UNIT 7: Exploitation

1 Introduction

- Exploitation is when interactions between two species are good for one species and bad for the other
  - Typically, the "exploiter" is taking resources from the other species
- Exploitation is widespread and highly diverse

Examples

- Antelopes graze on trees
- Lions eat antelopes
- Ticks feed on lions
- Swallows eat ticks
- Bacteria reproduce inside the swallow
- Viruses infect the bacteria ...

Types of exploitation

- These words are usually not used precisely, and I'm not going to test you on them
  - *Predation*: a *predator* kills and eats *prey*
  - *Parasitism*: a *parasite* lives on or in a *host* and makes use of host resources
    - Many parasites are *pathogens*, meaning that they cause disease
  - *Parasitoidism*: a *parasitoid* develops inside a host, but must kill the host to complete development
  - *Grazing*: a *grazer* takes food from another organism (typically a plant), and moves on

Borderline cases

- The categories listed above are useful, but not precise – and not used precisely
  - Do rabbits predate small plants, or graze them?
  - Are small insects on large trees grazers, or parasites?
  - Do intestinal worms in healthy people count as pathogens?
  - Anthrax is usually referred to as a parasite (or predator!), but should probably really be a parasitoid

More vocabulary

- Often interactions are grouped by the taxonomy of the species participating in the interaction
  - Herbivores eat plants
  - Carnivores eat animals
  - Micro-organisms are more likely than macro-organisms to be called parasites
  - Insects living on animals are more likely to be called parasites than insects living on plants

Exploiters and resources

- When we talk about exploitation in general, we will refer generically to the species being exploited as the **resource species**
- There is a strong analogy between resource species, and **abiotic** resources like water, light and nitrogen
  - Both benefit the species that use them
  - Both may, or may not, be depleted significantly by the activities of the species in question

1.1 Balance and equilibrium

- In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - **Answer:** As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - **Answer:** As exploiter population grows, the population of the resource species should decrease, which is bad for the exploiter
- Since each species has a negative effect on itself, these systems have a *tendency* to come to equilibrium
  - Equilibrium may be reached, or we may cycle around it

Equilibrium questions

- What factors determine the equilibrium levels of a resource-exploiter system?
- What factors determine whether neither, one or both species survive?
- What happens if people perturb the system (e.g., by eating a lot of one or the other species)?
- The equilibrium is of interest even if it is not reached:
  - if there are cycles, the equilibrium is what the system cycles around.

Reciprocal control

- Imagine a pair of exploiter and resource species whose population densities are mostly regulated by each other
  - The per capita growth rate of the exploiter population depends mostly on the density of the resource species
  - The per capita growth rate of the resource population depends mostly on the density of the exploiter species
- Poll: What will determine equilibrium values?
  - **<u>Answer</u>:** For equilibrium, each species must be at the density required to keep the *other* species balanced
  - **<u>Answer</u>:** We should have about as many foxes as required to control the rabbit population, and about as many rabbits as required to keep the fox population about constant.

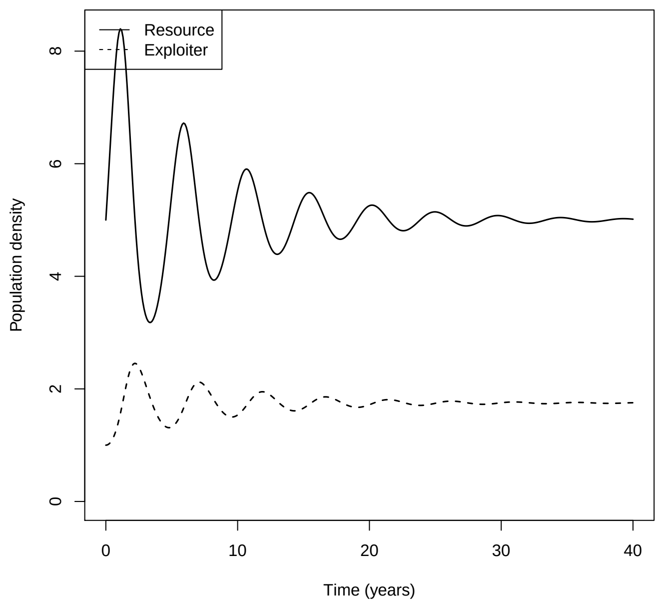
1.2 Tendency to oscillate

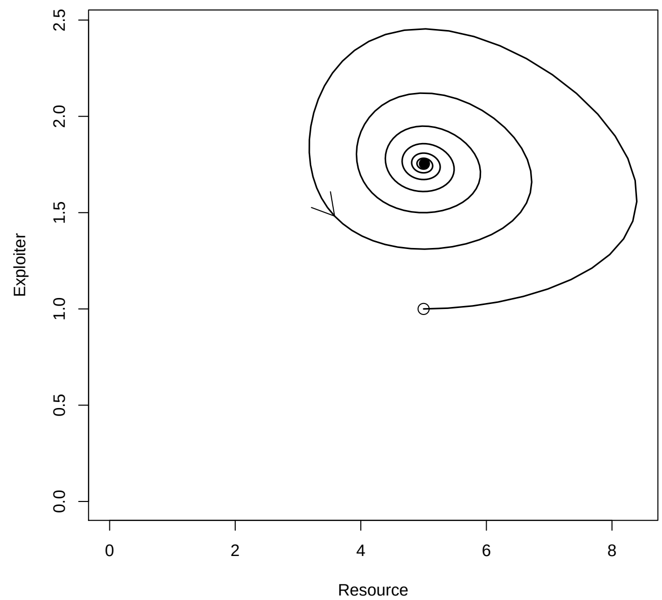
- In an exploiter-resource system, each species has an indirect, negative effect on itself
- This effect is delayed in time: it takes time for each species to respond to the other
- This means these systems have a tendency to oscillate
  - The same idea as from our population models, but with an explicit mechanism for delay
- There is a simple intuition for how these systems oscillate:
  - **<u>Answer</u>:** Exploiter goes up →Resource goes down →Exploiter goes down →Resource goes up →Exploiter goes up . . .

Persistence of oscillations

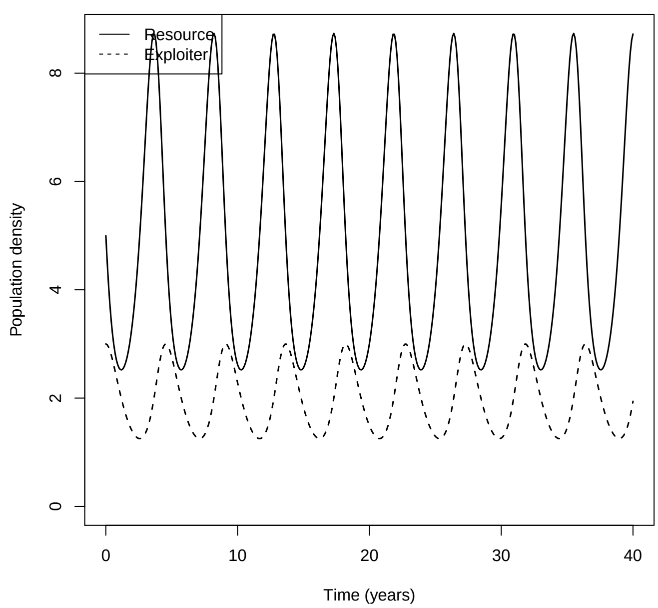
- Resource-exploiter systems have a *tendency* to oscillate
- In the simplest possible models, oscillations are **neutral**
  - e.g., they don't get larger or smaller
- In more realistic models, large oscillations will tend to get smaller
  - If small oscillations also tend to get smaller, we say that oscillations are **damped**
    * Oscillations which are not damped are **persistent**
  - If small oscillations tend to get larger, the system (usually) approaches a **limit cycle**

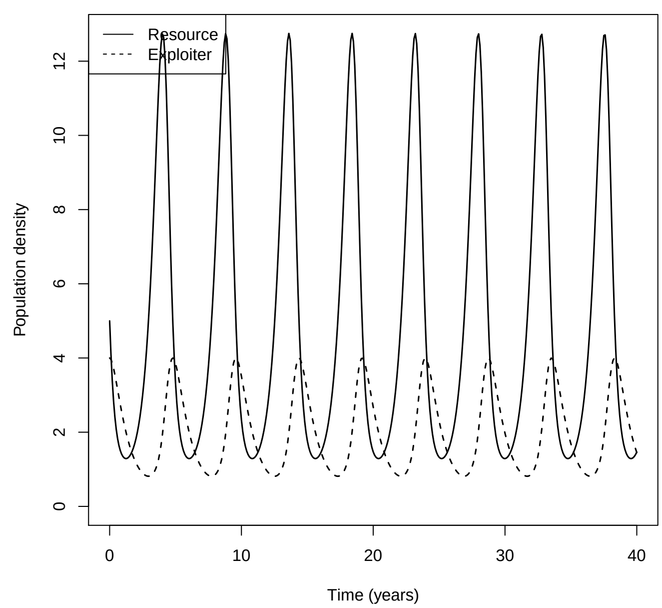
Damped oscillations



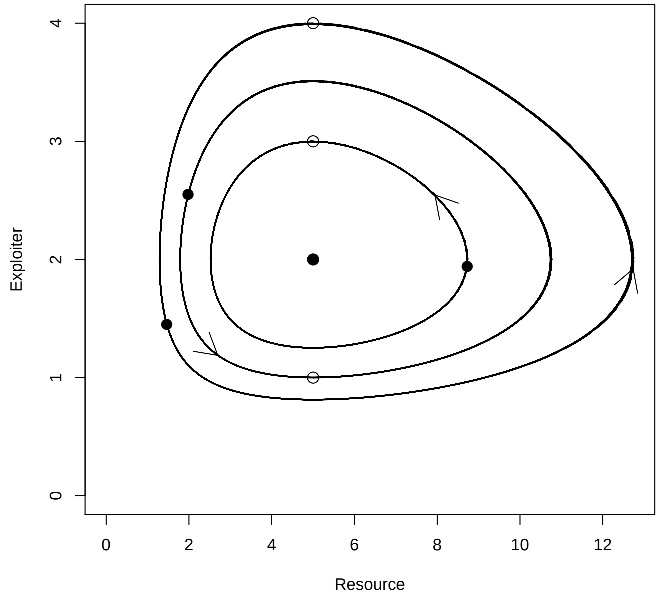


Neutral cycles

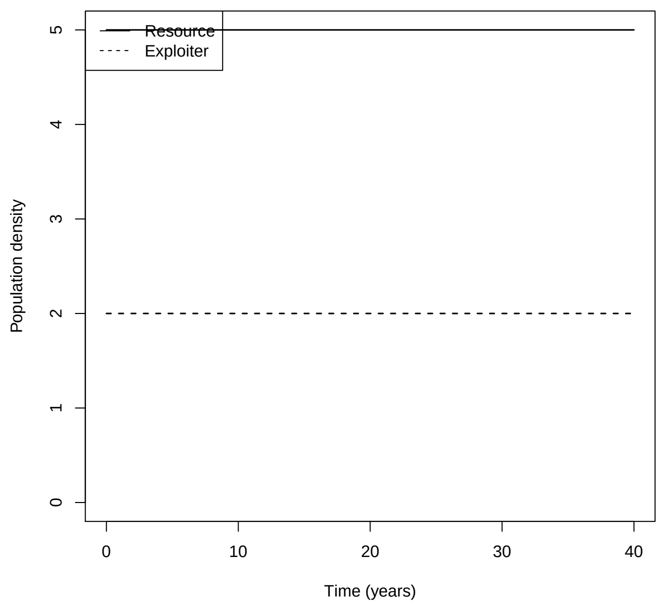




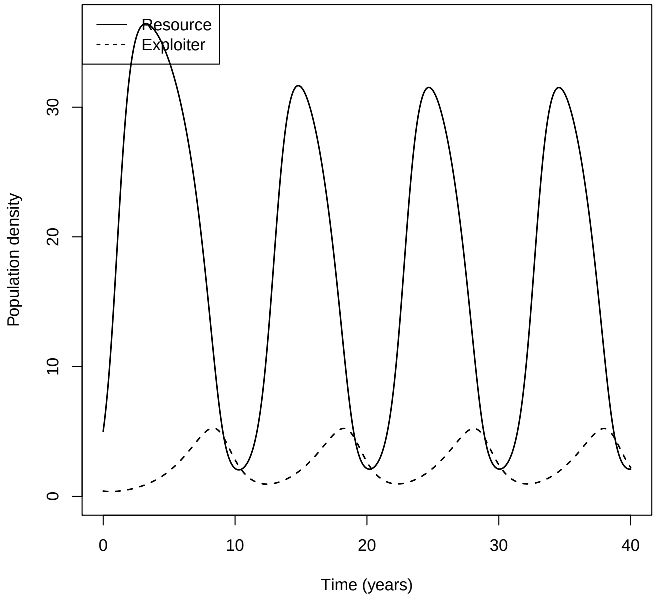
Neutral cycles

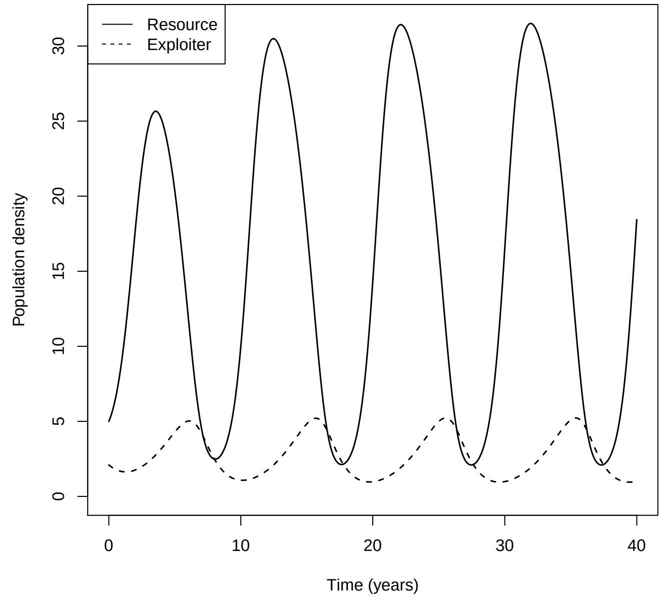


Comment slide: *Neutral cycles*

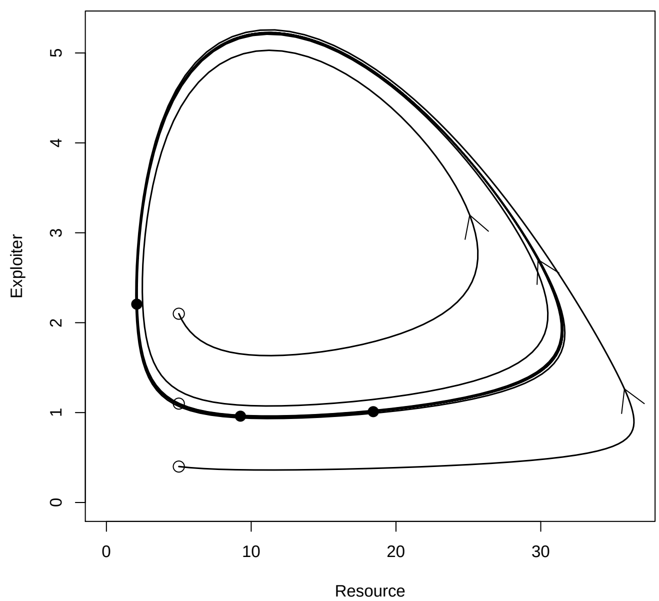


Limit cycles





Limit cycles



Neutral vs. limit cycles

- Poll: What is the difference between neutral cycles and limit cycles?
  - **Answer:** Neutral cycles have no tendency to get larger or smaller
    - **Answer:** Large cycles stay large, small cycles stay small
  - **Answer:** Limit cycles converge to a limit
    - **Answer:** Large cycles get smaller, small cycles get larger

2 A simple model

- We can investigate exploiter-resource systems using simple models
- Resource-species growth rate may depend on density of exploiter, or resource species, or both:
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
- Exploiter growth rate may depend on density of exploiter, or resource species, or both:
  - $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- At equilibrium:
  - **Answer:** $r_e = r_f = 0$
  - **Answer:** $r_f = N_e = 0$
  - **Answer:** $N_e = N_f = 0$
  - **Answer:** If $N_f = 0$, what happens to r_e?

Interactions

- What makes this a resource-exploiter system?
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - $\frac{dN_e}{dt} = r_e(N_e, N_f)N_e$
- **Answer:** We expect the resource species to be good for the exploiter (r_e goes up as N_f goes up)
- **Answer:** We expect the exploiter to be bad for the resource species (r_f goes down as N_e goes up)
- Mnemonic: e for exploiter, f for food.

Simplest model

- The simplest model of resource-exploiter interaction is when their per-capita growth rates only respond to each other.
  - $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$
- This is a pure **reciprocal control** model: resource growth rate depends only on exploiter density, and vice verse

Ratios

- This model assumes:
  - The rate at which individual fish get eaten depends on the total number of sharks
  - The rate at which individual sharks eat fish depend on the total number of fish
- The ratio of sharks to fish does not matter directly
- Does this make sense? What happens in the model if there are too many sharks, for example?
  - **Answer:** The number of fish will go down
  - **Answer:** *Then* the number of sharks will go down
  - **Answer:** Then the number of fish will go up ...

2.1 More detailed models

Resource populations

- Poll: Why might we expect resource population to affect per-capita growth rate of the resource species?
  - **Answer:** Competition for resources, territory, mates (density dependence)
  - **Answer:** Co-operation for protection, food-gathering (Allee effects)
  - **Answer:** Protection by numbers (predator satiation)

Exploiter populations

- Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - **Answer:** Competition for resources, territory, mates (density dependence)
  - **Answer:** Co-operation for protection, food-gathering (Allee effects)

Types of cycles

- The simplest models of reciprocal control lead to neutral cycles
  - Cycles starting from any starting point will go back through that starting point
  - These seem unrealistic; why should there be no tendency to spiral out or in for any cycle?
- To take the next step, we ask what factors will tend to:
  - make cycles get smaller (approach equilibrium)?
  - make cycles get larger (move away from equilibrium)?

2.2 Reciprocal control

- In this model, what happens to the *equilibrium* of this system if we reduce r_f, without changing r_e (for example, we start catching a lot more cod)?
  - **Answer:** The equation for change in N_e stays the same, so the equilibrium value of N_f must stay the same.
    - **Answer:** Unless N_e goes to zero!
  - **Answer:** The value of r_f has gone down, so we must increase it
    - **Answer:** by decreasing the number of exploiters

Reciprocal control

- In this model, what happens to the *equilibrium* of this system if we are at equilibrium, and then we reduce r_e without changing r_f (for example, we start killing sharks):
  - **Answer:** r_f doesn't change, so N_e must stay the same
  - **Answer:** r_e of the old equilibrium goes down, so N_f must increase
  - **Answer:** If we can't increase it enough, sharks go extinct, and fish increase to infinity.

Harvesting response

- Species under reciprocal control may respond to change in unexpected ways
- Imagine a community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- What will happen to these populations in the *short term* if people start fishing on a large scale (and catching large numbers of both sharks and fish)?
  - **Answer:** Populations will go down, because people are catching them

Harvesting equilibrium

- What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* if people start fishing on a large scale?
  - **Answer:** Shark population will go down (less sharks are needed to keep the fish in balance)
  - **Answer:** Fish population will go up (more fish are needed to keep the sharks in balance)

Real implications

- Until fairly recently, almost all species in the oceans were controlled primarily by interactions with other ocean species
  - Fishing food fish had little or no effect on the equilibrium number of fish at that **trophic level**
    - **Answer:** Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - **Answer:** *Increased the number of food fish*
- As fishing increases, this link is eventually broken
  - **Answer:** Fishing becomes an important regulator of ocean fish populations
  - **Answer:** Further increases in fishing can cause rapid declines in fish populations

3 Adding details

Resource density-dependence

- The most unrealistic aspect of the current model is that, in the absence of the exploiter, the resource species increases without limit
  - In reality, we would expect it, eventually, to be regulated.
- We can change our equations to allow the resource species to have a (negative) effect on itself:
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$

Predator satiation

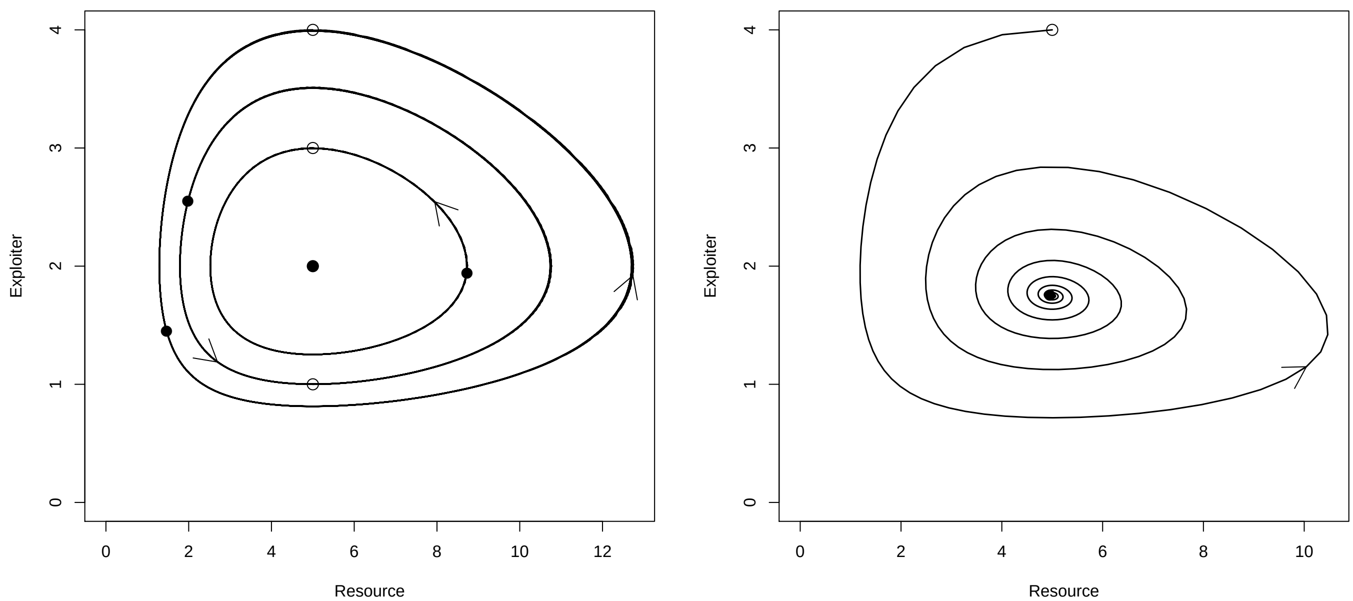
- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population
- What is the effect on feeding rates if the density of the *resource species* increases?
  - From the point of view of the exploiter?
    - **Answer:** Per-capita feeding goes up
  - From the point of view of the resource species?
    - **Answer:** Per-capita feeding goes down
  - Predator satiation means the resource species density can sometimes have a *positive* effect on its growth in the short term

3.1 Dynamics

Prey density dependence

- Reduces prey reproduction the most when prey numbers are highest
- Tends to pull cycles towards the middle
- Makes cycles get smaller, leading to **damped** cycles

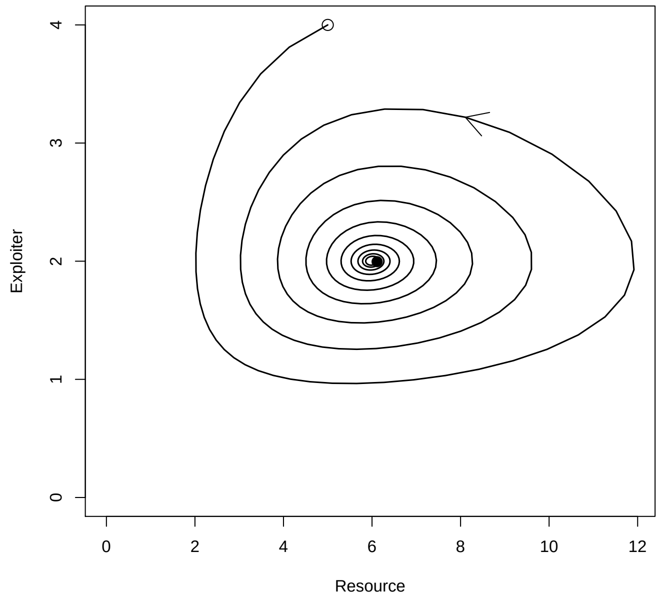
Prey density dependence



Predator density dependence

- Poll: If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?

Predator density dependence



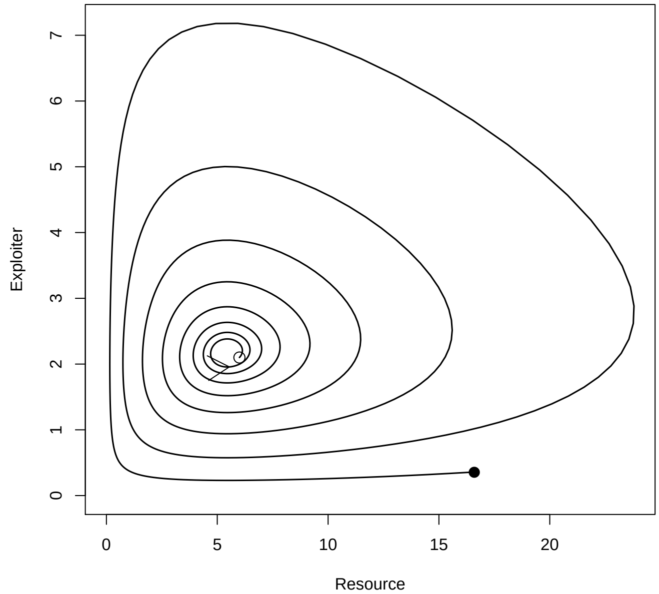
Predator density dependence

- Density dependence in the predator (exploiter species) has what effect on cycles?
  - **Answer:** Reduces predator reproduction when predators are the highest
  - **Answer:** This is not the same time as when prey are the highest, although we intuitively think that it is
  - **Answer:** Tends to cause damped cycles

Predator satiation

- Poll: The fact that predators can consume only limited amounts of prey has what effect on cycles?
  - **Answer:** Compared to neutral case, reduces predator reproduction when prey are the highest
  - **Answer:** Tends to make cycles get bigger
  - **Answer:** Without density dependence, makes cycles get bigger forever (oscillations increase to ∞)

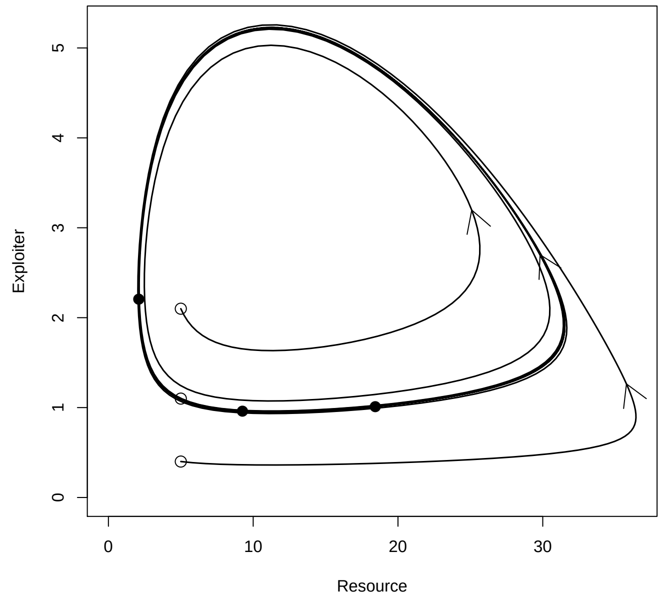
Predator satiation



Satiation with prey density dependence

- What sort of oscillations do we expect?
  - If density dependence is relatively strong?
    - **<u>Answer</u>:** Damped oscillations
  - If density dependence is relatively weak?
    - **<u>Answer</u>:** Close to equilibrium, we expect oscillations to increase
    - **<u>Answer</u>:** Far from equilibrium, density dependence takes over (prey cannot increase beyond their predator-free equilibrium) and oscillations decrease
    - **<u>Answer</u>:** We reach a "limit cycle" where the population oscillates

DD plus predator satiation



Oscillation summary

- *Neutral* cycles repeat from any starting point
- *Damped* cycles spiral in to the equilibrium.
- *Unstable* cycles spiral out forever
  - Biologically unrealistic
- A *limit cycle* is approached by spiralling out from near the equilibrium, and by spiralling in from far away
- Any oscillations that are not damped are called **persistent** — they don't go away

Oscillations in a complex system

- All resource-exploiter systems have a tendency to oscillate
- It often takes a long time for damped oscillations to die out, or for stable oscillations to converge
- Other stuff is going on at the same time
  - Other interactions
  - Environmental perturbations – weather, fire, people

Real-world implications

- If a resource-exploiter system is tightly linked, we expect to see some sort of noisy oscillations, with exploiter following resource (i.e., resource species goes up or down first)
- If the basic interaction leads to damped oscillations, we expect to see relatively small oscillations in reality
- If the basic interaction leads to stable oscillations, we expect to see relatively large oscillations in reality

3.2 Equilibria

Prey density dependence

- Imagine that the resource species has a negative effect on its own growth rate
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$
- What happens to the equilibrium if we start catching fish?
  - **Answer:** r_e doesn't change, so N_f can't change
  - **Answer:** r_f goes down and must be balanced by less sharks
- What if we start catching sharks?
  - **Answer:** r_e goes down, so N_f must go up
  - **Answer:** Increasing N_f decreases r_f, so N_e must go down

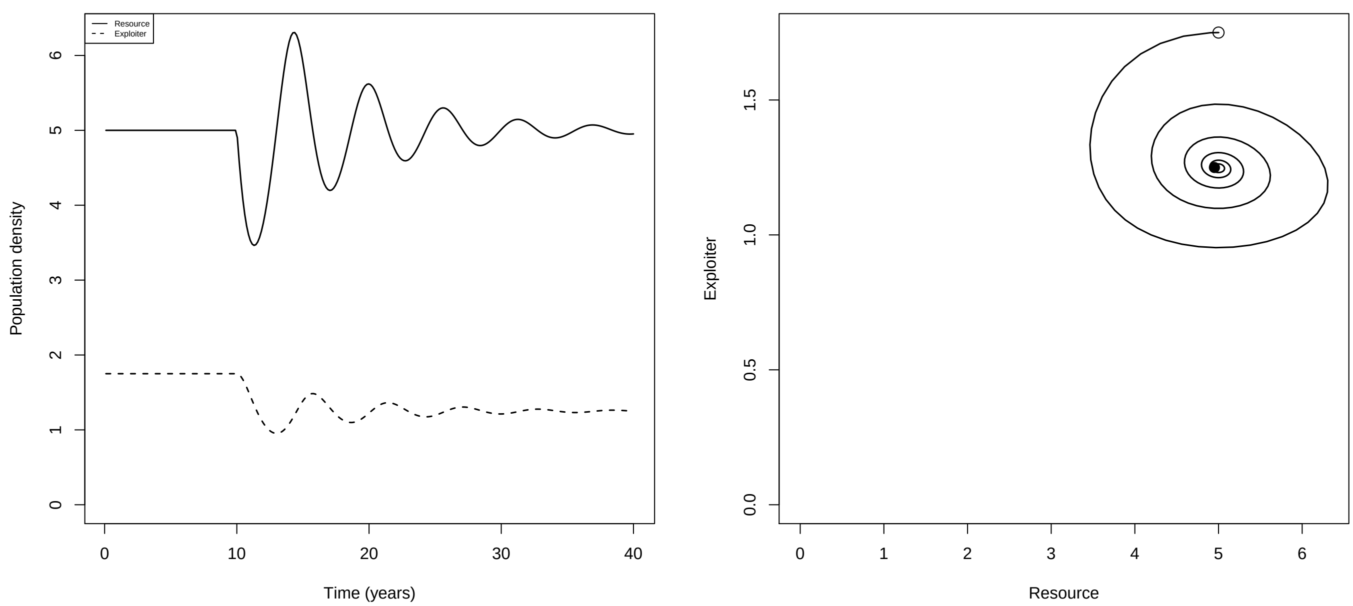
Predator satiation

- What if we also consider "satiation" – there is some limit to how much a predator can catch (or eat)
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$
- What happens to the equilibrium if we start catching fish?
  - **Answer:** r_e doesn't change, so N_f can't change
  - **Answer:** r_f goes down and must be balanced by less sharks
- What if we start catching sharks?
  - **Answer:** r_e goes down, so N_f must go up
  - **Answer:** Satiation: More fish means higher r_f means more sharks at equilibrium!
  - **Answer:** This is the opposite of what we see for density dependence, so we would have to ask which is the stronger effect in particular circumstances.

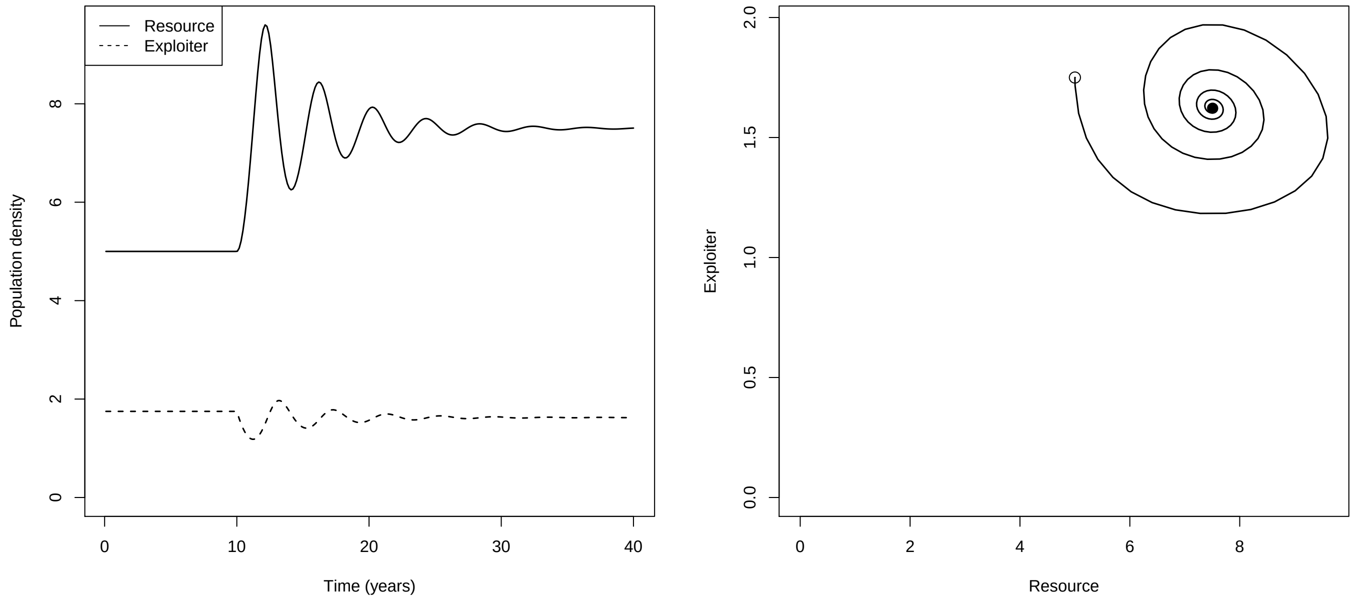
Examples

- Is reciprocal control realistic?
  - In the long term, catching fish isn't bad for fish populations? Feeding grouse doesn't improve long-term grouse populations?
- Poll: What happens *first* in this model if I start feeding grouse?
  - **<u>Answer</u>:** First we get more grouse, then we get more foxes, then we get less grouse, . . .
- Poll: What happens *eventually* in this model if I start feeding grouse?
  - **<u>Answer</u>:** Population eventually approaches (or orbits around) a new *equilibrium*, with more foxes, and the same amount of grouse as before

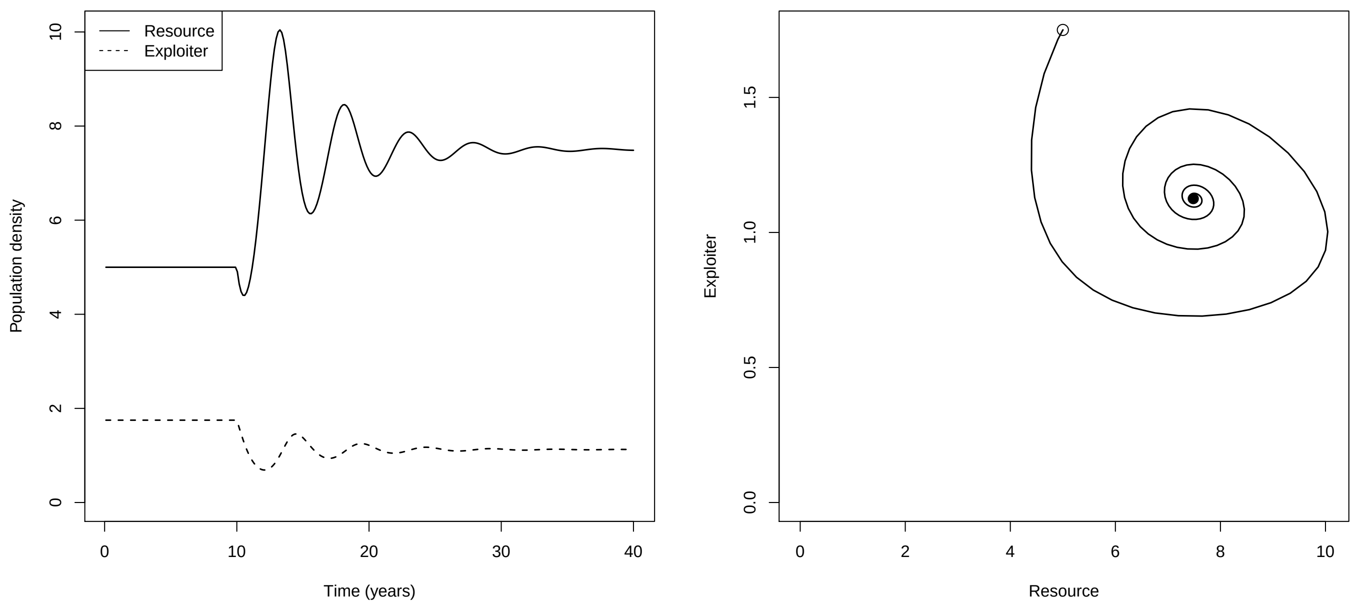
Harvesting dynamics



Harvesting dynamics



Harvesting dynamics



4 Who controls whom?

- These results tell us that how ecosystems respond to perturbation depends not only on the perturbation, but on how the ecosystems are regulated
- What controls populations of large fish in the ocean?

  - Sharks that eat them? Small fish that they eat?

- Studies of snowshoe hares
  - Very simple ecology: a few food species, one major predator
  - Food availability? Food edibility? Predators? Diseases?
- It's never a simple question

What controls ecosystem-level balance?

- Poll: Why is the earth green and the ocean blue?
  - **<u>Answer</u>:** The ocean could be green, and the earth could be brown
  - **<u>Answer</u>:** Why does the earth seem to be covered by plants, and the ocean doesn't?
- The question is: what trophic levels provide the primary control for which other trophic levels?
  - Top-down control theory: on land, herbivores are mostly controlled by carnivores, rather than by food
  - Plants fight back theory: plants invest enough in "defense" to escape herbivore control and compete with each other
- For each case, we can ask why the ocean is different