$$\hat{d}_i = \frac{d_i}{r}$$

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

Scale attack rates by conversion efficiency and resource traits

$$\hat{a}_i = \frac{a_i e_i K}{r}$$

IGPrey and IGPredator's attack rate on resource

$$\hat{\alpha} = \frac{\alpha e_2 K}{r}$$

IGPredator's attack rate on IGPrey

Metric of conversion efficiencies

$$\hat{f} = \frac{e_2 f}{e_1}$$

Scale time in terms of resource growth rate

$$\tau = rt$$

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

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

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

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

1. Mutual invasibility

2. Stability

Mutual invasibility: each species must be able to increase when rare when its competitor is at equilibrium with the resource

Mutual invasibility ==> coexistence is feasible (interior equilibrium exists)

2. **Stability**: interior equilibrium stable to small perturbations of species' abundances

Coexistence

1. Mutual invasibility analysis to determine feasibility of coexistence of equilibrium

2. Local stability analysis to determine whether internal equilibrium is an attractor

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

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

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)

1. Evaluate Jacobian at boundary equilibrium with Resource and Consumer 1 (environment for Consumer 2 when present in small numbers)

2. Compute the eigenvalues of the Jacobian

3. Find the dominant eigenvalue of Jacobian

Dominant eigenvalue of the Jacobian: per capita growth rate of Consumer 2 when it is rare and Consumer 1 is abundant

If dominant eigenvalue is positive, boundary equilibrium with resource and Consumer 1 is unstable

==> Consumer 2 (IGPredator) has a positive per capita growth rate when rare, can invade a community of resource and Consumer 1

Invasion criterion for consumer 2 (IGPredator)

Construct the Jacobian matrix for the three species community

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

Evaluate Jacobian 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

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

The dominant eigenvalue is the eigenvalue that has the largest absolute value.

Dominant eigenvalue of the Jacobian evaluated at the boundary equilibrium with the resource and Consumer 1 (IGPrey)

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

Per capita growth rate of Consumer 2 (IGPredator) when rare

Invasion criterion for consumer 2 (IGPredator)

IGPredator can invade when rare if:

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

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

When each consumer (IGPrey and IGPredator) can increase from initially 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:

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

Mutual invasibility when both criteria satisfied

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

Intraguild predation: two consumers compete for a common resource and also engage in a trophic interaction

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

How determine competitive superiority of IGPrey?

Use R* rule: consumer that reduces the resource to the lowest level is the superior competitor

R* for IGPrey and IGPredator

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

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

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

IGPredator has higher R*, but to persist on the resource it's R* < K

K=1 in non-dimensionalized model ➔ $R^*_{C2} < 1$

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

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

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

Invasion criterion for IGPrey:

IGPrey is the superior competitor

$$a_2(a_1d_2 - a_2d_1) - \alpha(a_2 - d_2) > 0$$

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   Intraguild predation

The IGPredator can invade when rare if

$$(a_1 - d_1)f\alpha > a_1(a_2d_1 - a_1d_2)$$

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:

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

Diagonal terms zero except for resource
(no self limitation in consumer species)

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 $A_1 A_2 - A_3 > 0$.

$A_1 = R^\star > 0,$

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

$$A_3 > 0 \text{ if}$$

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

A_3>0 always if f>1, i.e., gain to IGPredator from intraguild predation is greater than the gain to IGPrey from resource competition

$A_1 A_2 - A_3 > 0$ if

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

$$A_1 = R^\star > 0,$$

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

$A_3 > 0$ if

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

$A_1 A_2 - A_3 > 0$ if

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

Coexistence equilibrium stable to perturbations if two criteria are met

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

2. Consumer 2 (IGPredator) gains sufficient benefit from preying on Consumer 1 (high α and f)

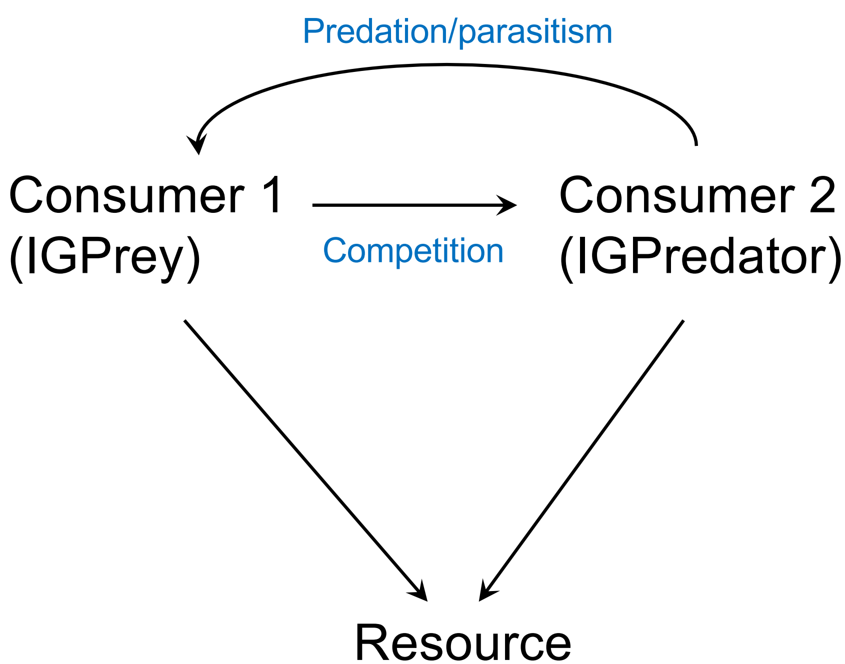
Inter-specific trade-off between competition and IGP necessary for coexistence

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

Key results

Inter-specific trade-off between competition and predation generates the negative feedback necessary for coexistence

IGPrey is superior competitor for basal resource, IGPredator can consume IGPrey (local niche partitioning)

Key results

IGPredator can exploit both resource and IGPrey

==> coexistence via resource partitioning

Resource partitioning --> intra-specific interactions relative to inter-specific interactions Key requirement for coexistence

Coexistence via non-linearity alone

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

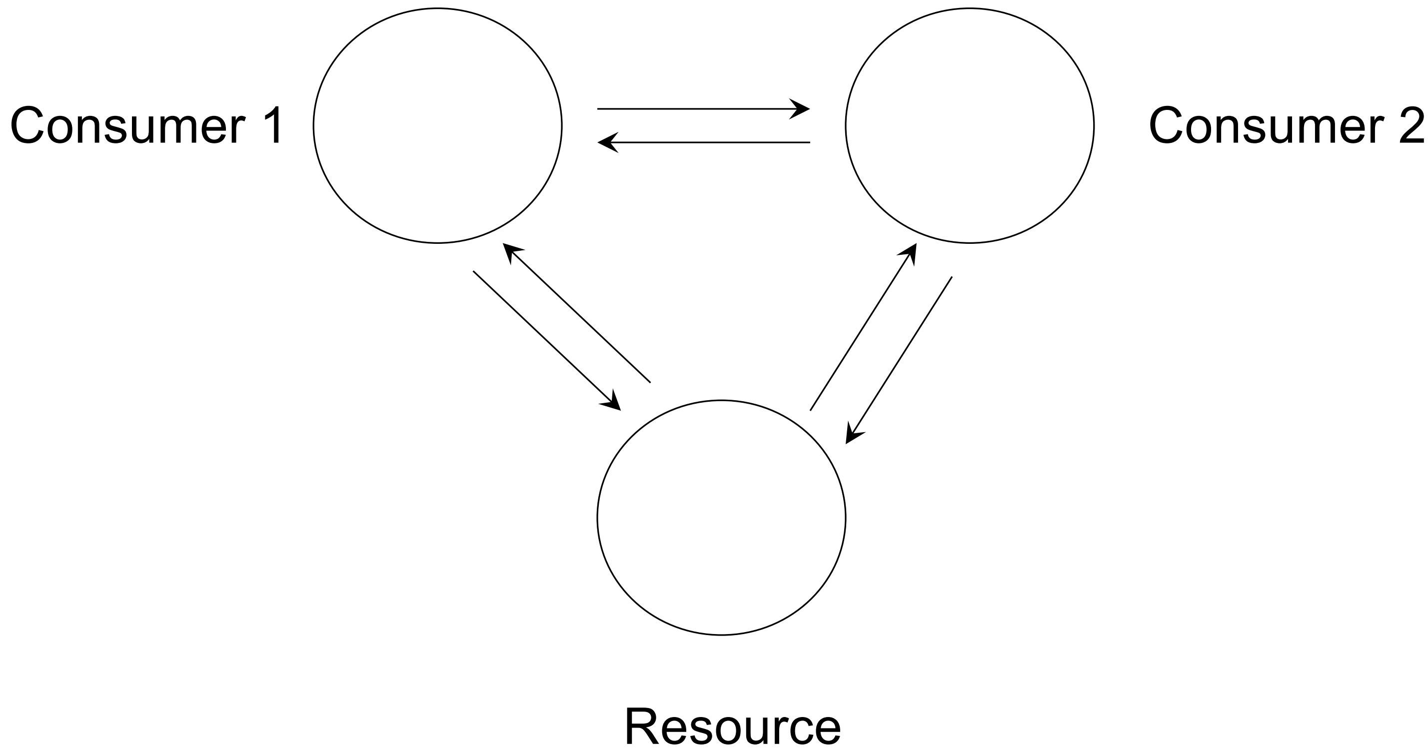
2. Relative non-linearity

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

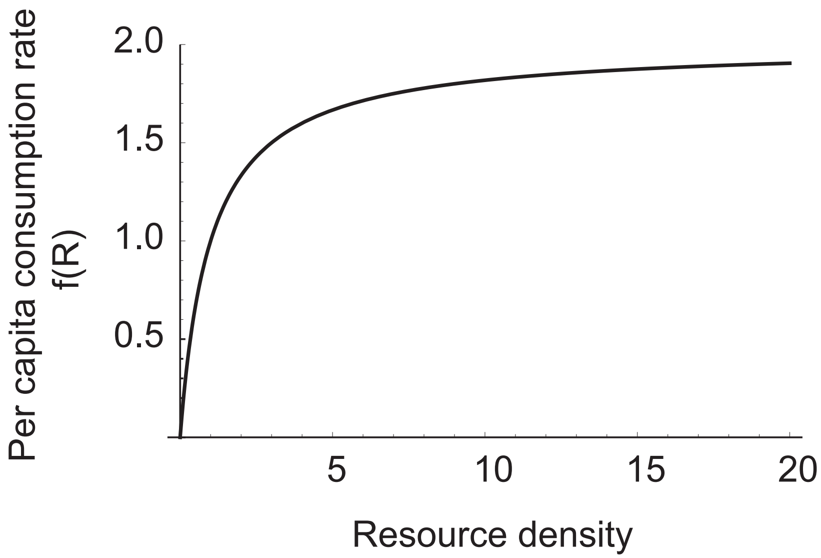
R^* rule: consumer species that drives resource abundance to the lowest level will exclude others

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

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

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

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

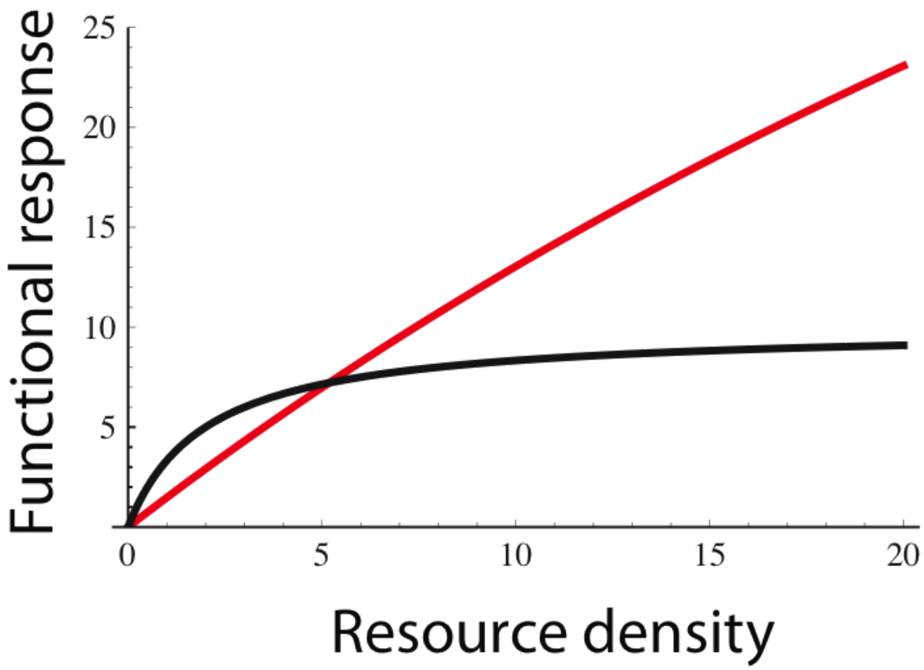
Consumers differ in the degree of non-linearity in their functional responses

Attack rate

Handling time

Longer handling time ==> more non-linear functional response

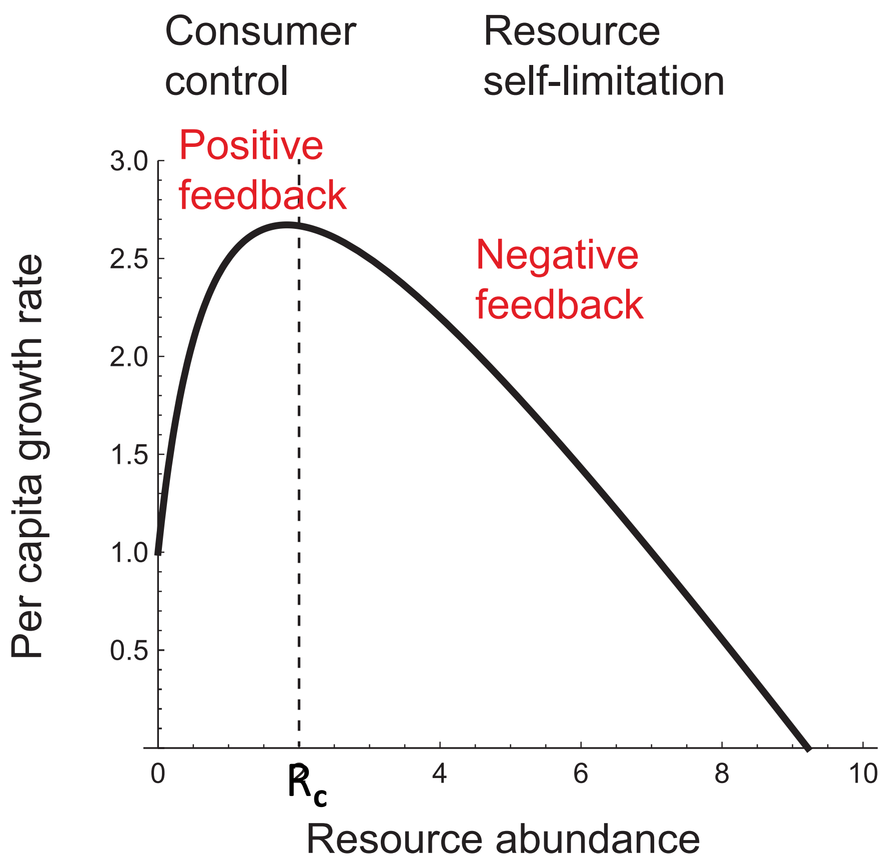
Non-linear functional responses



Consumer 2: shorter handling time

Consumer 1: longer handling time

Longer handling time ==> more non-linear functional response



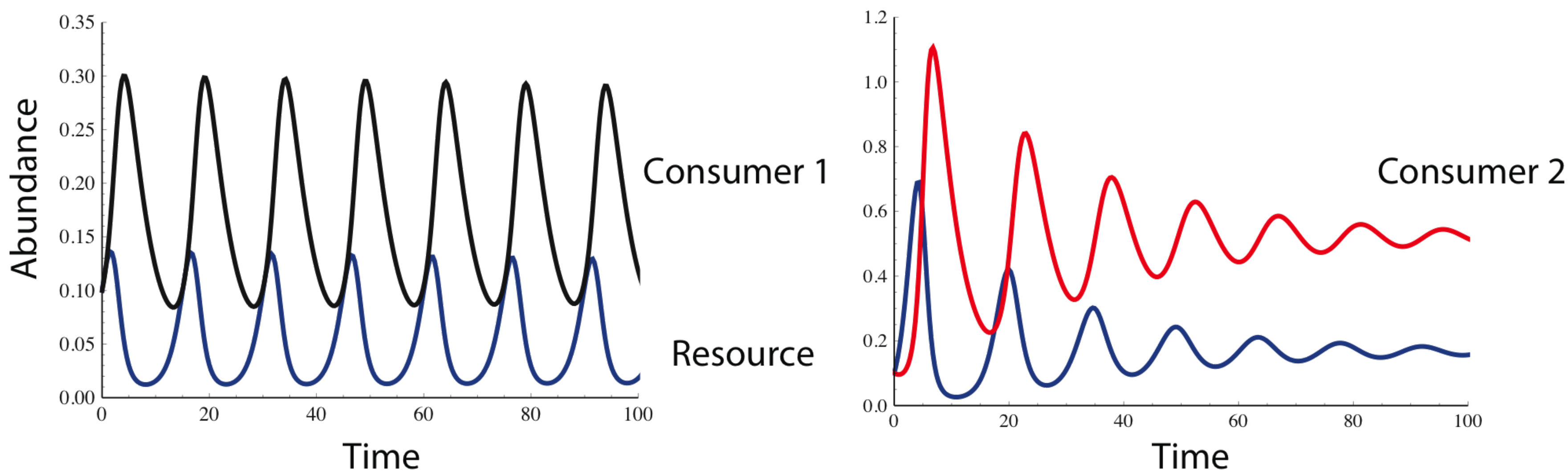
$$R^{\star} < R_c \Rightarrow \text{limit cycle oscillations}$$

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

Longer the handling time, more non-linear the functional response, stronger the consumer-resource oscillations

Consumer-resource dynamics when each persists in isolation with the resource (pairwise consumer-resource interaction)

Coexistence via non-linear functional responses



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

Armstrong and McGehee 1980

If consumers have linear functional responses (h=0), R* rule would operate and the consumer with the higher attack rate would exclude the other.

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^*s of both consumers each can invade when rare.

Coexistence occurs via a subtle form of resource partitioning

Consumer with the **less** non-linear functional response (**lower handling time**) is better at resource exploitation when resource abundance is high

Consumer with the **more** non-linear functional response (**higher handling time**) is 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 ✓

Coexistence via non-linearity alone in the absence of environmental variability

Negative feedbacks arising from species interactions enable stronger intra-specific competition relative to inter-specific competition