UNIT 6: 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
  - **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
- What will determine equilibrium values?
  - **Answer:** For equilibrium, each species must be at the density required to keep the *other* species balanced

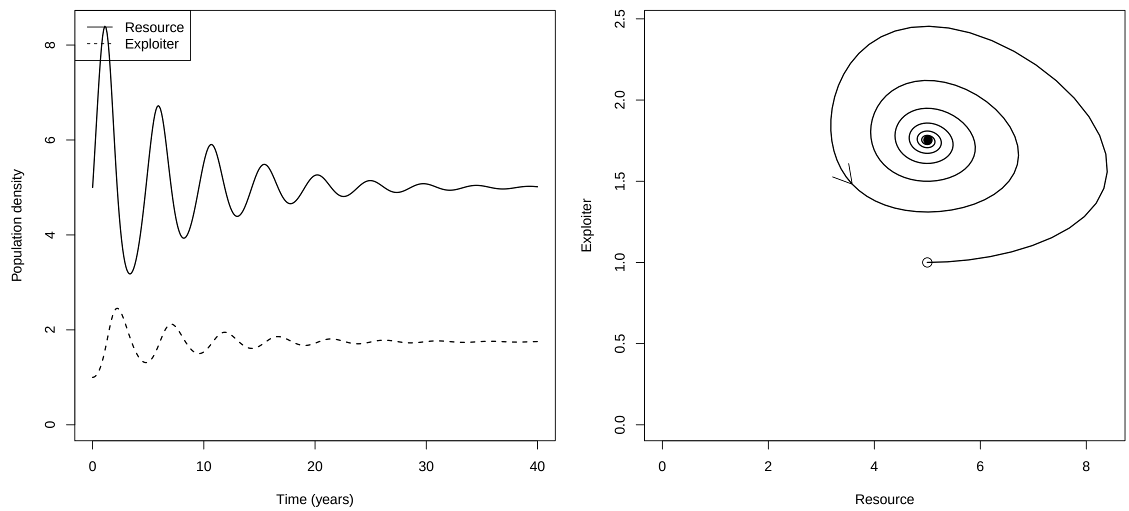
1.2 Tendency to oscillate

- 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:
  - **Answer:** Exploiter goes up →Resource goes down →Exploiter goes down →Resource goes up →Exploiter goes up . . .

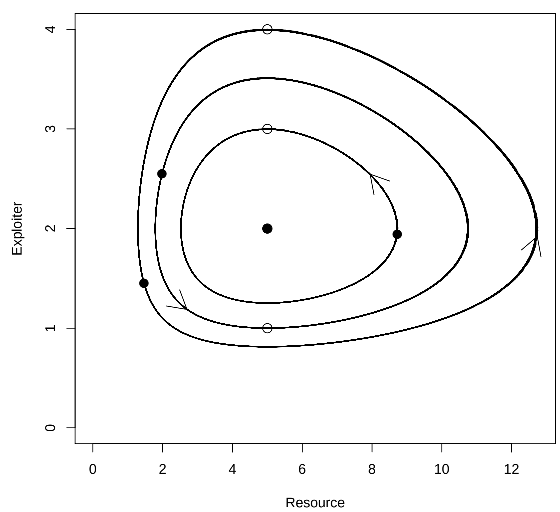
Persistence of oscillations

- Resource-exploiter systems have a *tendency* to oscillate
- In the simplest possible models, oscillations are *neutral*
- 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**
  - If small oscillations tend to get larger, we say that the system approaches a **limit cycle**

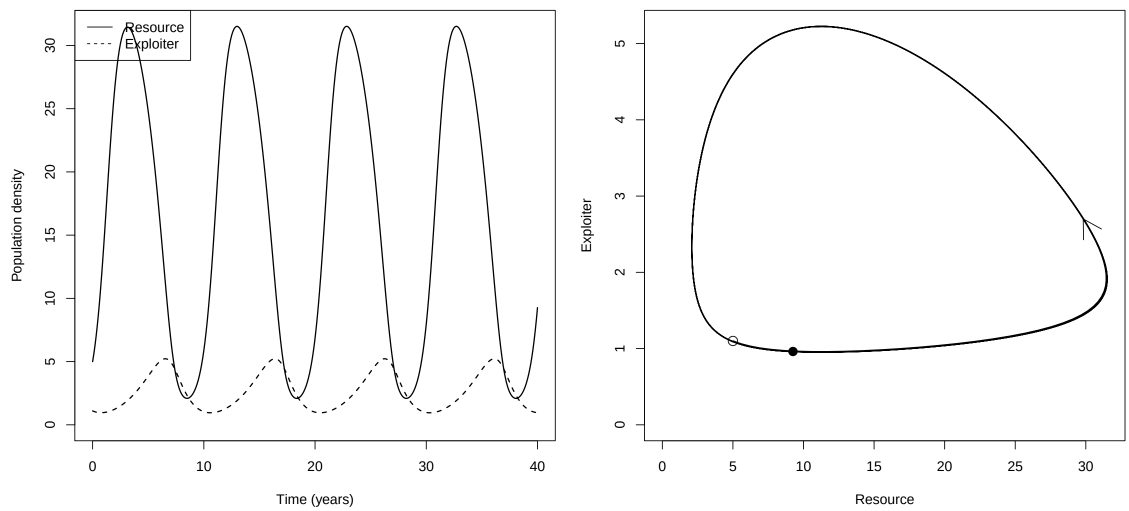
Damped oscillations



Neutral oscillations



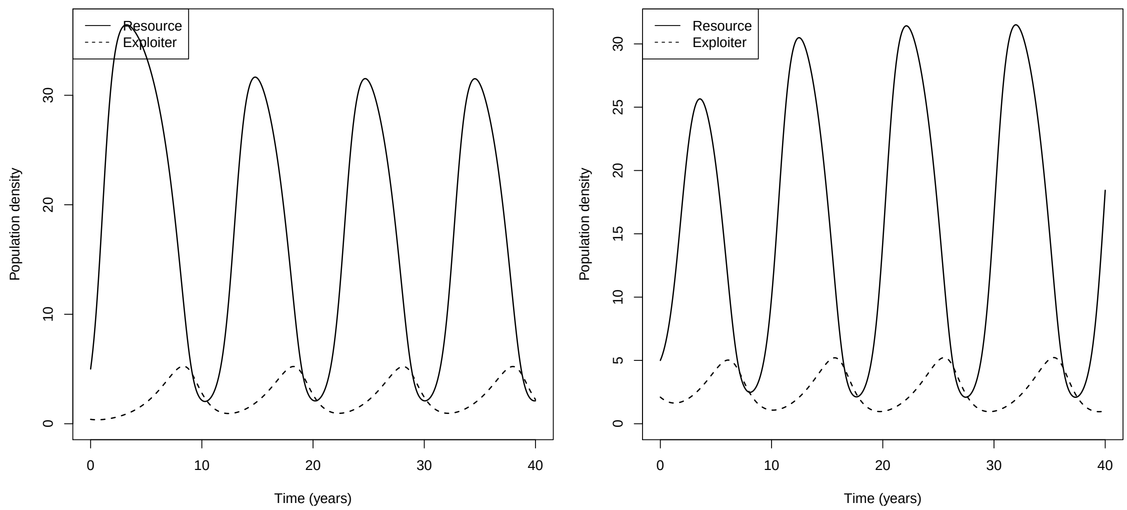
Limit cycles



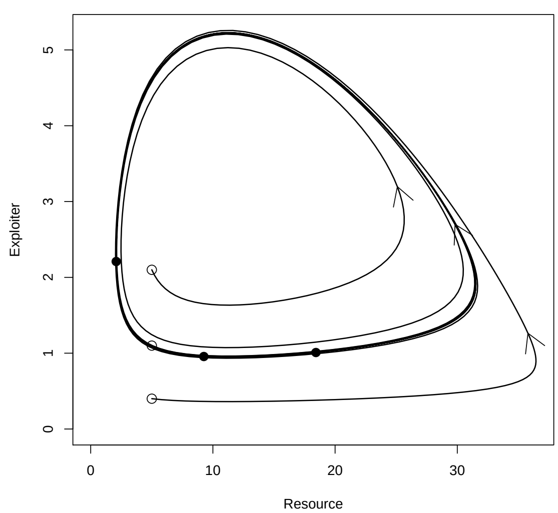
Neutral vs. limit cycles

- 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

Limit cycles



Limit cycles



2 Models

- We can investigate exploiter-host 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:** $N_e = N_f = 0$

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)

Simplest model

- The simplest model of resource-exploiter interaction is that 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

- 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)

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
  - **<u>Answer</u>:** If we have ten times as many fish, sharks will eat ten times as fast; not always possible for the sharks
- We address this problem with the same equations as above, but now the resource species can sometimes have a positive effect on itself, especially when exploiter densities are low.

3 Equilibrium and balance

3.1 Reciprocal control

- Imagine
  - $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$
- Exploiter per-capita growth rate depends *only* on resource density, and vice verse
- 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)?

- **<u>Answer</u>:** The equation for change in N_e stays the same, so the equilibrium value of N_f must stay the same.
  - **<u>Answer</u>:** Unless N_e goes to zero!
- **<u>Answer</u>:** The value of r_f has gone down, so we must increase it
  - **<u>Answer</u>:** by decreasing the number of exploiters

Reciprocal control

- Imagine:
  - $\frac{dN_f}{dt} = r_f(N_e)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$
- If we are at equilibrium, and then we reduce r_e without changing r_f (for example, we start killing sharks):
  - **<u>Answer</u>:** r_f doesn't change, so N_e must stay the same
  - **<u>Answer</u>:** r_e of the old equilibrium goes down, so N_f must increase
  - **<u>Answer</u>:** 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)?
  - **<u>Answer</u>:** 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

3.2 More detailed models

Resource species density dependence

- In a more realistic system, we expect some effect of the resource species 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?
  - **<u>Answer</u>:** r_e doesn't change, so N_f can't change
  - **<u>Answer</u>:** r_f goes down and must be balanced by less sharks
- What if we start catching sharks?
  - **<u>Answer</u>:** r_e goes down, so N_f must go up
  - **<u>Answer</u>:** 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?
  - **<u>Answer</u>:** r_e doesn't change, so N_f can't change
  - **<u>Answer</u>:** r_f goes down and must be balanced by less sharks
- What if we start catching sharks?
  - **<u>Answer</u>:** r_e goes down, so N_f must go up
  - **<u>Answer</u>:** Increasing N_f could increase or decrease r_f, so N_e could go up or down!

3.3 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?

- Why is the earth green and the ocean blue?
  - **Answer:** The ocean could be green, and the earth could be brown
  - **Answer:** 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

4 Oscillatory behavior

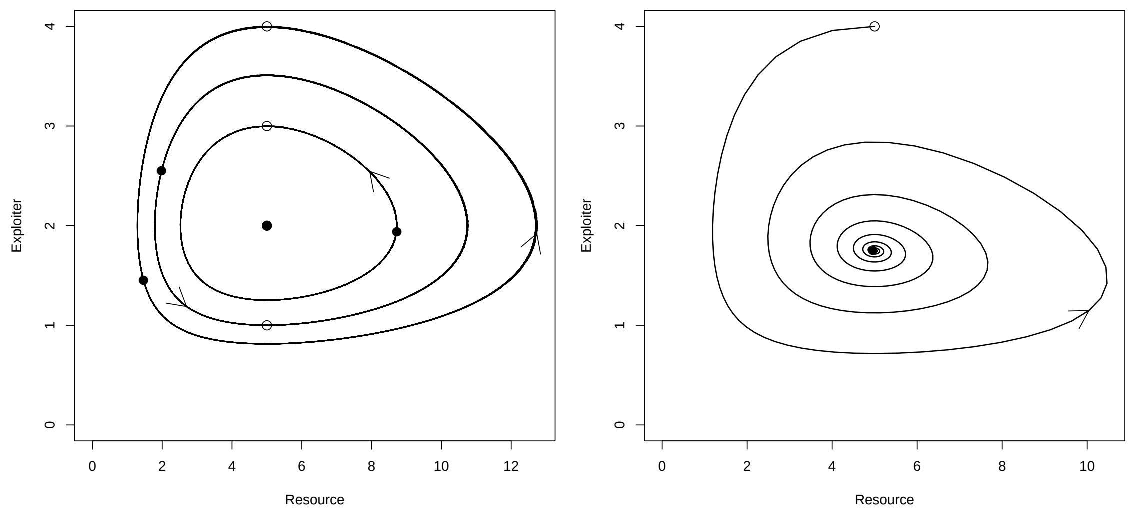
Simplest model

- 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?
- What factors will tend to make cycles get smaller (approach equilibrium)?
- What factors will tend to make cycles get larger (move away from equilibrium)?

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

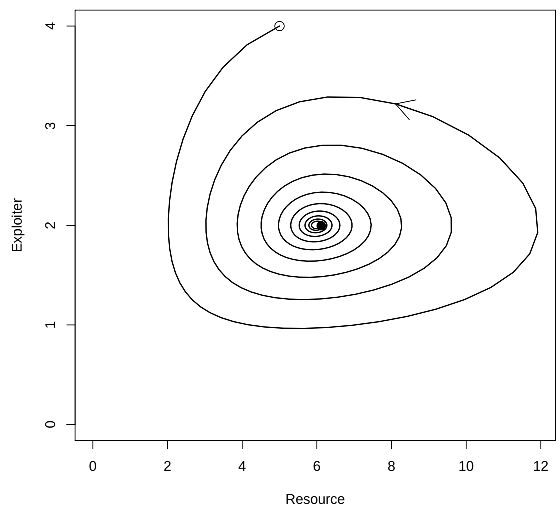
Prey density dependence



Predator density dependence

- 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?
  - **<u>Answer</u>:** Reduces predator reproduction when predators are the highest
  - **<u>Answer</u>:** This is not the same time as when prey are the highest, although we intuitively think that it is
  - **<u>Answer</u>:** Tends to cause damped cycles

Predator satiation

- What is the effect on feeding rates if the density of the *resource species* increases?
  - From the point of view of the exploiter?
    * **<u>Answer</u>:** Per-capita feeding goes up
  - From the point of view of the resource species?
    * **<u>Answer</u>:** Per-capita feeding goes down

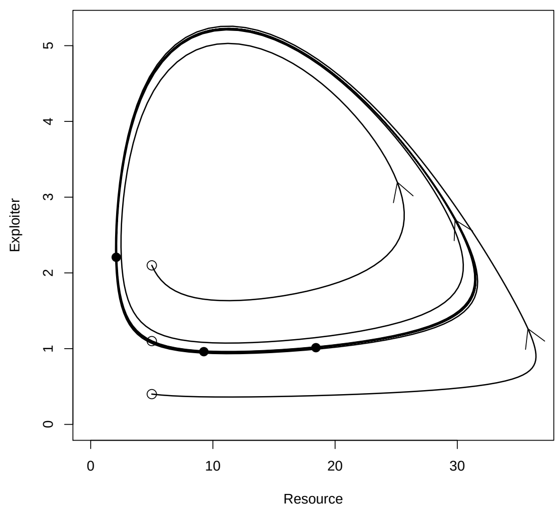
Predator satiation

- 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 ∞)
- No pictures

Satiation with prey density dependence

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

DD plus predator satiation



4.1 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

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

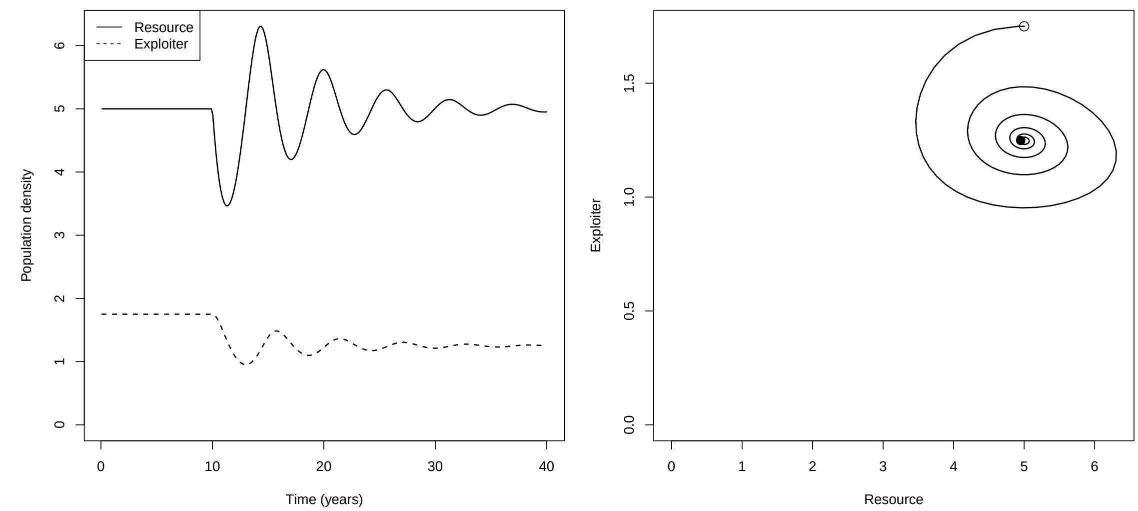
Real-world implications

- 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

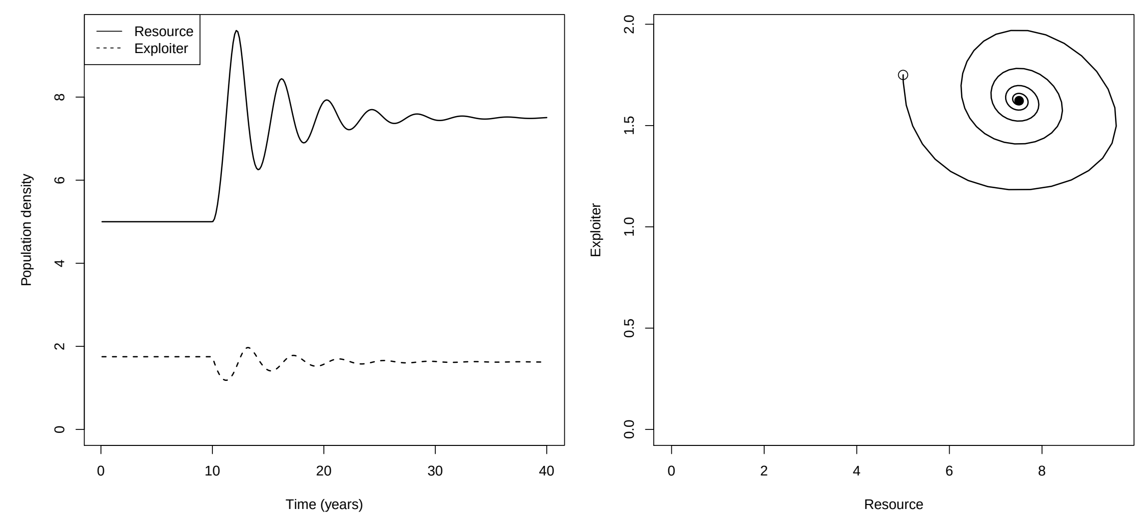
5 Harvesting examples

- 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?
- What happens *first* in this model if I start feeding grouse?
  - **Answer:** First we get more grouse, then we get more foxes, then we get less grouse, ...
- What happens *eventually* in this model if I start feeding grouse?
  - **Answer:** Population eventually approaches (or orbits around) a new *equilibrium*, with more foxes, and the same amount of grouse as before

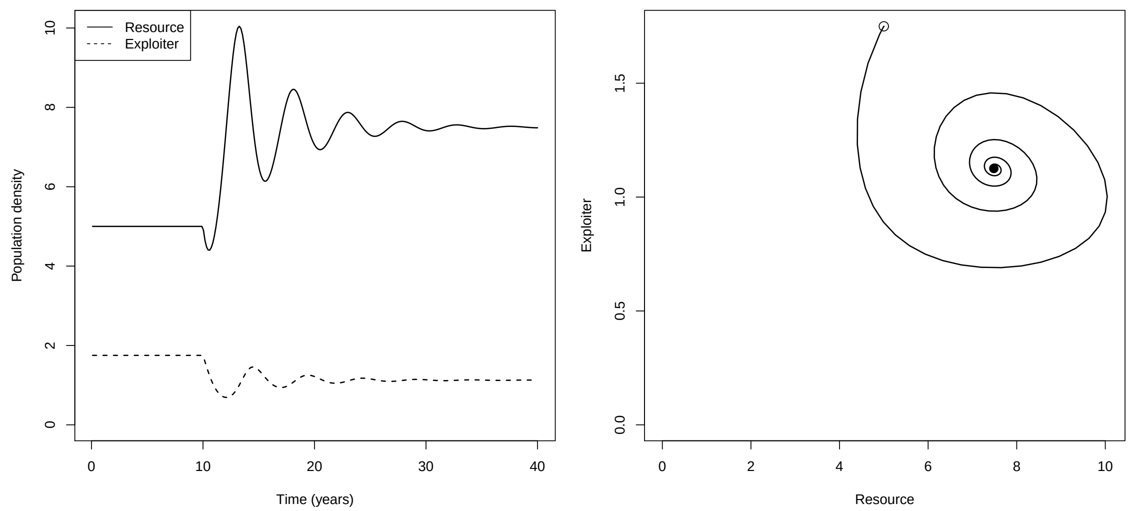
Harvesting dynamics



Harvesting dynamics



Harvesting dynamics



Resource
Exploiter
Population density
Time (years)
0
2
4
6
8
10
0
10
20
30
40
Exploiter
Resource
0.0
0.5
1.0
1.5
0
2
4
6
8
10