Questions in Consumer-Resource Interaction Theory

1) When do we expect consumer-resource interactions to drive one species to extinction (i.e., unstable)?

2) When do we expect top-heavy interactions or biomass pyramids?

Above questions in terms of the influence of resource productivity & C-N interaction strength
The Rosenzweig-MacArthur (RM) Consumer-Resource Model

1) Resource grow logistically in absence of consumer

2) Type II functional response

3) Biomass growth of consumer is a fraction of consumption function “you are what you eat”

*Model produces a range of dynamics (excitable and non-excitable) and ends up being a good model to examine the role of other biological structure
The RM Predator-Prey Model

\[
\frac{dN}{dt} = rN(1 - \frac{N}{K}) - \frac{aNC}{N + b}
\]

\[
\frac{dC}{dt} = e\frac{aNC}{N + b} - mC
\]

- \(N\) = resource biomass density (e.g., kg/m\(^2\))
- \(C\) = consumer biomass density
- logistic growth
- Type II consumption rate
- Growth rate
- Maintenance cost or loss in biomass
- \(e\) = efficiency of conversion into consumer biomass
- \(m\) = biomass loss rate per unit of \(C\)

*Growth rate* and *Type II consumption rate*
Consumer-Resource Theory

(i) Graphical Analysis (Phaseplane)

(ii) 4 Qualitatively Different Dynamical Outcomes

- consumer cannot persist
- stable equilibrium – non-excitabale dynamics
- stable equilibrium \( \rightarrow \) excitabale (oscillatory decay)
- cycles \( \rightarrow \) excitabale

(iii) Relationship to C:R biomass pyramids

(iv) Some Model Experiments

**How do the dynamics change as we increase productivity (K)?**

**How do the dynamics change as we increase interaction strength?**

(v) Some stabilizing factors

(vi) Lab and Field Results
(i) Graphical Analysis: Phaseplane

\[ \frac{dN}{dt} = rN(1 - \frac{N}{K}) - \frac{aNC}{N+b} \]

N-isocline \( \rightarrow \) \( \frac{dN}{dt} = 0 \)

i.e., given parameter values (e.g., \( r, K, a \))
then isocline is the combination of 
C & N densities that imply N is not

Growing \( \frac{dN}{dt} = 0 \)

\[ C = r(1 - \frac{N}{K})(N+b) \]

\[ a \]
(i) Graphical Analysis

\[
dC/dt = eaN/(N+b) - dC
\]

C-isoclone \( \Rightarrow dC/dt = 0 \)

i.e., the combination of C & N densities that imply C is not growing

\[
dC/dt = 0
\]

when

\[
N = \frac{bd}{ea-d}
\]
(i) Graphical Analysis

Understanding the flows around the isoclines start to unfold how C and N change through Time.

Red dot is equilibrium.
(i) Graphical Analysis

Solutions on the phaseplane can be interpreted as changes through time (time series – densities vs. time)

Phaseplane C vs. N

Time Series C vs Time

N vs Time
(ii) 4 qualitative outcomes to this model:

(1) **Cyclic dynamics (excitable):** occurs whenever consumer isocline \( \frac{dC}{dt} = 0 \) lies to the left of the peak on the resource \( \frac{dN}{dt} = 0 \) isocline.
(ii) 4 Basic outcomes to this model:

(2) Stable equilibrium dynamics (excitable with oscillatory decay): occurs whenever consumer isocline ($dC/dt=0$) lies to the right of the peak on the resource ($dN/dt=0$) Isocline, but not near $N=K$ (see next case)
(ii) 4 Basic outcomes to this model:

(3) **Stable equilibrium dynamics (non-excitable):** occurs whenever consumer isocline \((dC/dt=0)\) lies WELL to the right of the peak on the resource \((dN/dt=0)\) Isocline (i.e., it is relatively close to \(N=K\))
(ii) 4 Basic outcomes to this model:

(4) Resource goes to carrying capacity, $K$, & consumer goes extinct.
“In each case, increasing the supply of nutrients or energy tends to destroy the steady state. Thus man must be very careful in attempting to enrich an ecosystem in order to increase its food yield. There is a real chance that such activity may result in decimation of the food species that are wanted in greater abundance.”

M. Rosenzweig

*Paradox of enrichment* …

Science, 1971
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

![Diagram](attachment:image.png)

- $dN/dt = 0$:
  - $dC/dt = 0$
  - Consumer $(C)$ does not exist
- Very low $K$'s (similar to low productivity)

`Resource (N)`
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

- Low $K$'s: stable equilibrium (non-excitable)
  - Consumer & resource persist and maintain constant densities through time

\[
\begin{align*}
\frac{dC}{dt} &= 0 \\
\frac{dN}{dt} &= 0
\end{align*}
\]
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

**Diagram:**

- $dN/dt=0$
- $dC/dt=0$

**Moderate $K$'s:**

- Stable equilibrium (excitable; oscillatory decay)
- Consumer & resource persist and maintain constant densities through time
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

![Graph showing resource (N) and consumer (C) dynamics.](graph)

- **$dN/dt=0$**
- **$dC/dt=0$**
- **High $K$’s**: unstable equilibrium (excitable; oscillations)
- Cycles and can reach low densities periodically
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

CV shows same stability pattern

\[ \lambda \] (eigenvalue)

Rapid return (more resilient, more stable)

$K$ (surrogate for resource productivity)
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase resource carrying capacity, $K$?

$\lambda$ (eigenvalue)

Rapid return (more stable)

Excitable domain
Destabilizing (complex eigenvalues)

Non-excitable Stabilizing (real eigenvalues)

K (surrogate for resource productivity)
As the system becomes more productive, consumer-resource interactions become less stable (more excited or oscillatory) and therefore more prone to extinction.

Density

Resource

Consumer

Low densities prone to extinction

time
What happens to mean consumer:resource density (or equilibrium densities) across resource carrying capacity (productivity)?

\[ \text{dN/dt} = 0 \]

Low C:N ratio

*Consumer can be dangerously low densities
What happens to mean consumer:resource density (or equilibrium densities) across resource carrying capacity (productivity)?

\[ \frac{dN}{dt} = 0 \]

C:N ratio increases with carrying capacity, K (productivity)
What happens to mean consumer:resource density (or equilibrium densities) across resource carrying capacity (productivity)?

C:N ratio increases with carrying capacity, $K$ (productivity)

System gets top-heavy & can be inverted
FULL STORY:

Top Heavy

C:R

C
N

λ
(return time)

More stable
Rapid return

Oscillations
Oscillatory decay

K
FULL STORY:

Top Heavy

C:R

C
N

Low productivity prone to “mean-driven extinction”

More stable
Rapid return

λ
(runtime)

K

High productivity prone to “variance instability” or “variance-driven extinction”

Suppression-Stability Trade-off
Summary:

Biomass Pyramids
Increased resource productivity tends to make consumer-resource interactions more top heavy (i.e., increases C:N density ratio)

Stability
(i) Increased resource productivity tends to make “non-excitile” consumer-resource interactions more stable

(ii) Increased resource productivity tends to make “excitable” consumer-resource interactions less stable
Last Class
Consumer-Resource Interaction Theory

Phaseplanes, Isoclines and Dynamics (vectors)

4 qualitatively different types of population dynamics

What is the influence of resource productivity on population dynamics/stability?

Paradox of Enrichment
Qualitative outcomes of Consumer-Resource Model:

(1) Resource goes to carrying capacity, $K$, & consumer goes extinct

Equilibrium: No consumer (C), resource (N) at carrying capacity, $K$
Qualitative outcomes of Consumer-Resource Model:

(2) Stable equilibrium dynamics (non-excitable): occurs whenever consumer isocline ($\frac{dC}{dt}=0$) lies WELL to the right of the peak on the resource ($\frac{dN}{dt}=0$) isocline (i.e., it is relatively close to $N=K$)

Equilibrium: low Consumer:Resource ($C:N$) biomass
Qualitative outcomes of Consumer-Resource Model:

(3) Stable equilibrium dynamics (excitable with oscillatory decay): occurs whenever consumer isocline ($dC/dt=0$) lies to the right of the peak on the resource ($dN/dt=0$) isocline, but not near $N=K$ (see previous case).

Qualitative outcomes of Consumer-Resource Model:

(4) Cyclic dynamics (excitable): occurs whenever consumer isocline \((dC/dt=0)\) lies to the left of the peak on the resource \((dN/dt=0)\) isocline.

Equilibrium: high Consumer:Resource \((C:N)\) biomass
LAST CLASS: SUMMARY

Increasing resource productivity makes top heavy biomass pyramids more stable. Rapid return.
LAST CLASS: SUMMARY

Top Heavy

C:R

Low productivity prone to “mean-driven extinction”

More stable
Rapid return

High productivity prone to “variance instability” or “variance-driven extinction”
Summary:

Biomass Pyramids
Increased resource productivity tends to make consumer-resource interactions more top heavy (i.e., increases C:N biomass ratio)

Stability
(i) Increased resource productivity tends to make “non-exitable” consumer-resource interactions more stable

(ii) Increased resource productivity tends to make “excitable” consumer-resource interactions less stable
Interaction Strength (IS): A Flux-based Measure

Interaction strength (IS):

- $IS_{CN} = -aN/(N+b)$
- $IS_{NC} = +faN/(N+b)$

the rate of flow of biomass (energy) per unit of consumer between consumer and resource
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase interaction strength? (actually change attack rate, a)

very low attack rate (a)
very weak IS
Consumer does not exist
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase interaction strength? (e.g., change attack rate, $a$)

- **dN/dt = 0**
- **dC/dt = 0**

- **Low attack rate’s ($a$)**
- **Low IS**
- **Stable equilibrium**
  - (non-excitatable)
  - *Low C:N* (consumer:resource)

Eltonian Biomass Pyramid
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase interaction strength? (actually change attack rate, a)

*moderate C:N (consumer:resource)

moderate attack rate’s (a)
moderate IS
Stable equilibrium
(excitable, oscillatory decay)

[Diagram]

Consumer (C)

Resource (N)
(iii) Some Model Experiments

How do we expect the dynamics of the system to change as we increase interaction strength? (actually change attack rate, a)

- High attack rate’s (a)
- strong IS
- cyclic dynamics
- *High C:N or
  Inverted biomass pyramid
Given excitable dynamics then:

As consumer-resource interaction strength increases, consumer-resource interactions tend to become more top heavy (high C:N biomass ratios) and less stable (more oscillatory) and therefore more prone to extinction.

As energy flow increases between consumer and its resource the interaction becomes more oscillatory (drives "runaway consumption" or overshoot dynamics)
Summary: The influence of increased energy flux, interaction strength or resource productivity

- Stabilizing in non-excitable zone
- Destabilizing in excitable zone

*See this in assignment#2*
A Corollary to Consumer-Resource Interaction Theory

If high energy flow between a consumer and its resource tends to destabilize the consumer resource interaction (excitable)

THEN anything that inhibits energy flow can act to stabilize the interaction against runaway consumption
Some Stabilizing Mechanisms in Consumer-Resource Theory

All stabilizing features involve a reduction in energy flow to the consumer (prevents it from building up lots of consumer biomass) or weakens the consumers influence on the resource

1) Refugia \(\rightarrow\) when resource densities are low resources become inaccessible (type III functional response)

   refuge in space, size, prey switching response

2) Consumer interference \(\rightarrow\) when consumers are at high densities (prey tend to be at low densities) interference lowers attack rates

3) Donor control \(\rightarrow\) consumers are given the “doomed surplus” but do not eat healthy resources/prey
Experiments and Field Results
Principle of Energy Flux & Paradox of Enrichment (Luckinbill 1973)

**Control**
- Oscillations cause extinction

**Manipulation**
- Reduced attack rates with methyl cellulose which made the water more viscous and slowed interaction rates

Excitable dynamics stabilized (persisted) by weakening IS & reducing K

K about 1000

K reduced to 400

http://www.youtube.com/watch?v=rZ7wv2LhynM
Productivity and stability (paradox of enrichment)


Production moved through all dynamic predictions. C extinction, Stable dynamics, oscillations and collapse due to oscillations.

*C density increased relative to N as predicted also (top heavy).
Daphnia Micrcosm Experiments (McCauley)

Daphnia feeding on phytoplankton under different nutrient inputs (changing K)

Get the paradox of enrichment

Showed less edible phytoplankton (bigger) less influenced (attack rate weaker \( \rightarrow \) weakens interaction strength)

Also found Daphnia have “resting eggs” that stabilize Daphnia-phytoplankton under low phytoplankton conditions (decouples or weakens the interaction)
Laboratory Consumer-Resource Experiments

1) Lab experiments are even more unstable than models

2) In general, find that experiments are consistent with the paradox of enrichment or principle of interaction strength/energy flux

3) In general, lab results are consistent with idea that weakening interaction strength (energy flow) begets more stable dynamics (excitable case)

4) Spatial scale and heterogeneity is important (e.g. Huffaker’s mite experiments)
Field Results:  
Principle of Interaction Strength/EnergyFlux or Paradox of Enrichment

Some field examples are consistent with these ideas but it has not been clearly shown in nature experimentally. Nature’s has “complexities” that likely prohibit the full expression of this instability (we will turn to this shortly).

Examples: Monocultures and Insect outbreaks  
e.g., Budworm on Balsam Fir cycles tend to be greater in Balsam Fir monocultures  
(greater productivity of firs, K, per unit area)

Called the Resource concentration hypothesis by entomological researchers
Field Results:
Principle of Interaction Strength/Energy Flux

Interaction strength and productivity in nature. Lynx are extremely mobile with high attack rates and Hares are very productive for their size, large cycles occur in this system.
Aquatic vs. Terrestrial:
Aquatic - small, more edible, high growth, high consumption rate
THEREFORE aquatic ecosystem have higher resource productivity and interaction strength (Global Population Dynamics Database; GPDD)

Herbivore:Plant Biomass Ratio
Higher in aquatic than terrestrial

More variable (high CV), less stable in aquatic ecosystems as well

Aquatic more top heavy and more variable dynamics
Field Results Summary

1) No controlled natural experiment that shows the paradox of enrichment or principle of energy flux (interaction strength)

2) BUT data suggestive that where we find wild cycles (high CV) and top heavy webs the results tend to be consistent with the theory - productive monocultures and pest outbreaks (High K) - aquatic versus terrestrial (aquatic have high K,a, etc.) - high attack rates and growth (e.g., lynx-hare)