Exploitation

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Introduction

Introduction

- **Exploitation** is when interactions between two species are good for one species and bad for the other
- Typically, the exploiter (*natural enemy*) is taking resources from the other species (*victim*)
- 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 ...
- (recycling via **donor-controlled** consumption)

Types of exploitation

- Not used precisely, and not testable
- **Predators** kill and eat **prey**
- **Parasites** lives on or in **hosts** (**symbiosis**) and use host resources
- **Pathogens** cause disease
- **Parasitoids** develop inside a host and kill it
- **Grazers** take resources from another organism but don't kill it

.	**symbiotic**	**kills host**
predator	no	yes
grazer	no	no

.	**symbiotic**	**kills host**
parasite	yes	no
parasitoid	yes	yes

Borderline cases

- Do rabbits predate small plants, or graze them?
- Are small insects on large plants grazers, or parasites?
- Do intestinal worms in healthy people count as pathogens?
- Anthrax is usually called a parasite (or pathogen), but should probably really be a parasitoid

More vocabulary

- Interactions can be grouped by the taxonomy of the interacting species
- Herbivores eat plants
- Carnivores eat animals
- Micro-organisms are more likely 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 call the exploitee the **resource species**
- Resource species are a lot like **abiotic** resources (e.g. water, light and nitrogen)
- Both benefit the species that use them
- Both may, or may not, be depleted significantly by the exploiter
- Name an important difference between biotic and abiotic resources

Balance and equilibrium

- In an exploiter-resource system, each species has an indirect, negative effect on itself

- Since each species has a negative effect on itself, these systems *tend* to reach equilibrium

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 useful even if it is not reached: if there are cycles, the equilibrium is what the system cycles around.

Reciprocal control

- Exploiter + resource species whose population densities are mostly regulated by each other
- *Per capita* growth rate of exploiter depends mostly on resource density
- *Per capita* growth rate of resource depends mostly on exploiter density
- What determines equilibrium values?

Tendency to oscillate

- In an exploiter-resource system, each species has an indirect, negative effect on itself
- Effect is *time-delayed*: each species takes time 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:
- Exploiter goes up → Resource goes down → Exploiter goes down → Resource goes up → Exploiter goes up ...

Persistence of oscillations

- Resource-exploiter systems *tend* to oscillate
- In the simplest models, oscillations are **neutral**
- In more realistic models, large oscillations will tend to get smaller
- If small oscillations also tend to get smaller, the oscillations are **damped**

- If small oscillations tend to get larger, the system approaches a **limit cycle**

Damped oscillations

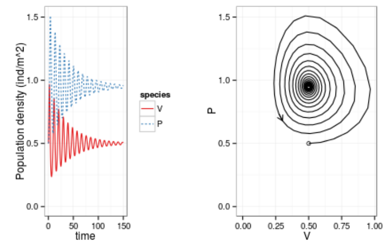

Figure 1: plot of chunk damped

Neutral oscillations

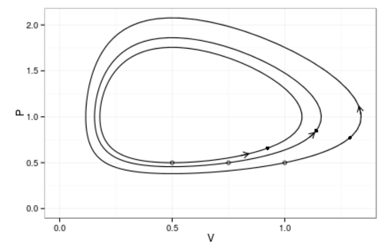

Figure 2: plot of chunk neutral

Limit cycles

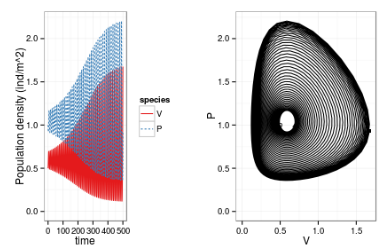

Figure 3: plot of chunk lim

Limit cycles (2)

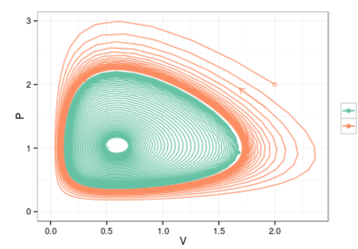

Figure 4: plot of chunk lim2

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
- Will use P (predator) and V (victim) (E and R are too confusing)
- $\frac{dV}{dt} = r_V(V, P) \cdot V$
- Exploiter growth rate may depend on density of exploiter, or resource species, or both:
- $\frac{dP}{dt} = r_P(V, P) \cdot P$
- At equilibrium:
- Can't have exploiter without resource!

Interactions

- What makes this a resource-exploiter system?
- $\frac{dV}{dt} = r_V(V, P) \cdot V$
- $\frac{dP}{dt} = r_P(V, P) \cdot P$
- What should happen to r_P as V increases?

Simplest model

- The simplest model of resource-exploiter interaction is that their *per capita* growth rates only respond to each other.
- $\frac{dV}{dt} = r_V(P) \cdot V$
- $\frac{dP}{dt} = r_P(V) \cdot P$
- 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?

More detailed models

Resource populations

- Why might the resource population affect *per capita* growth rate of the resource species?

Exploiter populations

- Why might the exploiter population affect *per capita* growth rate of the exploiter species?

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:
- $\frac{dV}{dt} = r_V(P, V) \cdot V$
- $\frac{dP}{dt} = r_P(V) \cdot P$
- Exploiter *per capita* growth still depends only on resource

Predator satiation

- Another conceptual problem with the model is the idea that exploiter feeding is proportional to size of the resource population

Reciprocal control: change resource

- Back to the simplest exploiter-victim model:
- $\frac{dV}{dt} = r_V(P) \cdot V$
- $\frac{dP}{dt} = r_P(V) \cdot P$
- What happens to the **equilibrium** if we reduce r_V without changing r_P (for example, we start catching more fish)?

Resource change

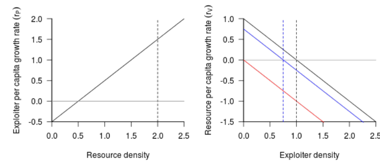

Figure 5: plot of chunk resource_chg

Reciprocal control: change exploiters

- If we're at equilibrium, and then reduce r_P without changing r_V (for example, we start killing sharks)
- What happens to the equilibrium?

Exploiter change

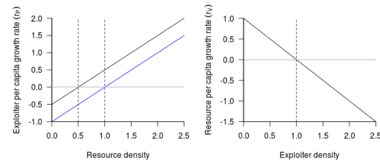

Figure 6: plot of chunk exploit_chg

Harvesting response

- Species under reciprocal control may respond to change in unexpected ways
- Community of sharks and large fish whose densities are primarily controlled by their exploitative interactions (the sharks eat the fish)
- What happens in the *short term* if people start catching large numbers of both sharks and fish?

Harvesting equilibrium

- What will happen to happen to these reciprocally controlled populations of sharks and fish in the *long term* under heavy fishing pressure?

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**

- As fishing increases, this link is eventually broken: "fishing down the food chain" (Pauly et al. 2001)

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
- $\frac{dV}{dt} = r_V(P,V)N_f$
- $\frac{dP}{dt} = r_P(V)P$
- What happens to the equilibrium if we start catching fish?
- What if we start catching sharks?

Predator satiation

- What if we also consider **satiation** (limit to how much a predator can catch, or eat)?
- $\frac{dV}{dt} = r_V(P,V)V$
- $\frac{dP}{dt} = r_P(V)P$
- What happens to the equilibrium if we start catching fish?
- What if we start catching sharks?

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?
- 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?
- What trophic levels provide the primary control for which other trophic levels?
- **Top-down** control: 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

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
- 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)?

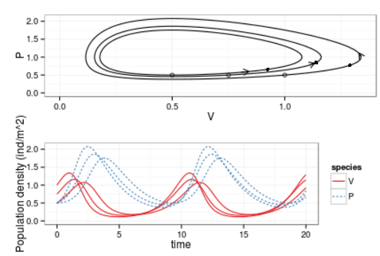

Figure 7: plot of chunk neutral2

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

Picture

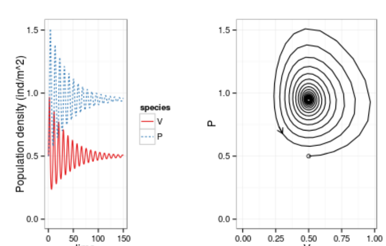

Figure 8: plot of chunk damped2

Predator density dependence

- If we go back to the reciprocal control model and add predator density dependence, what do we expect to see?

Predator density dependence

- Density dependence in the predator (exploiter species) has what effect on cycles?

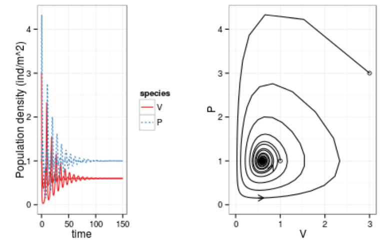

Figure 9: plot of chunk predDD

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?

Predator satiation

- What effect does the fact that predators can consume only limited amounts of prey have on cycles?

Satiation with prey density dependence

- What sort of oscillations do we expect?
- If density dependence is strong?
- If density dependence is weak?

Satiation+prey DD: low K

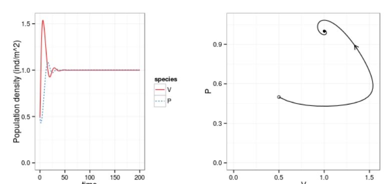
Figure 10: plot of chunk predsat2

Satiation+prey DD: high K

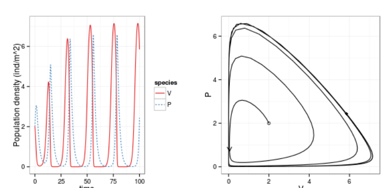
Figure 11: plot of chunk predsat3

Satiation+prey DD: high K, log scale

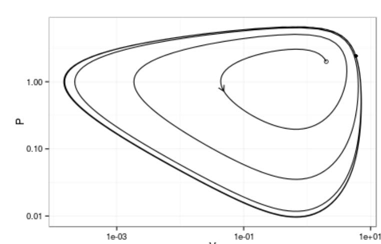

Figure 12: plot of chunk predsat4

Oscillation summary

- *Neutral* cycles repeat from any starting point (reciprocal control)
- *Damped* cycles spiral in to the equilibrium (density-dependence alone)
- *Unstable* cycles spiral out forever (satiation alone)
- Biologically unrealistic
- *Limit cycles* spiral out from near the equilibrium, and spiral in from far away (satiation + density-dependence)

Chaos in a three-species food chain

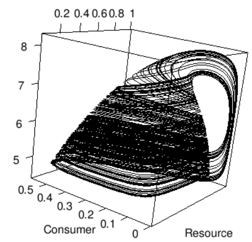

Figure 13: (Hastings and Powell 1991)

Oscillations in the real world

- All resource-exploiter systems have a tendency to oscillate
- Damped oscillations take a while to die out, or stable oscillations to converge
- Other stuff is going on at the same time
- Seasonal variation
- 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

References

Hastings, Alan, and Thomas Powell. 1991. "Chaos in a Three-Species Food Chain." *Ecology* 72 (3): 896–903.

Pauly, Daniel, Ma. Lourdes Palomares, Rainer Froese, Pascualita Sa-a, Michael Vakily, David Preikshot, and Scott Wallace. 2001. "Fishing down Canadian Aquatic Food Webs." *Canadian Journal of Fisheries and Aquatic Sciences* 58 (1) (January): 51–62. doi:10.1139/f00-193. http://www.nrcresearchpress.com/doi/abs/10.1139/f00-193.