

Indirect interactions

Key concepts

- Interaction chains versus modification chains
- Apparent competition
- Indirect mutualism
- Top down versus bottom up regulation
- Keystone species
- The Janzen-Connell hypothesis

Beyond species pairs

In previous chapters, we've seen how the interaction between pairs of species can have profound impacts on their fates. In addition to some intuitive results, we've encountered concepts such as the paradox of enrichment, and the variable outcomes associated with antagonistic interactions. This chapter extends our knowledge of interaction pairs to a larger number of species. The emphasis is on examples with a tractable number of species (often three) where we can understand novel mechanisms (those that cannot occur among pairs of species in isolation).

These novel mechanisms can be summarized as *indirect interactions*. At their simplest they involve three species: a donor species, a transmitter species and a receiver species. The donor is the species that initiates a direct interaction with the transmitter species. This affects the direct interaction between the transmitter species and the receiver species.

Interaction chains and modification chains

There are qualitative differences between the kinds of adjustments that occur to the transmitter species. When the population size of the



Figure 1: Moths illuminate our understanding of many indirect interactions, including indirect mutualism and apparent competition

Trait-mediated indirect effects represents a growing area of ecological research

transmitter species is altered due to the donor species, we refer to an interaction chain. When the donor species causes some other change in the transmitter species (e.g. behavioral or genetic), we refer to a modification chain (or trait-mediated indirect effect). Here, we focus primarily on interaction chains.

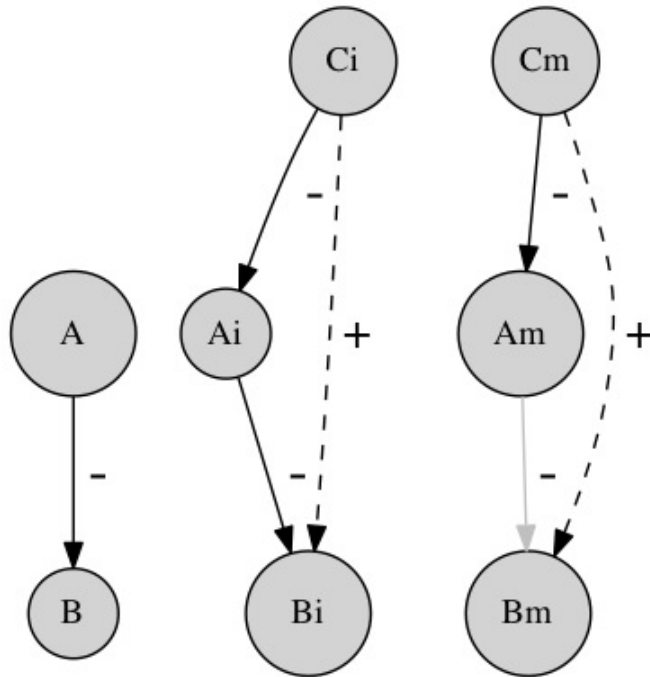


Figure 2: The enemy of my enemy is my friend. When species A and B are alone, A has a negative effect on B keeping B's population size relatively small. The addition of species C leads to a change in species A, reducing the negative direct impact of A on B. This can either be because species C reduces the population size of species A (an interaction chain) or through some other method (a modification chain, e.g., modifying the behavior of species A). In either case, C has a positive indirect effect on B (dashed arrows).

Exploitation competition

Our earlier chapter on competition introduced resource competition and R^* theory. In such situations, the two competing species are not fighting or necessarily interfering with each other in any direct way, yet the presence of one species (that with the lower R^* value) has a profound effect on the other species. While this is technically an indirect interaction, it is sufficiently common and with its own theory that it is treated separately.

Apparent competition

One of the most well-studied interaction chains is *apparent competition*. In a previous chapter, we learned that competition is $-/-$ interaction where both species incur a fitness loss. Two species that share a natural enemy can exhibit what looks like competition but is really an indirect interaction mediated by the shared natural enemy. The two

moth species *Plodia interpunctella* and *Ephestia kuehniella* are both viable hosts to the parasitoid wasp *Venturia canescens*.

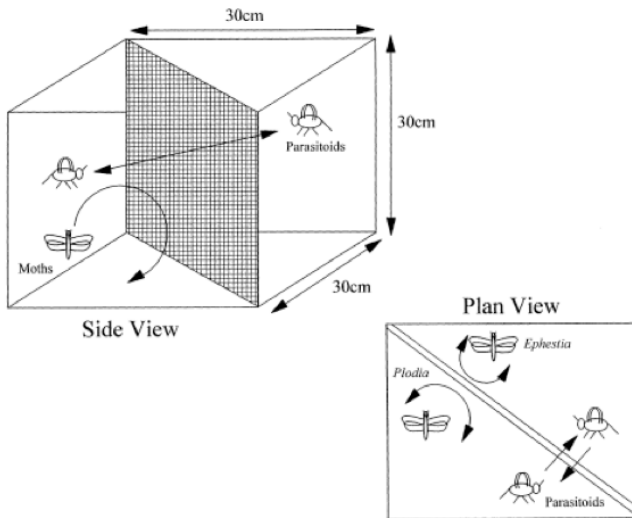


Figure 3: Experimental set up used by Bonsall and Hassell, 1998, *J. Anim. Ecol.*, in which the parasitoid could move freely between the two halves of the cage (but the host species could not). Equal resources were provided to both sides of the cage.

In an experimental set up, Bonsall and Hassell (1998) divided cages in half with nylon mesh. Each half was occupied by equal numbers of larvae of one or the other moth species. Because of the difference in body size, the parasitoid wasp was able to pass through the nylon mesh but the moths were not. Each half of the cage (i.e., each moth species) had the same amount of food resources and since the two species were not in contact, there was no direct competition between them. Control cages were also used which had one of the moth species in one half of the cage, with the other half empty of moths.

In the control cages, each moth species coexisted with the parasitoid wasp. However in cages with both moth species, the moth populations would drop to very low density and sometimes extinction. Each moth species stimulated the population size of the parasitoid (by acting as host to its eggs) and each paid the cost in additional parasitization (relative to control cages). Thus we observe the presence of both moth species having a negative impact on each other. This has the same appearance as competition, but in this case is mediated by direct interactions between each moth species and the parasitoid and only indirect (apparent) competition between the two moth species.

Indirect mutualism

The yucca plant *Yucca glauca* is pollinated by the moth species *Tegeticula yuccasella*, which uses its specialized mouth parts to push pollen into the stigma. Even though this moth will also oviposit eggs into the flowers (sometimes resulting in flower loss by larval seed con-

sumption), it is a net gain to the yucca plant which relies on its specialist pollinator. A second moth species *Tegeticula corruptrix* does not pollinate the yucca but will predate its seeds in the same way as its relative. The interaction of the second moth species and the yucca plant is a net loss the plant.

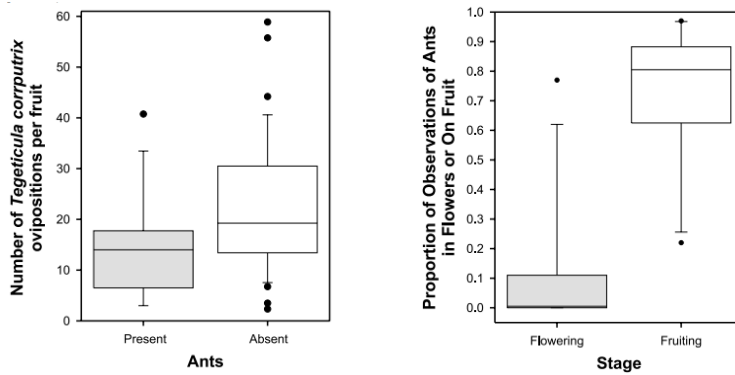


Figure 4: Research by Perry et al. 2004, Can. J. Zool. showed that by spending a significant amount of time around the fruiting bodies of the plant, the ant reduces the amount of egg-laying by the non-pollinating moth.

Wood ants in the genus *Formica* are often found on this same yucca plant. They cause minor damage to the plant's leaves by feeding on them. However, the ants deter the seed-predating moth while the pollinating moth will still visit plants with ants. So when the non-pollinating moth is present, the ant and the yucca have an indirect mutualism (the ant deters the non-pollinating moth, facilitating the pollination from the other moth species; the ant receives the benefit of a food resource with only minor damage to the plant). In the absence of the non-pollinating moth, the interaction between ant and yucca is of a more predator-prey nature.

Trophic cascades & bottom-up versus top-down control

The section on apparent competition reinforces an observation we made earlier while studying predator-prey interactions: organisms at a higher trophic level can have a profound impact on the prey or hosts at lower levels. Also, we've learned from resource competition that the limiting resources can have equally profound effects on consumer species. This set of observations has led ecologists to ask whether the forces that regulate populations and communities originate from basal resources or top predators.

Energy flow from basal trophic resources such as plants need to be transferred to higher trophic levels by consumption (herbivores consume plants, predators consume herbivores). However, appreciation of indirect interactions led ecologists to see that predators can help the plants to flourish by keeping their herbivore populations in check. The "green world" hypothesis, puts forward the idea that as well as

organisms like predators relying on energy flow from plants, the plants also rely on predators to prevent plant over exploitation by herbivores. Since the basal resources are pre-requisite to the formation of a species community, it is argued that competition for such resources is a major factor in structuring communities, but when resources are not limiting, predation and similar top-down forces are important.

The idea that the presence or absence of top predators will affect the lower trophic levels (herbivores and plants) in alternating ways is known as a trophic cascade. Figure 2 illustrates the idea where B is the basal (plant) trophic level, A is the intermediate herbivore level and C is the predator level. In the absence of C, herbivores suppress plant population sizes. In the presence of C, herbivore populations are kept in check allowing the plant populations to grow to relatively large sizes.

Keystone species

Keystone species are those species that have a disproportionately large effect on their environment (relative to their abundance), typically affecting many other species in the community. Keystone species typically achieve this role through a combination of direct and indirect interactions.

The keystone sea otter *Enhydra lutris* is a predator of sea urchins. Unchecked, sea urchins will prey on kelp. By keeping the sea urchin population relatively low, kelp forests can develop. These dynamic, productive ecosystems are home to many marine species. The direct act of predation by the sea otter has positive indirect effects on the kelp and the species that live in the kelp forest. Keystone species don't have to be predators. Ecosystem engineers like the beaver indirectly create habitat for numerous other species.

The Janzen-Connell hypothesis

The Janzen-Connell hypothesis proposes that host-specific natural enemies (such as predators or parasites) puts a premium on dispersal of offspring as far away as possible from their parents. The idea (published independently by the ecologists Janzen and Connell) is primarily applied to static organisms like trees, where the offspring can develop at variable distances from the parent due to variation in seed dispersal. Seeds that disperse short distances are vulnerable to specialized natural enemies, whereas those that disperse greater distances will escape. Seeds of different plant species will benefit from this mechanism. The space around a tree that is inhospitable to its own offspring opens up as available habitat for other species. Consequently, the tree

species that are not hosts to the natural enemy benefit indirectly from the direct host-natural enemy interaction.

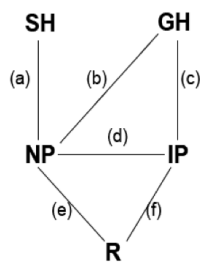
Test yourself

- What is the difference between interaction chains and modification chains?
- How would apparent competition between two hosts of a shared parasite operate?
- How does the Janzen-Connell hypothesis lead to an indirect interaction?

Further reading

- Bonsall and Hassell. 1998. The population dynamics of apparent competition in a host-parasitoid assemblage. *J. Anim. Ecol.*
- Perry, Mondor and Addicott. 2004. An indirect mutualism: ants deter seed predators from ovipositing in yucca fruit. *Can. J. Zool.*

Homework



The diagram on the left represents a community with a resource (R), native plant (NP), invasive plant (IP), specialist herbivore (SH) and generalist herbivore (GH). The lines (a-f) represent direct interactions between 2 species.

(i) Which line(s) indicate positive indirect effects on the invasive plant?

(ii) Which line(s) indicate negative direct effects on the invasive plant?

(iii) Is there "apparent competition" between the 2 plant species?