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. Why?

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- 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?

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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:

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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**

  - If small oscillations tend to get larger, we say that the system approaches a **limit cycle**
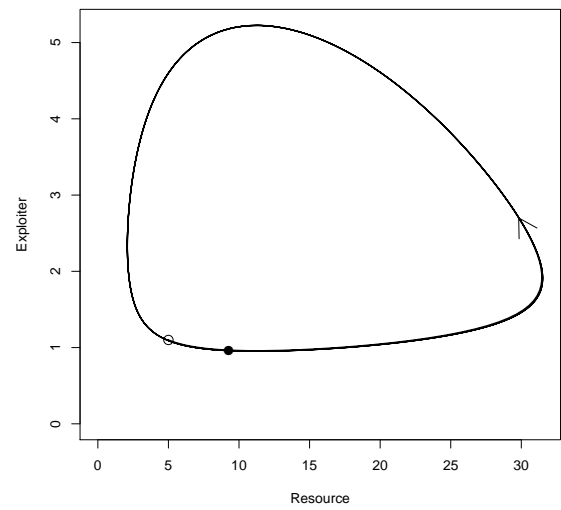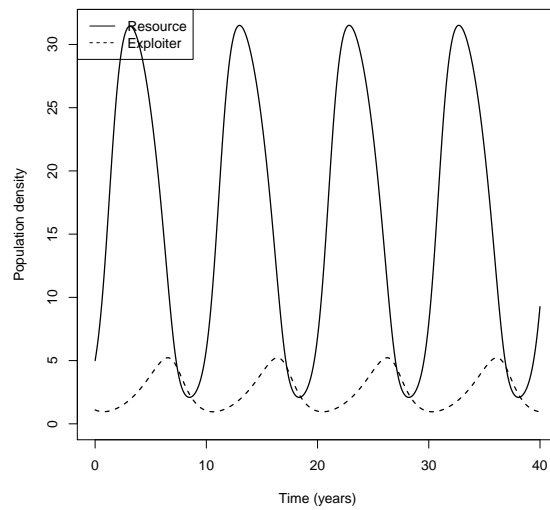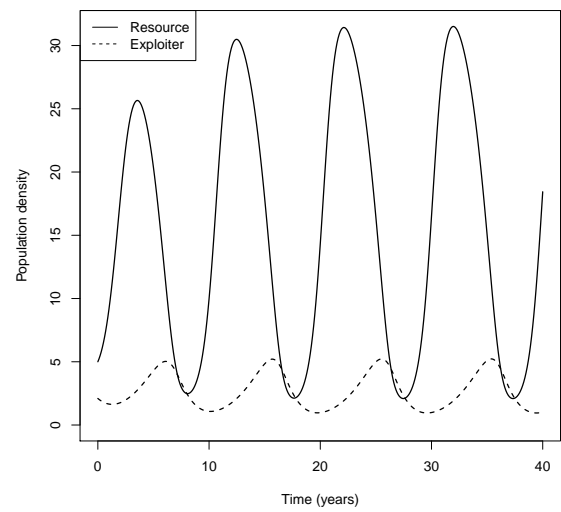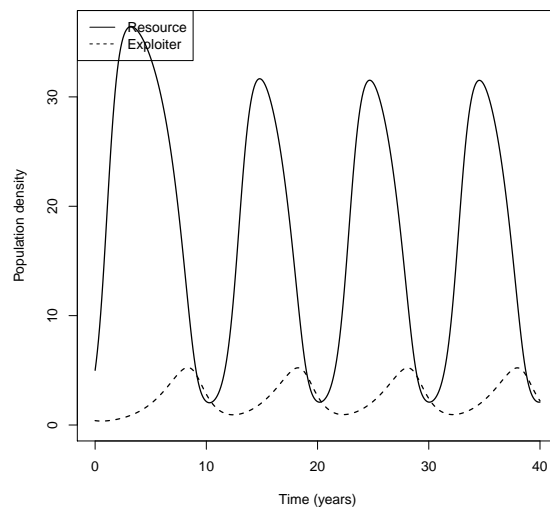
Damped oscillations
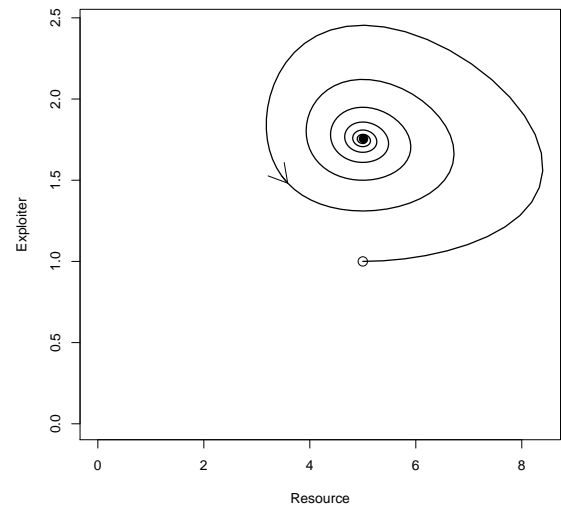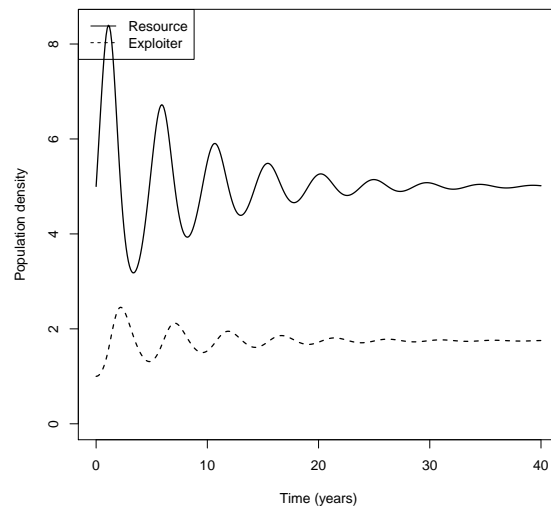
Neutral oscillations
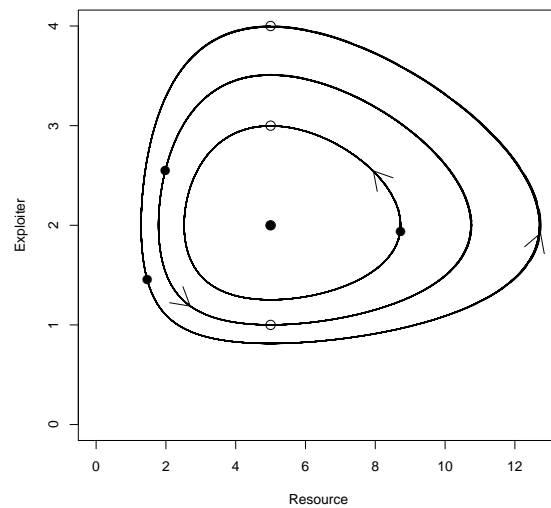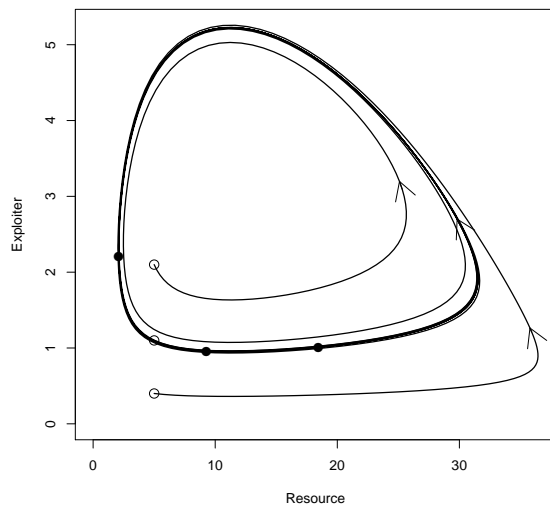

Limit cycles

Limit cycles

Limit cycles

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Neutral vs. limit cycles

- What is the difference between neutral cycles and limit cycles?

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2 Models

- 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:

$$- \quad \frac{dN_e}{dt} = r_e(N_e, N_f)N_e$$

- At equilibrium:

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Interactions

- What makes this a resource-exploiter system?

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

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- Mnemonic: e for exploiter, f for food.

  $-$ r is already in too much demand

Simplest model

- The simplest model of resource-exploiter interaction is that their per-capita growth rates only respond to each other.

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

- 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?

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2.1 More detailed models

Resource populations

- Why might we expect resource population to affect per-capita growth rate of the resource species?

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Exploiter populations

- Why might we expect exploiter population to affect per-capita growth rate of the exploiter species?

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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

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- 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

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

- DIAGRAMS

- 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)?

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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):

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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)?

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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?

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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**

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    - Catching sharks directly had little or no effect on the number of sharks

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- As fishing increases, this link is eventually broken

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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?

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- What if we start catching sharks?

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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?

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- What if we start catching sharks?

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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?

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- 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 Examples

4.1 Oscillation

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

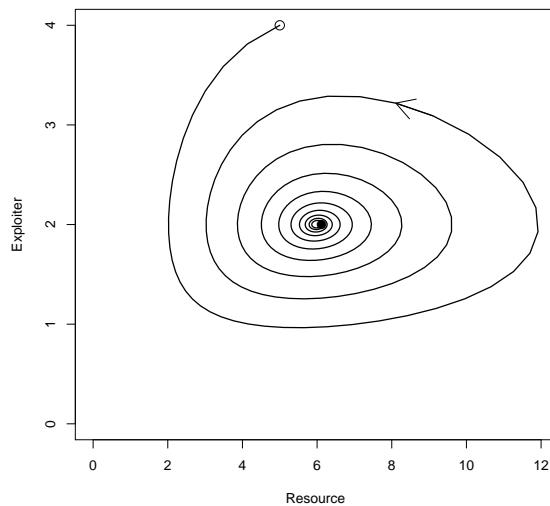- Makes cycles get smaller, leading to **damped** cycles

Prey density dependence
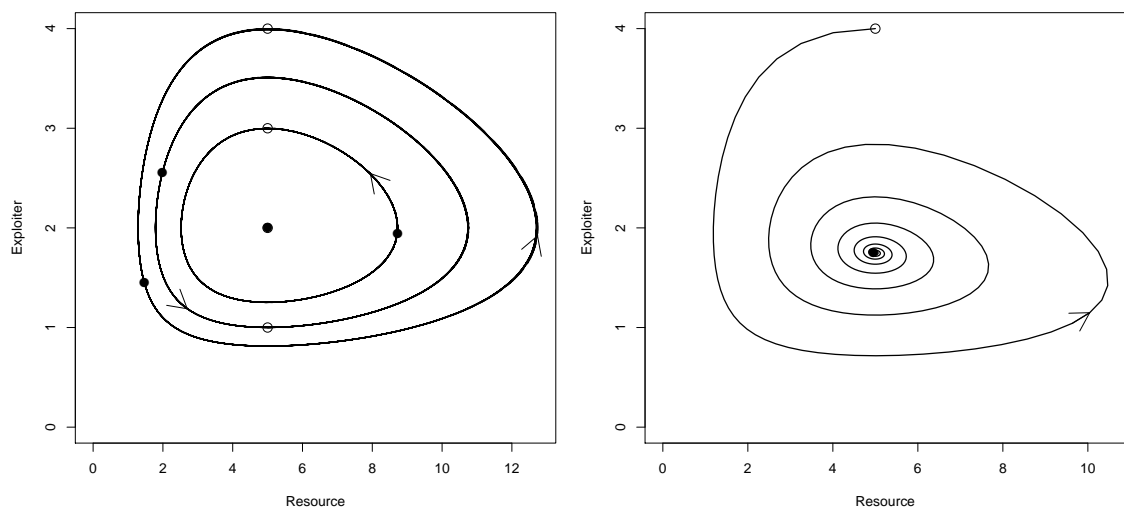
Predator density dependence

- 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?

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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?

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    – From the point of view of the resource species?

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Predator satiation

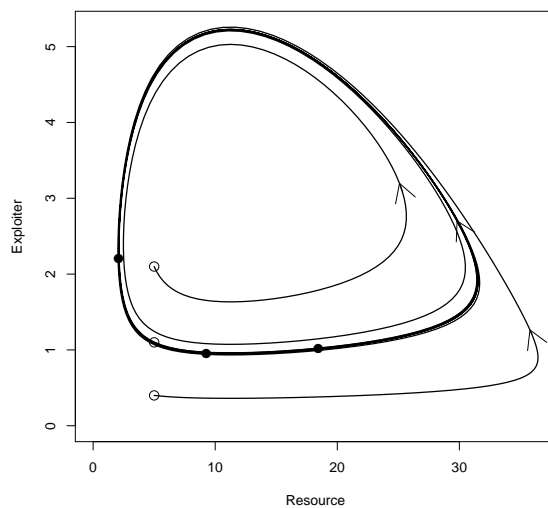- The fact that predators can consume only limited amounts of prey has what effect on cycles?

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- No pictures

Satiation with prey density dependence

- What sort of oscillations do we expect?

    - If density dependence is strong?

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    - If density dependence is weak?

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DD plus predator satiation

Oscillation summary

- *Neutral* cycles repeat from any starting point

- *Damped* cycles spiral in to the equilibrium.

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- *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
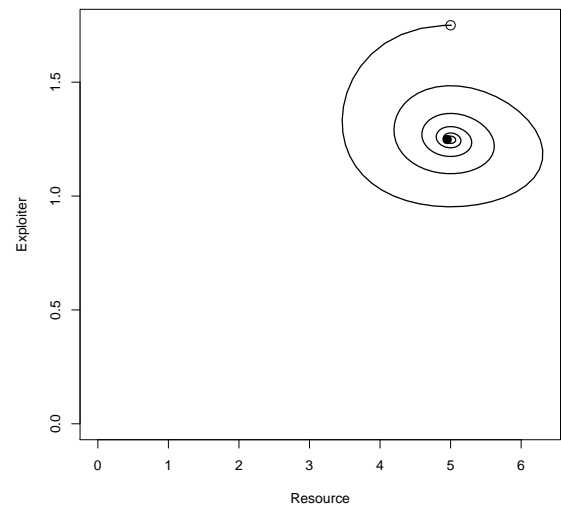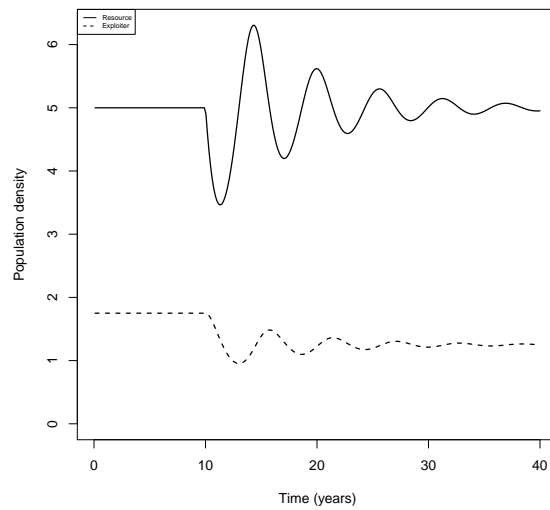 – Environmental perturbations – weather, fire, people

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
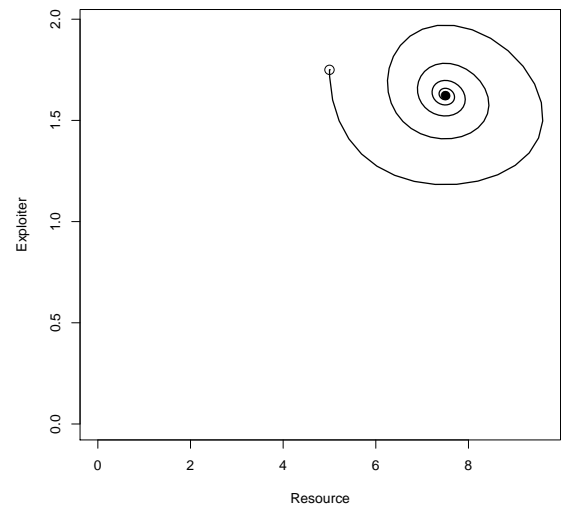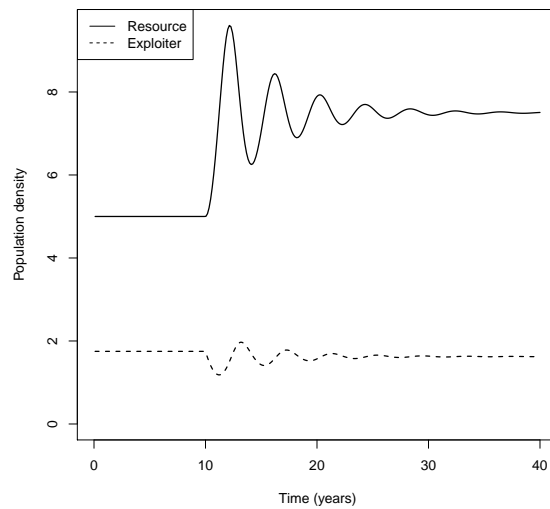
4.2   Harvesting examples

- 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?

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- What happens *eventually* in this model if I start feeding grouse?

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Harvesting dynamics

Harvesting dynamics

Harvesting dynamics