A mathematical perspective of community ecology

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Mechanisms that maintain diversity

Diversity: Species coexistence

Coexistence: Non-linear dynamics * Environmental heterogeneity

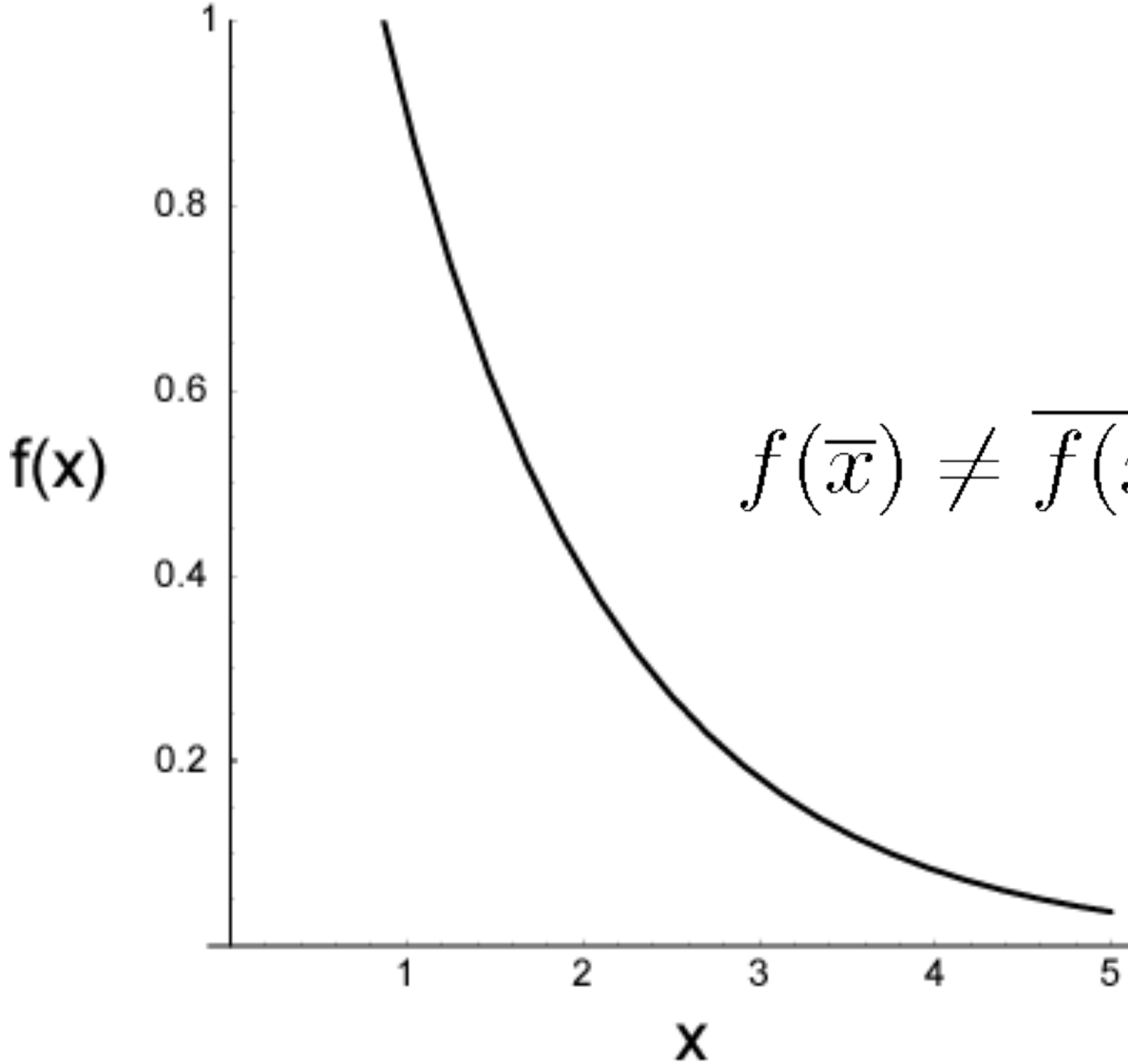
(density-dependence) (temporal, spatial)

Coexistence mechanisms

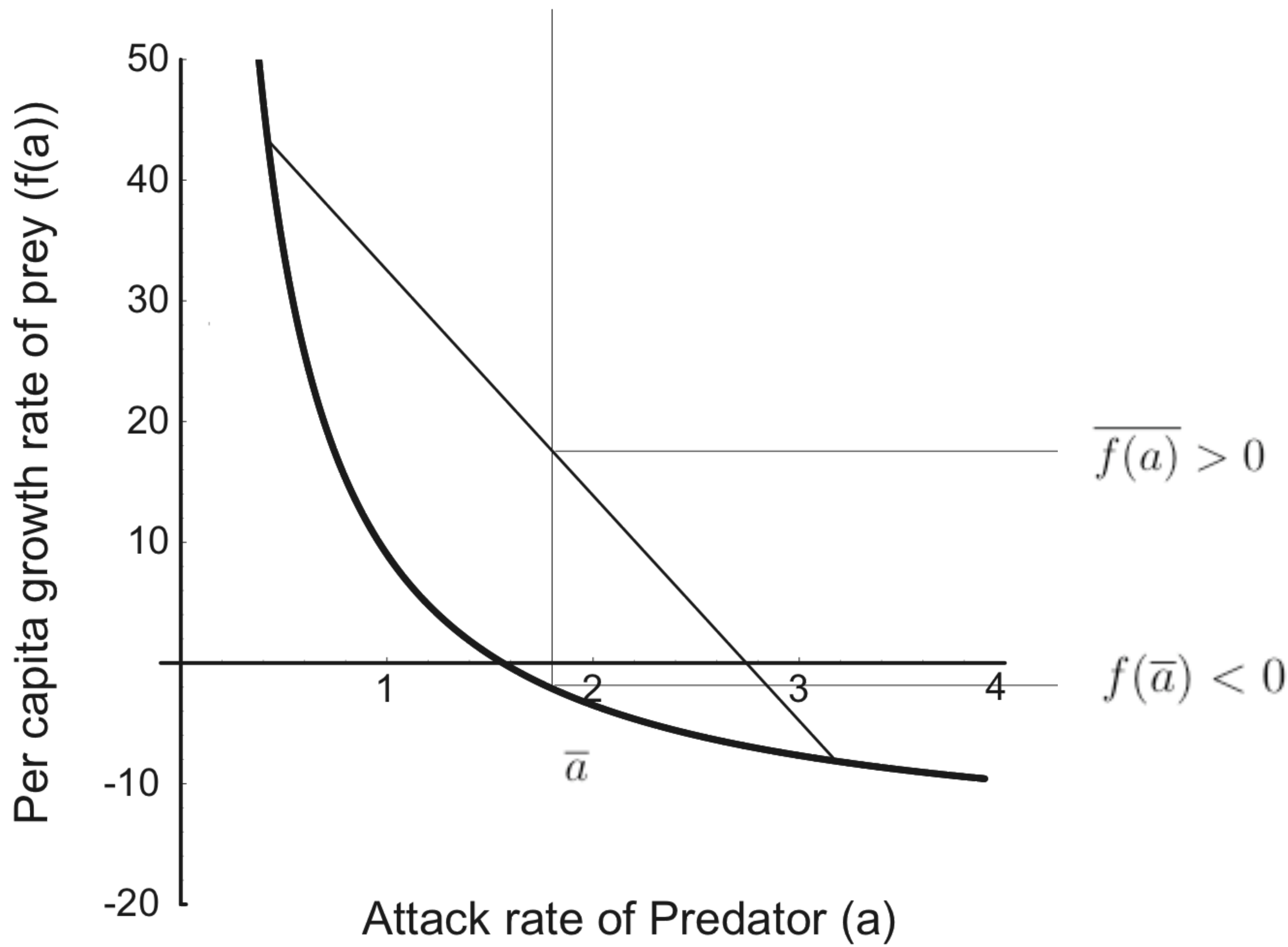
1. Non-linearity:
   negative feedback
   (negative density-dependence)

2. Heterogeneity
   (Jensen's inequality)

Jensen's Inequality



$$f(\overline{x}) \neq \overline{f(x)}$$


50
40
30
20
10
-10
-20
1
2
3
4
Per capita growth rate of prey (f(a))
Attack rate of Predator (a)
$\overline{f(a)} > 0$
$f(\overline{a}) < 0$
$\overline{a}$

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:

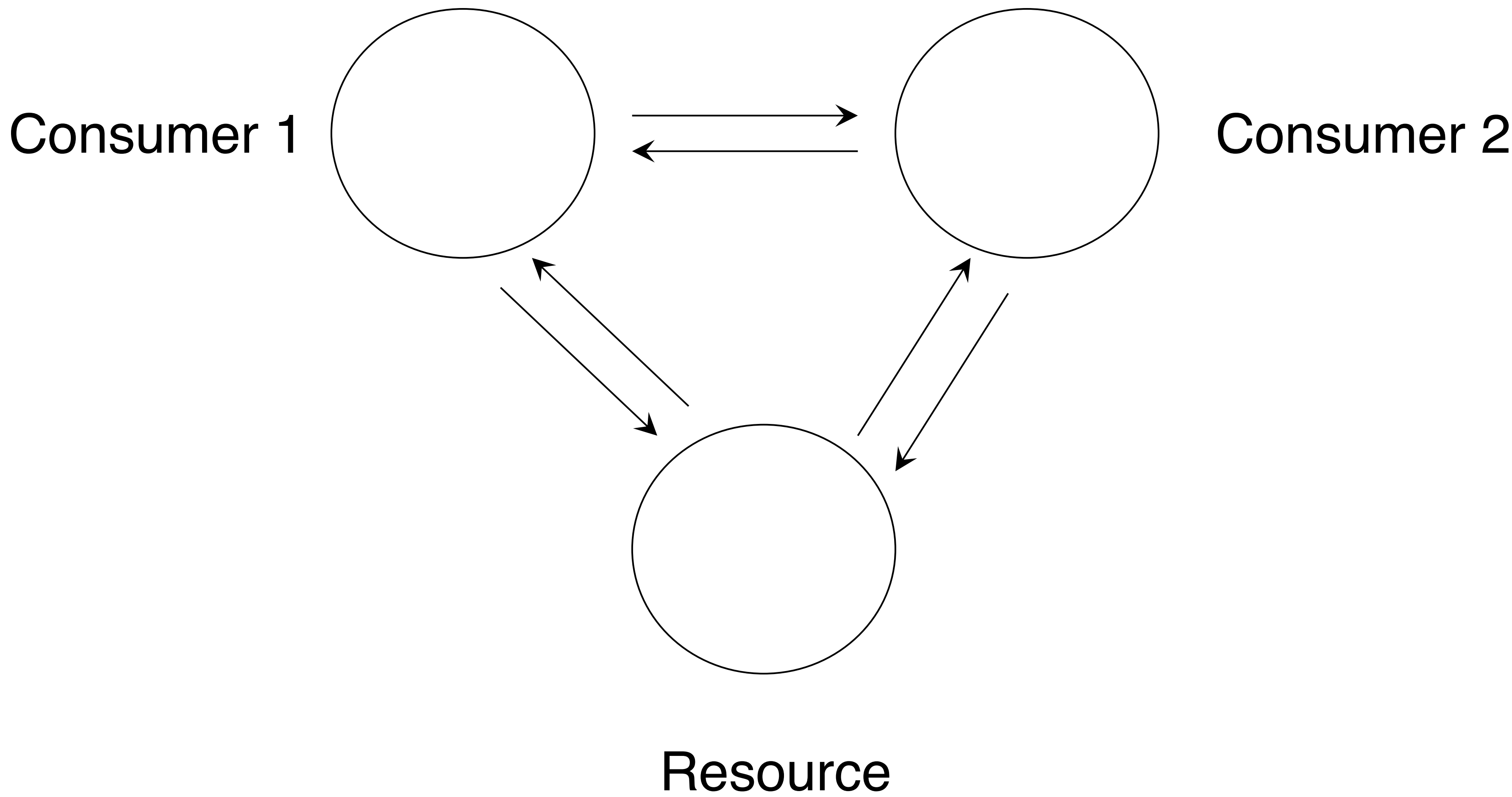
Exploitative competition (-/-)
Apparent competition (-/-)
Mutualism (+/+)
Consumer-resource (+/-)

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



Exploitative competition

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

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

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

Coexistence:

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

Stability: coexistence equilibrium stable to perturbations

Exploitative competition

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

Invasion criteria:

$$\frac{d_1}{e_1 a_1} < \frac{d_2}{e_2 a_2}$$ Consumer 1

$$\frac{d_2}{e_2 a_2} < \frac{d_1}{e_1 a_1}$$ Consumer 2

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:

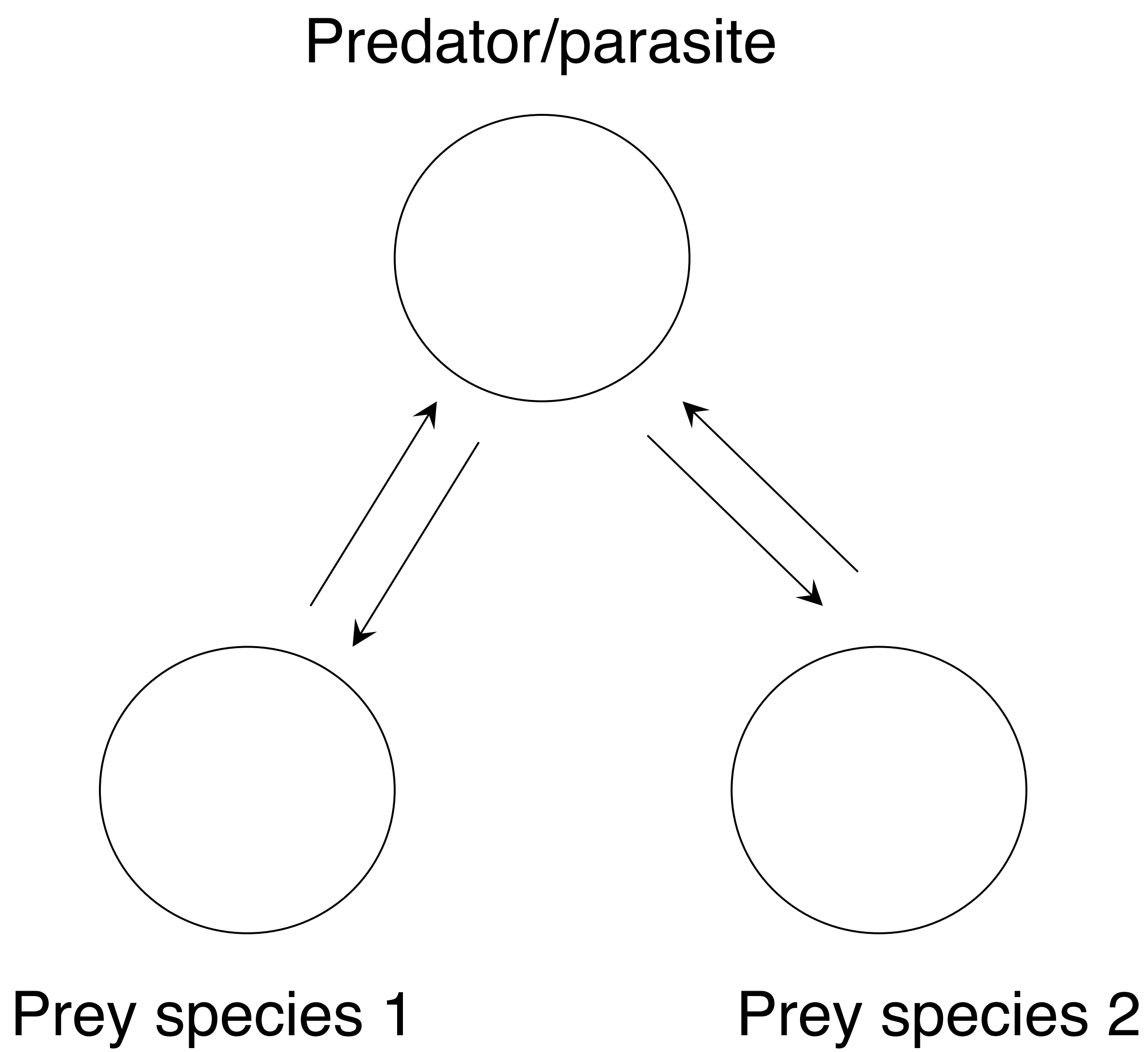
Exploitative competition (-/-) ✓
Apparent competition (-/-)
Mutualism (+/+)
Resource-consumer (-/+)

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



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

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

Invasion criteria:

$$\frac{r_1}{a_1} > \frac{r_2}{a_2}$$ Consumer 1

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

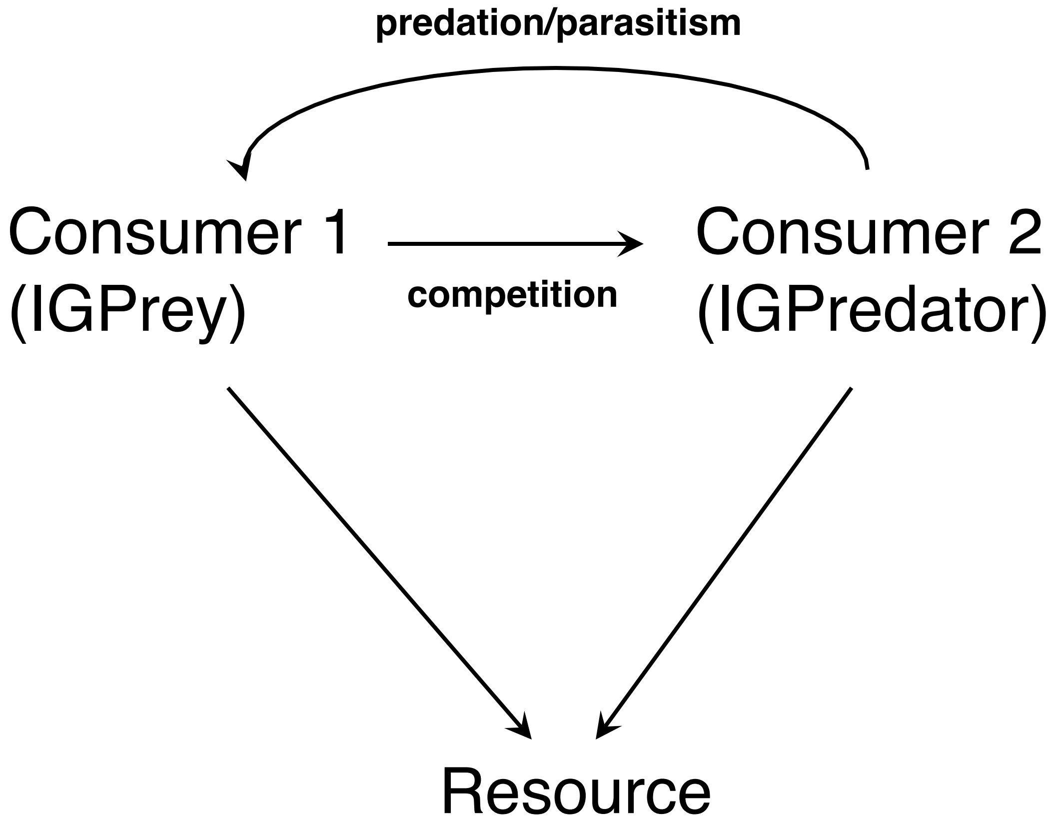
1. Inter-specific trade-offs (R^*, P^*)

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

Negative feedback: local niche partitioning ==>

Intra-specific > inter-specific

Coexistence via non-linearity: trade-offs



Intraguild predation

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

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

Boundary equilibria

Resource and Consumer 1 (IGPrey):

$$R^{\star} = \frac{d_1}{e_1}, C_1{}^{\star} = \frac{a_1 - d_1}{a_1^2}, C_2{}^{\star} = 0$$

Resource and Consumer 2 (IGPredator):

$$R^{\star} = \frac{d_2}{e_2}, C_1{}^{\star} = 0, C_2{}^{\star} = \frac{a_2 - d_2}{a_2^2}$$

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:

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

Invasion criterion for IGPredator:

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

Mutual invasibility

Recall: $R_{C_1}{}^{\star} = \frac{d1}{a1}, R_{C_2}{}^{\star} = \frac{d2}{a2}$

Consider IGPrey to be the superior resource competitor.

Then,

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

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

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

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

Then 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

IGPredator can invade when rare if:

$$(\mathrm{a}_1 - d_1) f \alpha > a_1(a_2 d_1 - a_1 d_2)$$

Intraguild predation | Resource competition

Coexistence:

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

Stability: coexistence equilibrium stable to perturbations ?

Coexistence equilibrium

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

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

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

Stability of coexistence equilibrium

Jacobian matrix for the three species community:

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

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

$$A_1 = R^\star,$$

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

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

Stability of coexistence equilibrium

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

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

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

$A_3 > 0$ if

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

$A_1 A_2 - A_3 > 0$ if

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

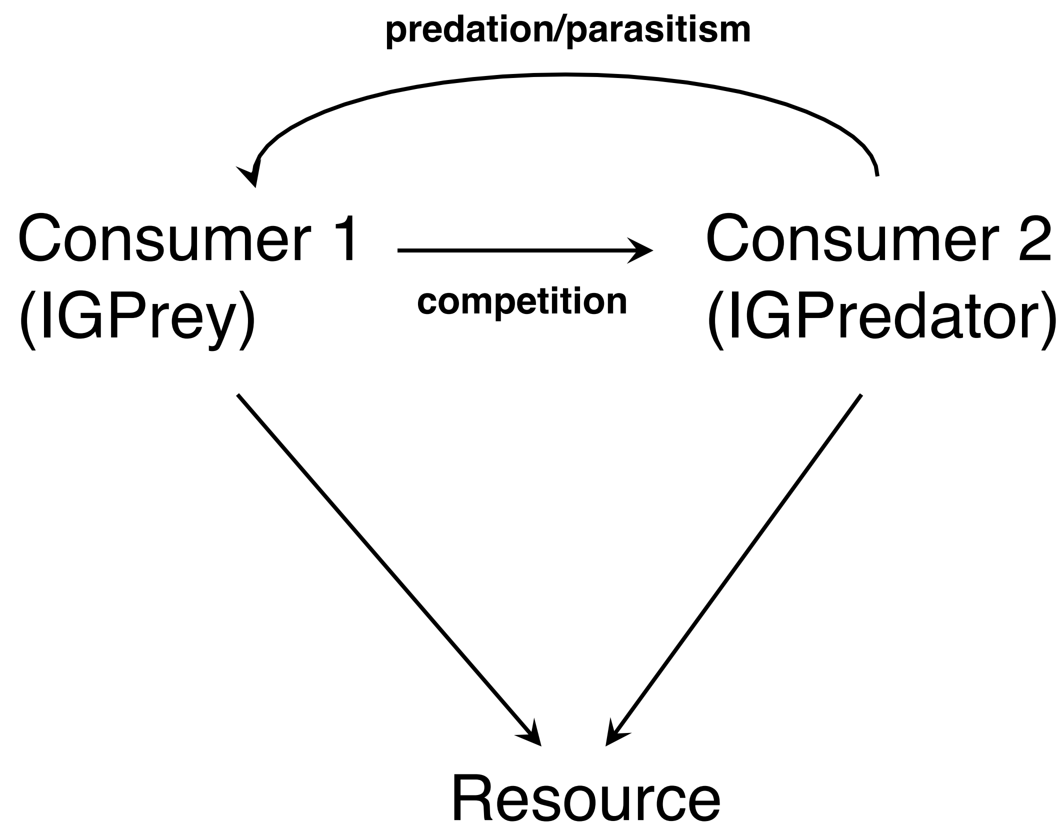
Stability of coexistence equilibrium

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: trade-offs



Intraguild predation

Coexistence via non-linearity: trade-offs

Interactions with competition and predation: intraguild predation

Coexistence: negative feedback via inter-specific trade-off

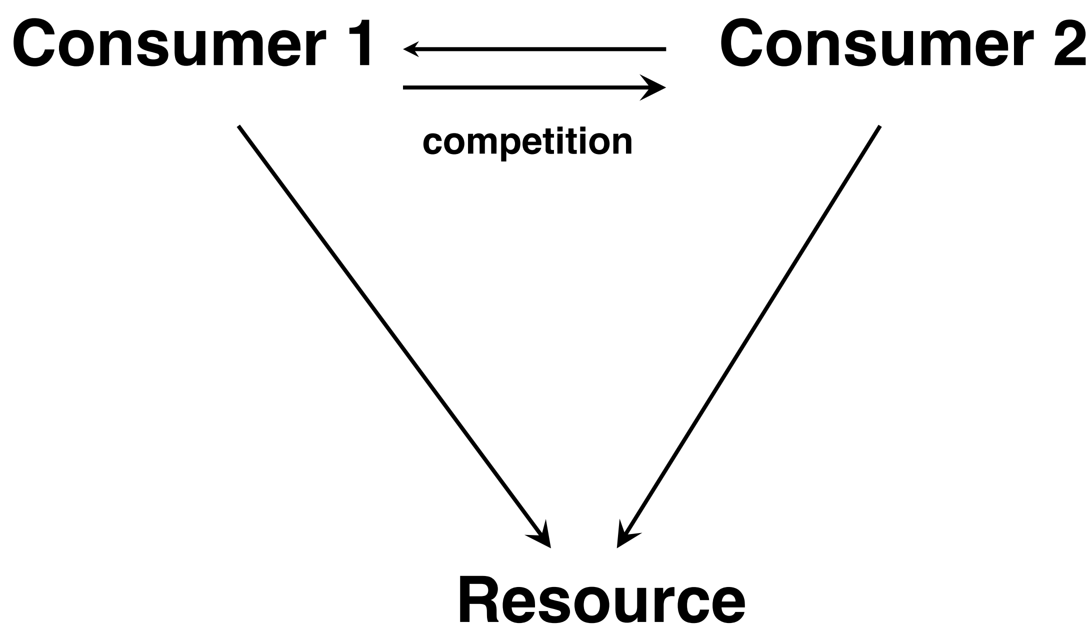
IGPrey is superior competitor for basal resource, IGPredator can consume IGPrey (local niche partitioning)

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



Exploitative competition

Exploitative competition

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

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

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

Linear functional responses

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

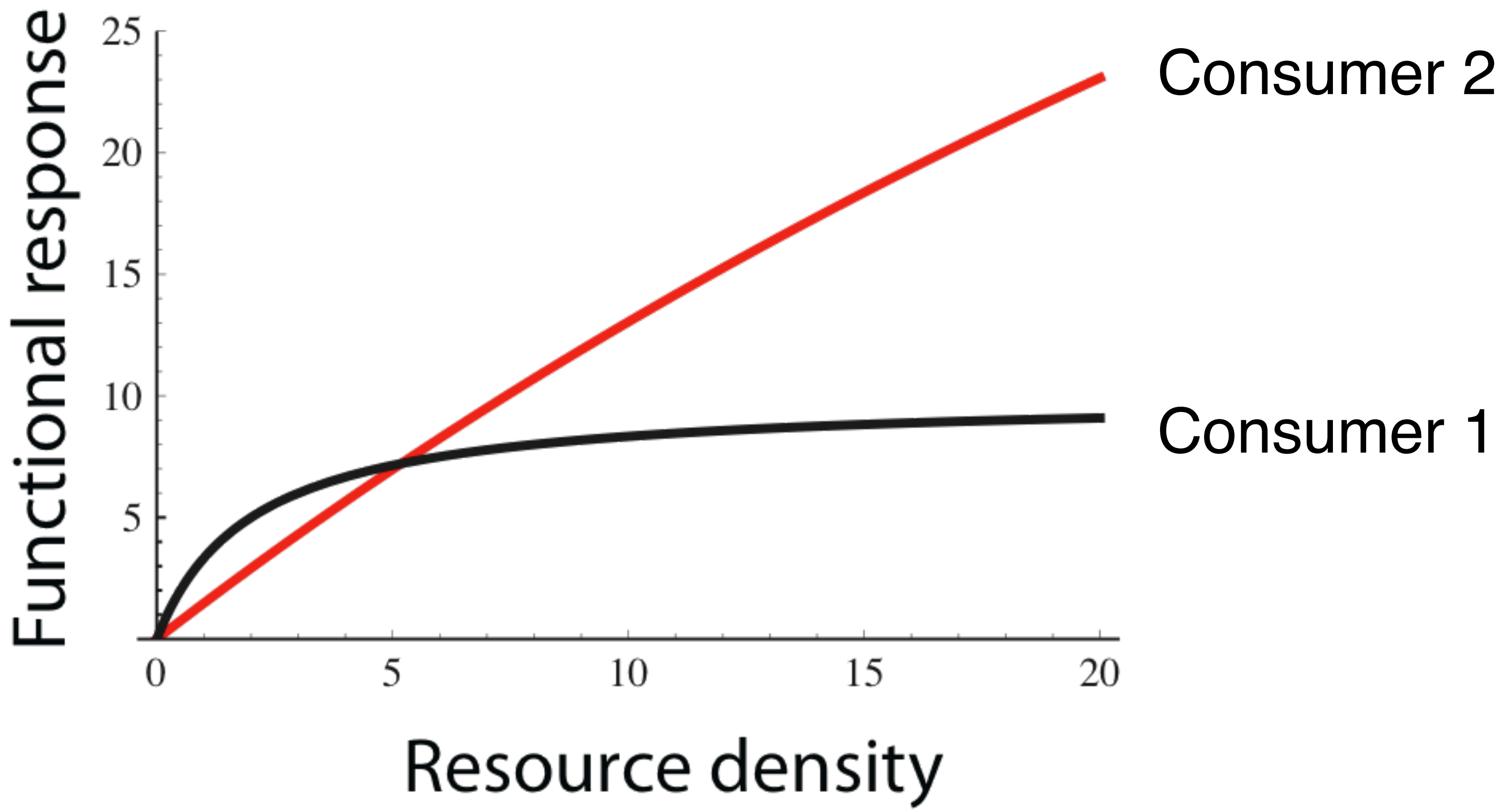
Exploitative competition with non-linear functional responses

$$\frac{dR}{dt} = rR\left(1 - \frac{R}{K}\right) - \frac{a_1 RC1}{1 + a_1 T_{h_1} R} - \frac{a_2 RC2}{1 + a_2 T_{h_2} R}$$

$$\frac{dC_1}{dt} = e_1 \frac{a_1 RC1}{1 + a_1 T_{h_1} R} - d_1 C_1$$

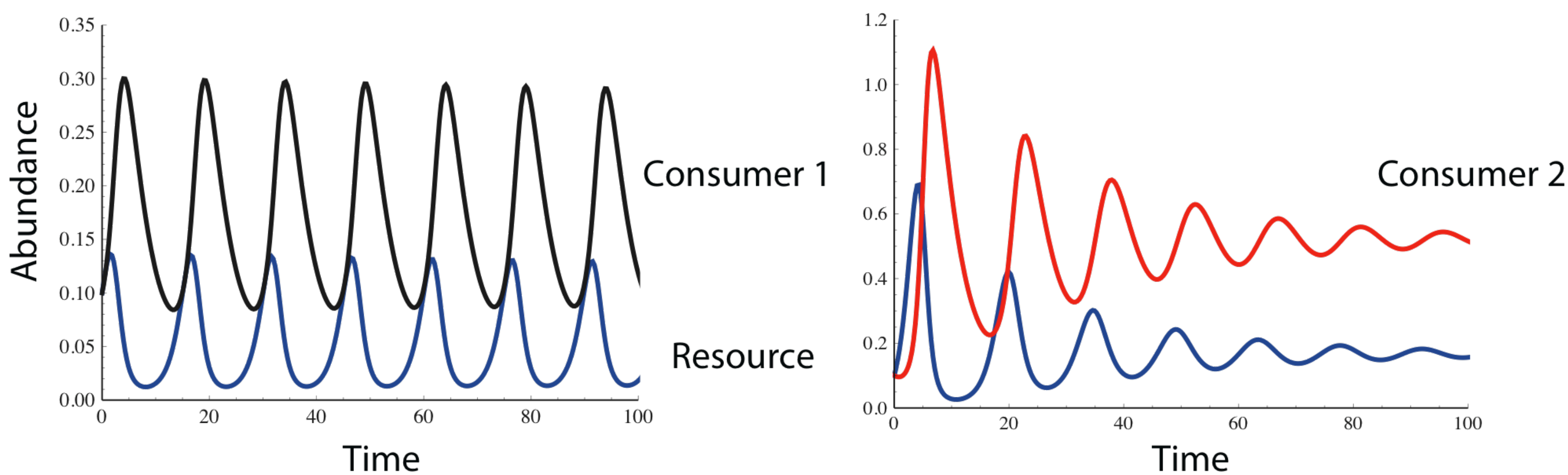
$$\frac{dC_2}{dt} = e_2 \frac{a_2 RC2}{1 + a_2 T_{h_2} R} - d_2 C_2$$

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)