# UNIT 7: Exploitation

# Outline

# 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 ...

# *Exploitation examples (present)*

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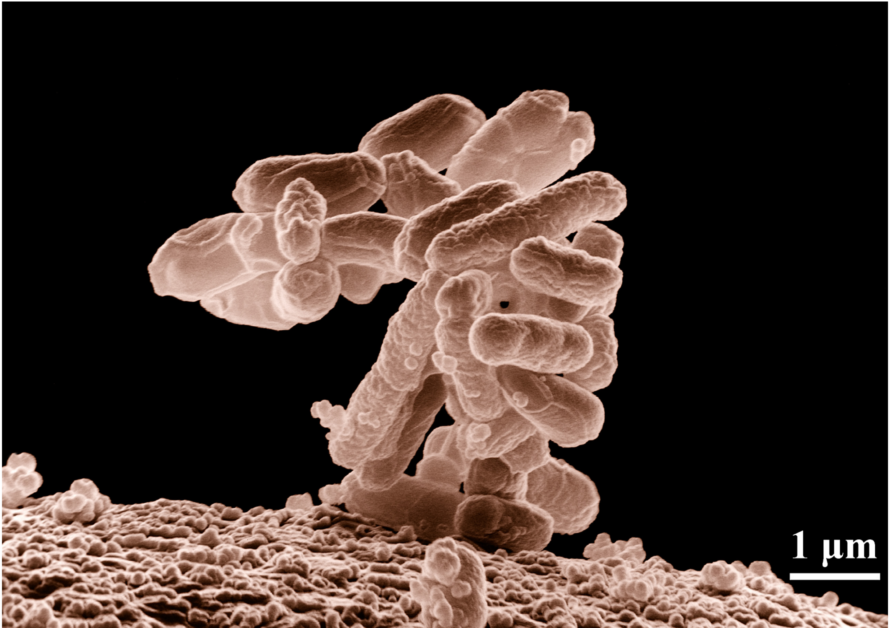


# Exploitation examples (present)

# 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

# Outline

# Balance and equilibrium

- In an exploiter-resource system, each species has an indirect, negative effect on itself. Why?
  - * As resource species population grows, the number of exploiters should increase, which is bad for the resource species
  - * 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?
  - * For equilibrium, each species must be at the density required to keep the *other* species balanced
  - * 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.

# Outline

# 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
  - * Exploiter goes up $\rightarrow$Resource goes down $\rightarrow$Exploiter goes down $\rightarrow$Resource goes up $\rightarrow$Exploiter goes up ...

# Outline

# 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:
  - * $r_e = r_f = 0$
  - * $r_f = N_e = 0$
  - * $N_e = N_f = 0$
  - * If $N_f = 0$, what happens to $r_e$?

# Interactions

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

# Resource-exploiter interactions (present)

# *Resource-exploiter interactions (present)*

# 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?
  - * The number of fish will go down
  - * *Then* the number of sharks will go down
  - * Then the number of fish will go up ...

# Outline

# *How do populations affect their own growth rates? (present)*

# Resource populations

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

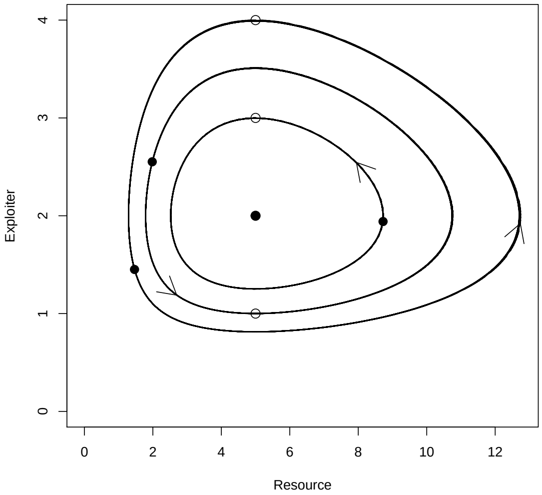
# Exploiter populations

- Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?
  - * Competition for resources, territory, mates (density dependence)
  - * 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)?

# *Neutral cycles (present)*



# Outline

# 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)?
  - * The equation for change in $N_e$ stays the same, so the equilibrium value of $N_f$ must stay the same.
    - * Unless $N_e$ goes to zero!
  - * The value of $r_f$ has gone down, so we must increase it
    - * 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):
  - * $r_f$ doesn't change, so $N_e$ must stay the same
  - * $r_e$ of the old equilibrium goes down, so $N_f$ must increase
  - * If we can't increase it enough, sharks go extinct, and fish increase to infinity.

# *People and the ocean (present)*

# 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)?
  - * 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?
  - * Shark population will go down (less sharks are needed to keep the fish in balance)
  - * 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**
    - * Decreased the number of sharks
  - Catching sharks directly had little or no effect on the number of sharks
    - * *Increased the number of food fish*
- As fishing increases, this link is eventually broken
  - * Fishing becomes an important regulator of ocean fish populations
  - * Further increases in fishing can cause rapid declines in fish populations

# Outline

# *How do populations affect their own growth rates? (present)*

# 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:
  - $\frac{dN_f}{dt} = r_f(N_e, N_f)N_f$
  - $\frac{dN_e}{dt} = r_e(N_f)N_e$

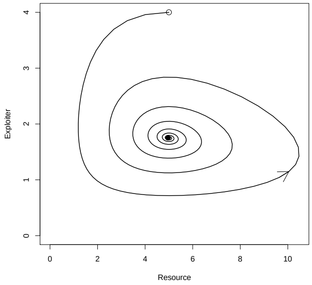
# Predator satiation

- 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?
    - * Per-capita feeding goes up
  - From the point of view of the resource species?
    - * 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

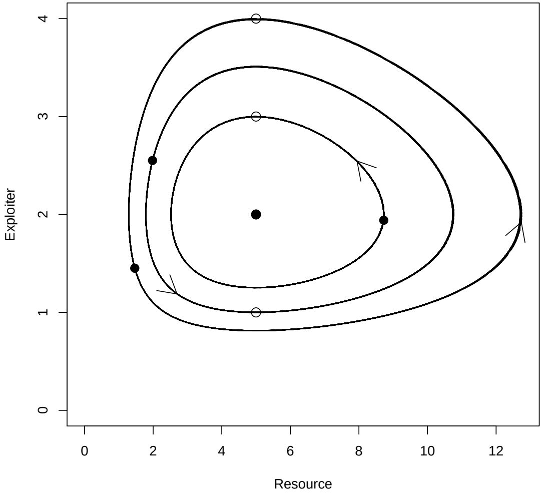
# Outline

# Prey density dependence

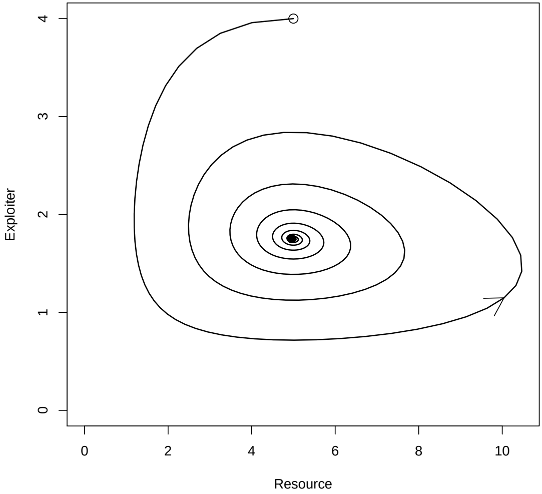
- Reduces prey reproduction the most when prey numbers are highest
- Tends to pull cycles towards the middle
- Makes cycles get smaller, leading to **damped** cycles



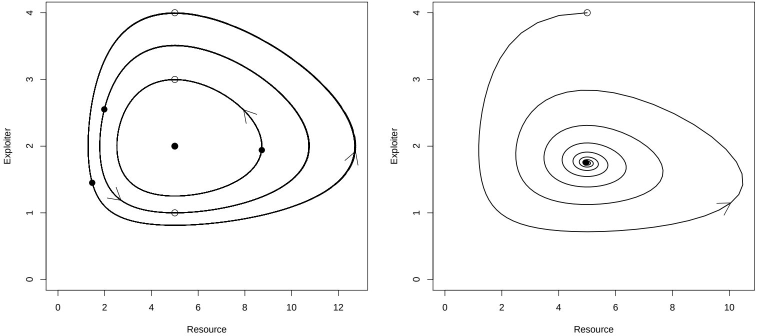
# Neutral cycles (present)



# Prey density dependence (present)

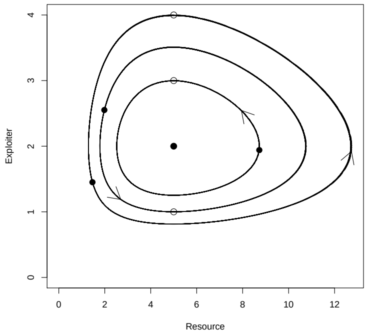


# Prey density dependence

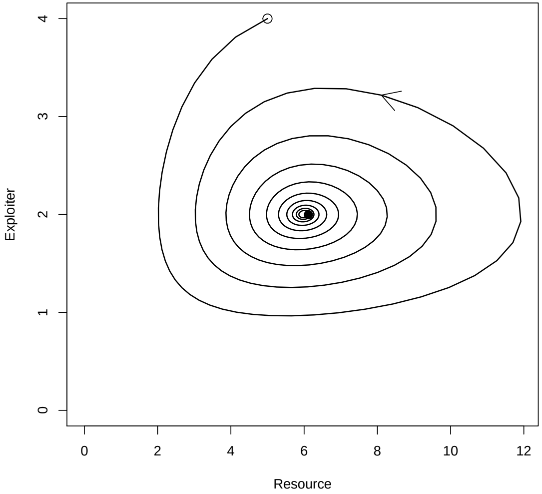


# Predator density dependence

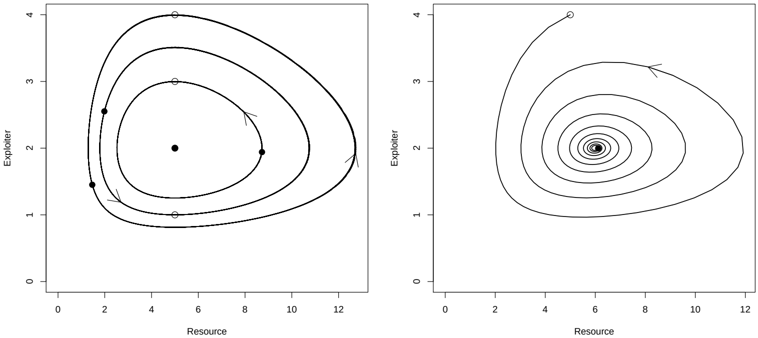
- If we go back to neutral cycles, and add predator density dependence, do we expect cycles to spiral out, or spiral in?



# Predator density dependence

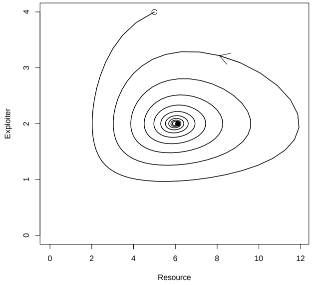


# *Predator density dependence (present)*



# Predator density dependence

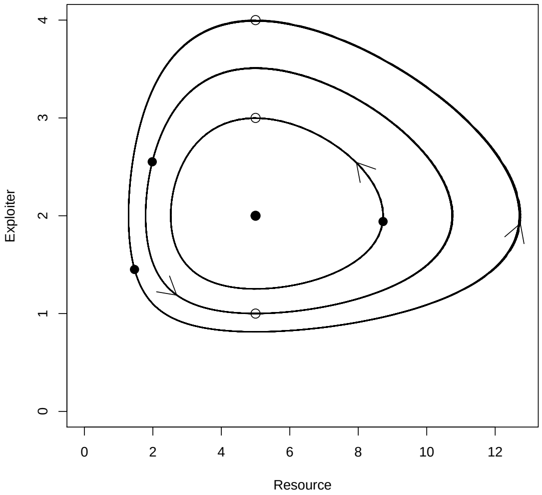
- Density dependence in the predator (exploiter species) has what effect on cycles?
  - * Reduces predator reproduction when predators are the highest
  - * This is not the same time as when prey are the highest, although we intuitively think that it is
  - * Tends to cause damped cycles



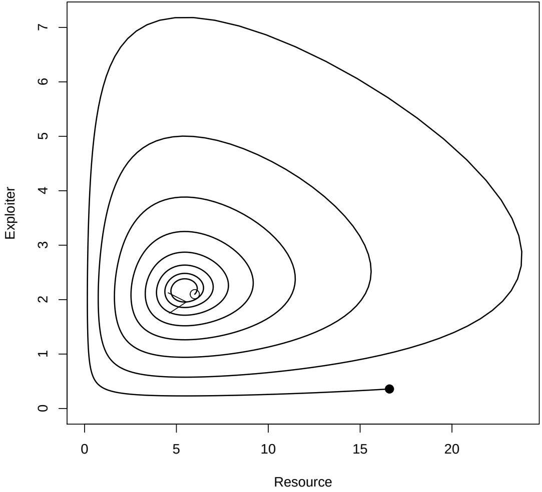
# Predator satiation

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

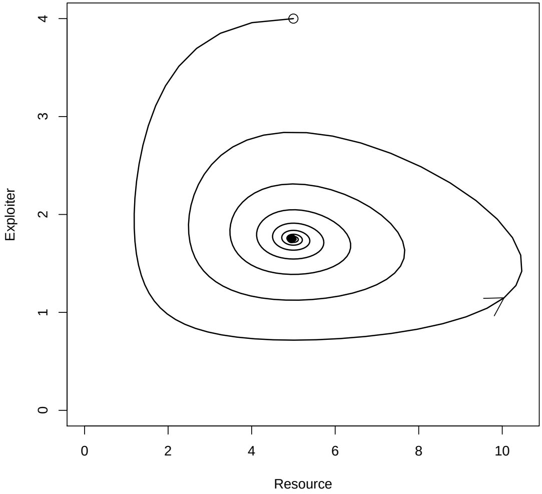
# Neutral cycles (present)



# Predator satiation



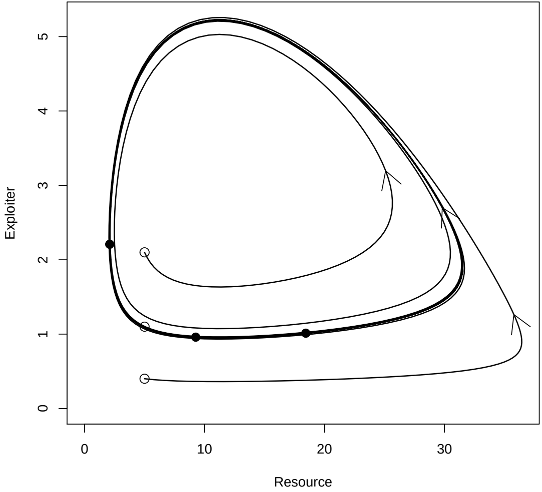
# Prey density dependence (present)



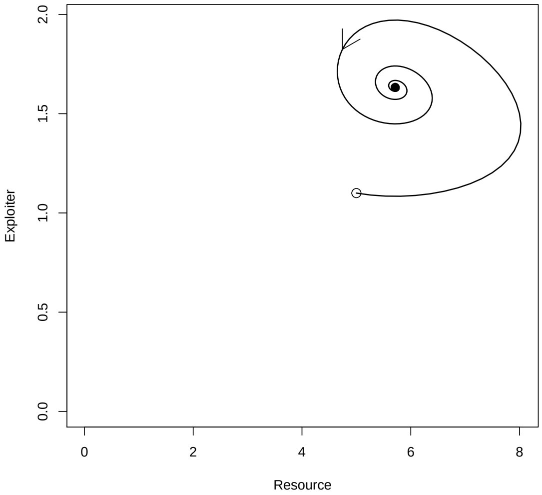
# Satiation with prey density dependence

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

# Density dependence plus predator satiation



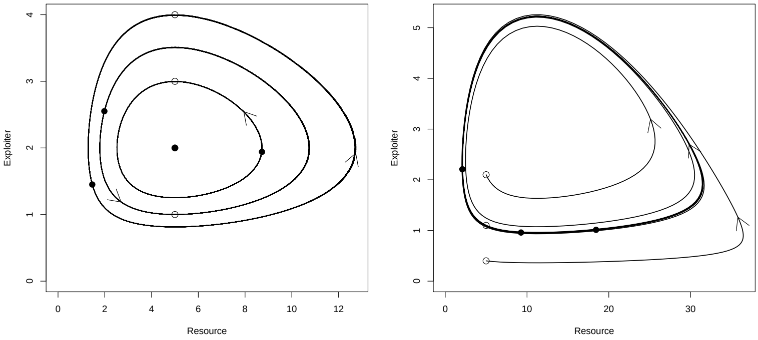
# Density dependence plus weak predator satiation



# 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

# Neutral vs. limit cycles (repeat)



# 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

# Outline

# 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?
  - * $r_e$ doesn't change, so $N_f$ can't change
  - * $r_f$ goes down and must be balanced by less sharks
- What if we start catching sharks?
  - * $r_e$ goes down, so $N_f$ must go up
  - * Increasing $N_f$ decreases $r_f$, so $N_e$ must go down

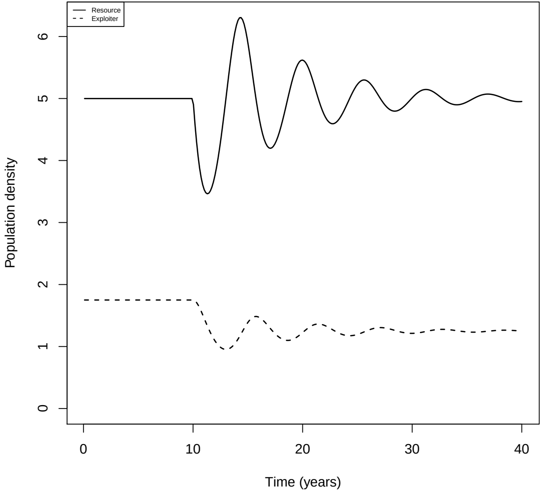
# Predator satiation

- 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?
  - * $r_e$ doesn't change, so $N_f$ can't change
  - * $r_f$ goes down and must be balanced by less sharks
- What if we start catching sharks?
  - * $r_e$ goes down, so $N_f$ must go up
  - * Satiation: More fish means higher $r_f$ means more sharks at equilibrium!
  - * 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?
- What happens *first* in this model if I start feeding grouse?
  - * 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?
  - * Population eventually approaches (or orbits around) a new *equilibrium*, with more foxes, and the same amount of grouse as before

# Harvesting dynamics (present)



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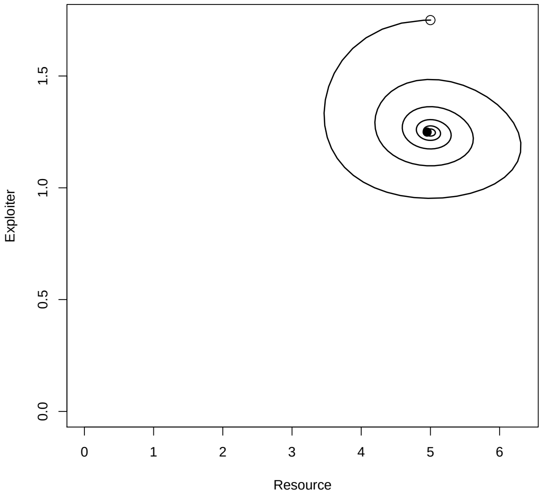

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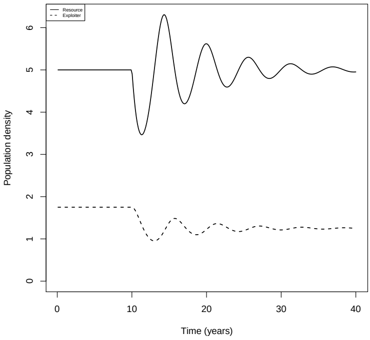


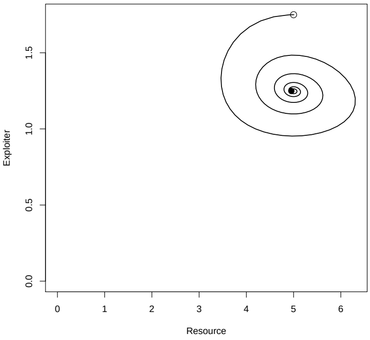

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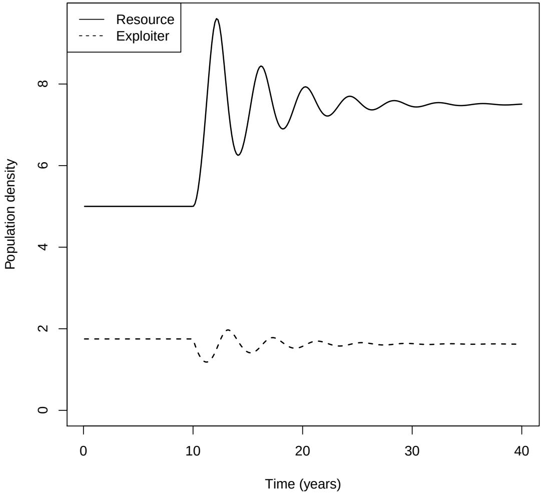

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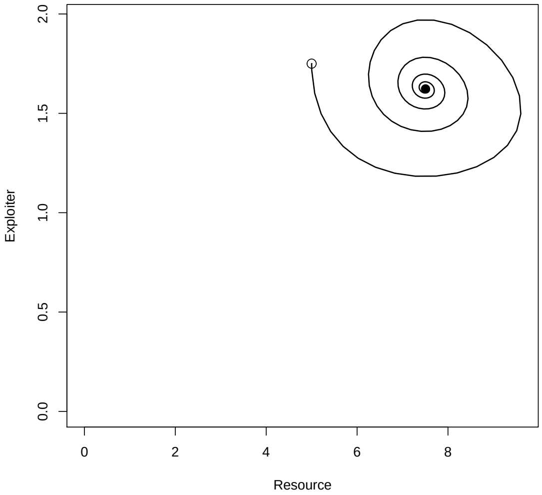

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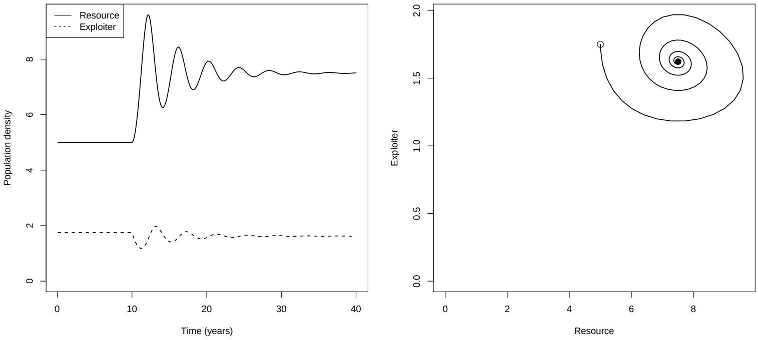

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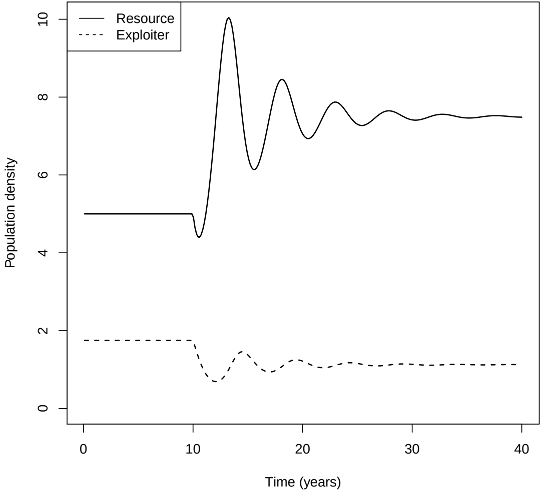

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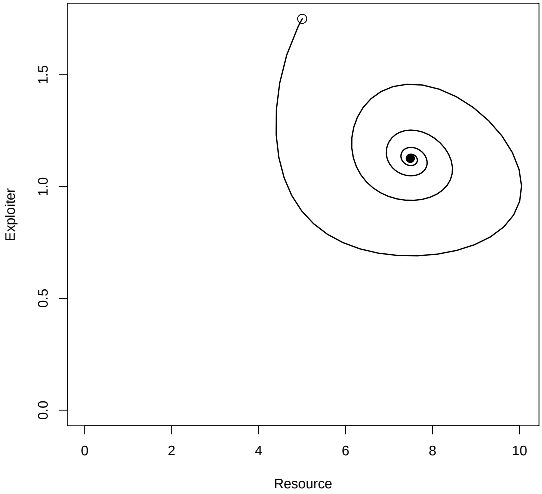

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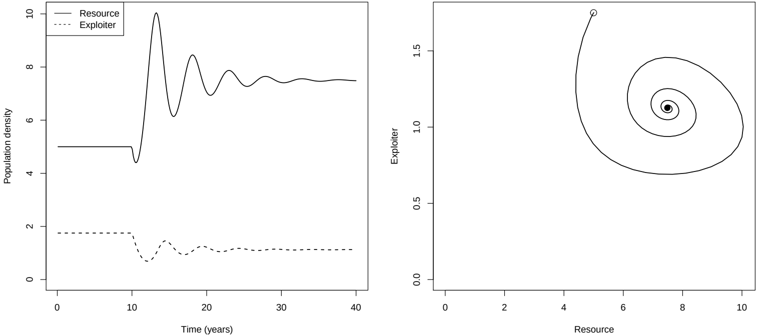
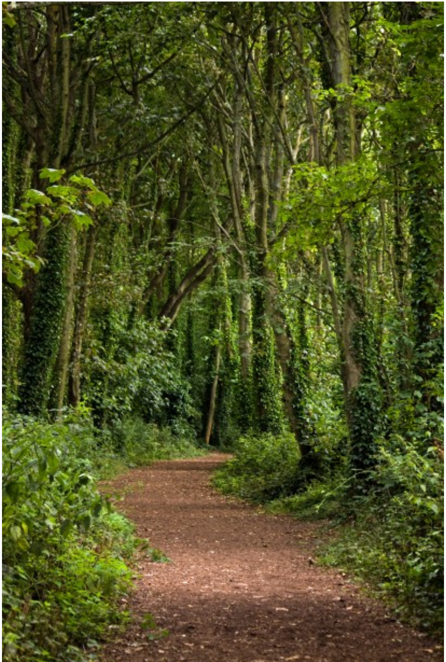


# Outline

# 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? (present)



# What controls ecosystem-level balance?

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

# *What controls ecosystem-level balance? (present)*