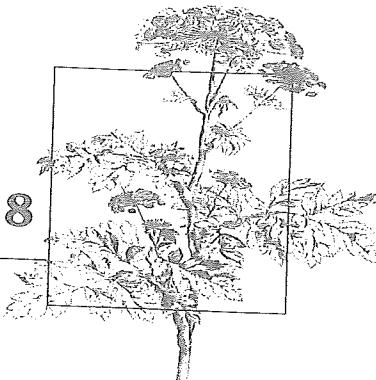


in the absence of their interactions is crucial as the restoration of tailings or landfills. Not only the introduction of endophytic fungi, importance of community structure and area is in need of

## CHAPTER 8



## Indirect Effects

### OVERVIEW

Pairwise interactions between species, such as competition, predation, and mutualism, underestimate the complexity of indirect interactions that can propagate through chains of three or more species in complex communities. Indirect effects describe how the consequences of pairwise direct interactions between species are transmitted to other species either through behavioral modifications, altered spatial distributions, or altered abundances in the food web. Indirect effects are a logical consequence of the fact that interacting species are embedded in larger food webs. Indirect effects can complicate interpretations of community-level experiments, since responses to the additions or removals of species can result from direct and indirect effects. However, knowledge of the potential pathways of indirect interactions can be used to generate testable hypotheses that can illuminate which indirect interactions probably account for a particular response.

**I**NDIRECT EFFECTS occur when the influence of one species, the donor, is transmitted through a second species, the transmitter, to a third species, the receiver (Abrams 1987). The observed effect is indirect if the donor influences the receiver through an intermediate species. Complex interactions including both direct and indirect effects are possible, and perhaps likely. Indirect effects can involve changes in a whole host of properties of species.

The most common effects materialize as changes in steady-state abundance, but indirect effects can influence the dynamics, behavior, or even the genetics of the receiver. Indirect interactions potentially occur in any complex community in which chains of three or more interacting species exist, in other words, in all but the simplest communities. Although much of the theory discussed previously in this book has focused on the ways in which pairs of species interact, for example, as abstracted by competition coefficients or functional responses, species are connected in chains or webs of interactions with many other species. As we shall see later in this chapter, indirect interactions, or indirect effects, can complicate the interpretation of ecological experiments, especially when chains of indirectly interacting species are not taken into account. Indirect effects can also complicate the interpretation of experimental introductions or removals of species in complex systems. Despite some of the problems that arise, indirect effects are potentially an integral part of the workings of most complex natural communities. This means that questions about the strength and commonness of indirect effects are of fundamental interest to community ecologists.

There is as yet no generally accepted terminology for the various kinds of indirect effects (Miller and Kerfoot 1987; Strauss 1991; Wootton 1994c).



#### Two basic kinds of indirect effects.

Wootton (1993, 1994c) makes a useful distinction between two basic kinds of indirect effects that focuses on whether the transmitting species changes in abundance or changes in its per capita effect on the receiver. An **interaction chain indirect effect** occurs when a species indirectly affects others as a consequence of changes in the abundance of an intermediate transmitter species (Figure 8.1). For example, if species A negatively affects species B, and species C reduces the abundance of species A, then species C will have an indirect positive effect on species B. In contrast, an **interaction modification indirect effect** occurs when a donor species changes the per capita effect of the transmitter on the receiver without changing the abundance of the transmitter (see Figure 8.1). Such effects might arise if species C changes some other attribute of species A—behavior or size, for example—thereby changing the per capita effect of species A on species B. Of course, these two kinds of indirect effects are not mutually exclusive, and mixed effects could occur in which both the abundance and per capita effect of the transmitter change.

The distinction between indirect effects involving interaction chains and interaction modifications can be clarified by a hypothetical example framed in terms of simple models of interacting species. Consider a simple three-level food chain, with a top predator that indirectly affects primary producers in the bottom level through direct effects on the herbivores in the second trophic

state abundance, even the genetics of many complex communities exist, in other parts of the theory discussed, in which pairs of interaction coefficients or strengths of interactions between indirect interactions of ecological interacting species are not included. The interpretation of complex systems, are potentially an important part of communities. This is true of indirect effects.

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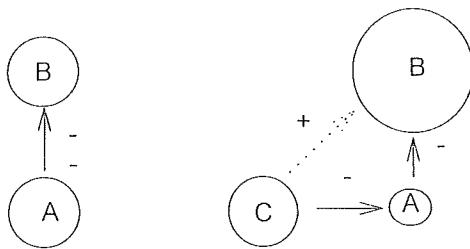
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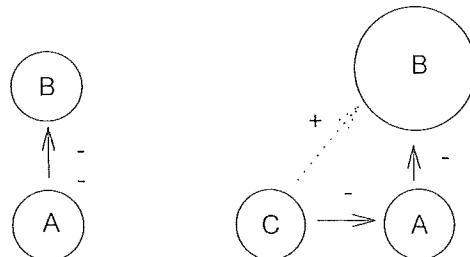
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#### A. Interaction Chain Indirect Effect



#### B. Interaction Modification Indirect Effect



**FIGURE 8.1.** Graphical representations of indirect effects involving interaction chains (A) and interaction modifications (B). Direct effects are indicated by solid arrows, with the sign of the interaction indicated by + or -. Indirect interactions are shown by dashed arrows. Population sizes are indicated by the relative sizes of the circles denoting each species.

level. If the effect is due solely to reduced abundance of the herbivores, then the effect is an interaction chain indirect effect, which could be represented simply by a change in herbivore density in a functional response term for herbivores feeding on producers. However, the top predators might not reduce herbivore abundance and might instead reduce the per capita consumption of producers. Such an interaction modification indirect effect could be represented as a change in the herbivore per capita attack rate within the functional response, instead of a change in herbivore abundance. While this example focuses on predator-prey interactions, similar logic would apply to systems of competitors or mutualists and distinguishes between processes affecting **densities** of interacting species versus **per capita impacts**, such as competition coefficients or attack rates, that relate species densities to the intensity of interspecific interactions.

Some of the interactions already considered in previous chapters are examples of indirect effects. These interactions, and some additional ones,

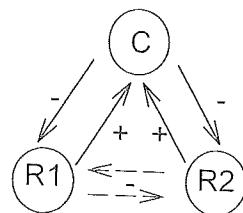


## Examples of indirect effects.

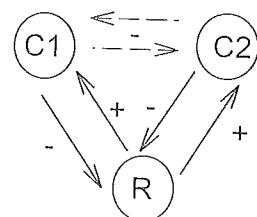
are outlined graphically in Figure 8.2 to illustrate why they are indirect. For example, purely **consumptive competition** between two species, when the contested resource is a third species, is a kind of indirect effect (see Figure 8.2). In contrast, direct chemical competition between two species involving chemical inhibition of one species by another clearly would not be an indirect interaction. The outcome of **keystone predation**, in which a predator enhances the abundance of one or more inferior competitors by reducing the abundance of a superior competitor, is another kind of indirect effect. The positive effect of the predator on inferior competitors is mediated through its negative impact on an intermediate species, the superior competitor.

Other kinds of indirect interactions are of sufficient interest that they have acquired specific names. These interactions are described in greater detail below and include **apparent competition**, **indirect mutualism**, and **indirect commensalism**. The ideas of Hairston et al. (1960) and Fretwell

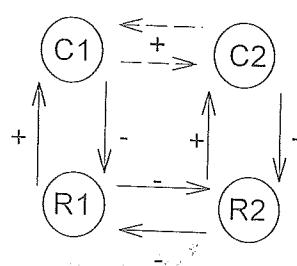
## A. Apparent Competition



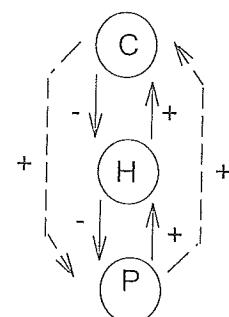
## B. Consumptive Competition



## C. Indirect Mutualism



## D. Trophic Cascade



**FIGURE 8.2.** Some of the major kinds of indirect effects. Direct effects between pairs of species are indicated by solid arrows, whereas indirect effects are shown as dashed arrows. C indicates consumer species, and R indicates resource species in the interactions diagrammed in (A), (B), and (C). In (D), P indicates primary producers, H indicates herbivores, and C indicates top consumers or predators.

in Figure 8.2 are indirect. For **competitive competition**, when the consumer is removed (see Figure 8.2). In situations involving chemical interactions, an indirect interaction may enhance the abundance of a species with a positive effect or have a negative impact.

interest that they described in greater detail in greater mutualism, and

Competition

ade

between pairs of dashed arrows. Interactions indicated by solid lines indicate her-

(1977) about the relative importance of competition and predation in regulating populations of species in different trophic levels describe another kind of indirect effect, called a **trophic cascade**. Here the abundance of primary producers is thought to be indirectly regulated by top predators in food chains with three or more trophic levels. In short chains with only two levels, the regulation would be a direct effect. Other interaction modification indirect effects, called **higher-order interactions**, refer to changes in the ways in which pairs of species interact that are caused by the presence of other species. Although very complex indirect effects involving feedback through large numbers of species can be imagined and modeled, the majority of well-studied indirect effects typically involve chains of only three or four interacting species.

## APPARENT COMPETITION

Robert Holt (1977) first described the conditions that might promote an indirect effect called **apparent competition**, in which the presence of multiple noncompeting prey species elevates predator abundance above levels maintained by single prey species, which increases predation pressure on multiprey

assemblages (see Figure 8.2). Apparent competition can occur where two noncompeting species share a predator on some higher trophic level. In the absence of predators, each prey species is regulated by purely intraspecific density-dependent mechanisms, and neither prey species competes, directly or indirectly, with the other. The scenario assumes that predator abundance depends on total prey abundance, so that where more species of noncompeting prey coexist, they should support more predators than in situations where only a single prey species occurs. Predators consume prey at a rate that increases with predator abundance. This can lead to a situation in which both prey species occur at lower densities when they occur together than when they occur separately. Although this pattern would have the outward appearance of interspecific competition, since the prey are less abundant in sympatry than in allopatry, the prey do not compete, directly or indirectly. Lower abundance in sympatry is caused entirely by the greater abundance of predators supported by both prey populations together than by either prey population alone. This idea is interesting, but does it happen? There are very few studies designed specifically to test for apparent competition. Two studies suggest that apparent competition can in fact occur.

Russell Schmitt (1987) described a likely case of apparent competition involving marine invertebrates dwelling in rocky reefs off the coast of southern California. At first glance, the pattern in this system appears consistent

with habitat segregation resulting from competition between two groups of prey, sessile bivalves (*Chama* and *Mytilus*) and mobile gastropods (*Tegula* and *Astrea*). The bivalves occur mostly in areas described as high-relief reefs, where they find some shelter from predators among crevices in the rocks. The gastropods are more abundant in low-relief reefs composed of rocky cobbles, and they usually do not seek shelter in crevices. However, competition between the two bivalves and gastropods seems very unlikely. The bivalves and gastropods consume different kinds of food. The bivalves filter particles from the water and the gastropods scrape algae from the rocks. Competition for space is also unlikely, because bivalves and gastropods favor different substrates. Gastropods forage on the surface of the rocks, whereas bivalves occupy crevices. A diverse array of invertebrate predators, including lobsters, octopods, and whelks, prey on both bivalves and gastropods. The gastropods appear much more vulnerable to predators, and both predators and bivalves appear to be more abundant on high-relief reefs.

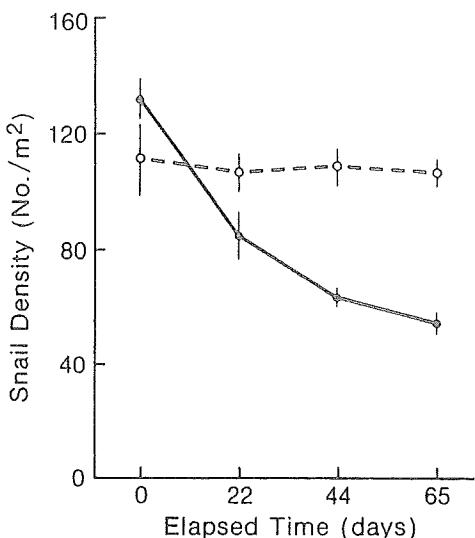
To test whether predators become more abundant when prey from both habitats are available, Schmitt transferred the bivalves *Chama* and *Mytilus* to the gastropod-dominated rocky cobble reefs and observed the impact of this transfer on gastropod mortality and predator abundance. Additional bivalves were added over time to offset losses to predators and maintain a high density of prey. It was not possible to perform the reciprocal transfer of gastropods to the high-relief reefs where *Chama* and *Mytilus* usually occurred; therefore, to measure possible interactions between the bivalves and gastropods at low predator densities, Schmitt transplanted bivalves to areas with high and low natural densities of gastropods. As expected, transplants of bivalves to cobble reefs increased predator abundance. Relative to control areas that did not receive bivalves, gastropod densities declined significantly over the 65-day duration of the experiment (Figure 8.3). Gastropods had a similar indirect negative effect on bivalves, with more bivalves being consumed by predators in areas of high gastropod density ( $45.1 \text{ snails/m}^2$ ) than in areas of low snail density ( $4.7 \text{ snails/m}^2$ ). The results are consistent with a somewhat asymmetric indirect negative effect of bivalves on snails, mediated by the rapid aggregation of predators in areas with high densities of their preferred prey, the bivalves.

Sharon Lawler (1993a) also found evidence for apparent competition between two prey species in a laboratory study of interactions among protists. Lawler examined interactions between two prey species, the flagellate *Chilomonas* and the ciliate *Tetrahymena*, and their shared predator, the ciliate *Euplotes*. *Chilomonas* and *Tetrahymena* coexist in laboratory microcosms, which suggests that competition is not sufficiently intense to drive either species extinct under these conditions. Each species, when occurring in the absence of the other prey, also managed to coexist with predators for long periods of time. *Euplotes* attained much higher densities when it fed on

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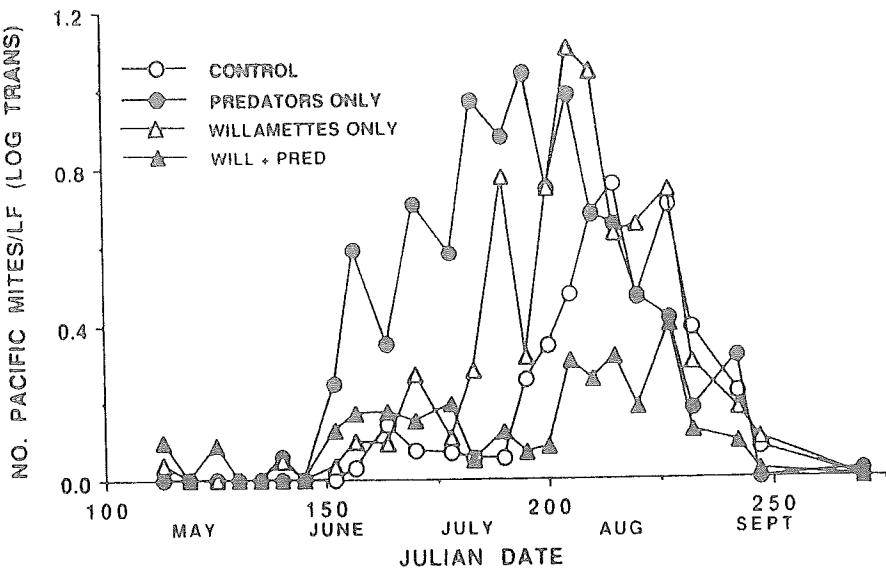


**FIGURE 8.3.** Decrease in gastropod density (solid circles) at sites receiving alternate prey (bivalves) contrasted to unchanged gastropod densities (open circles) at control sites without alternate prey. The decrease is attributed to apparent competition. (Reprinted from Schmitt, 1987, with permission of the Ecological Society of America.)

*Tetrahymena*, which suggests that *Tetrahymena* is a better food source than *Chilomonas*. However, when both prey species occurred together with *Euplotes*, *Chilomonas* was rapidly eliminated, apparently because the presence of *Tetrahymena* led to a predator density that was sufficient to drive *Chilomonas* extinct.

Holt and Lawton (1994) have recently reviewed evidence for indirect effects resulting from shared predators. They point out that although the potential consequences of natural enemies for shared prey have long been recognized, there have been surprisingly few quantitative studies of these interactions. Much of the evidence for apparent competition that they review is anecdotal, consisting of observations of high mortality among certain focal prey when alternate prey are also more abundant. There is a great need for experimental studies of apparent competition. Apparent competition may have important practical implications in managed agricultural communities. For example, attempts at biological control might be made more effective by creating situations in which introduced predators remain at higher densities by virtue of being able to feed on multiple prey species. This is, in fact, counter to the usual strategy, in which a very specific predator of a particular prey is sought.

Karban et al. (1994) have found that under some circumstances, predators are more effective at controlling a certain target prey when they are released together with an alternate prey than when released alone. They studied the effectiveness of a predatory mite, *Metaselia occidentalis*, used to



**FIGURE 8.4.** Enhanced reduction of target prey (Pacific mites, which feed on grapevines) by predators when predators are introduced on grapevines together with an alternate prey (Willamette mites). The enhanced reduction may be a consequence of apparent competition mediated by the presence of an alternate prey species. (Reprinted from Karban et al., 1994, with permission. © Springer-Verlag.)

control infestations of herbivorous Pacific mites (*Tetranychus pacificus*) feeding on grapevines. They found that introduction of the predatory mite together with an alternate food source, the Willamette mite (*Eotetranychus willamettei*) resulted in a much greater reduction in the abundance of Pacific mites than when the predator is introduced in the absence of the alternate prey (Figure 8.4). Karban et al. emphasize that a result consistent with apparent competition occurred only once in the course of several such introductions. They suggest that the low frequency of this kind of apparent competition in their field trials may reflect the impact of poorly understood aspects of environmental variation on these indirect effects.

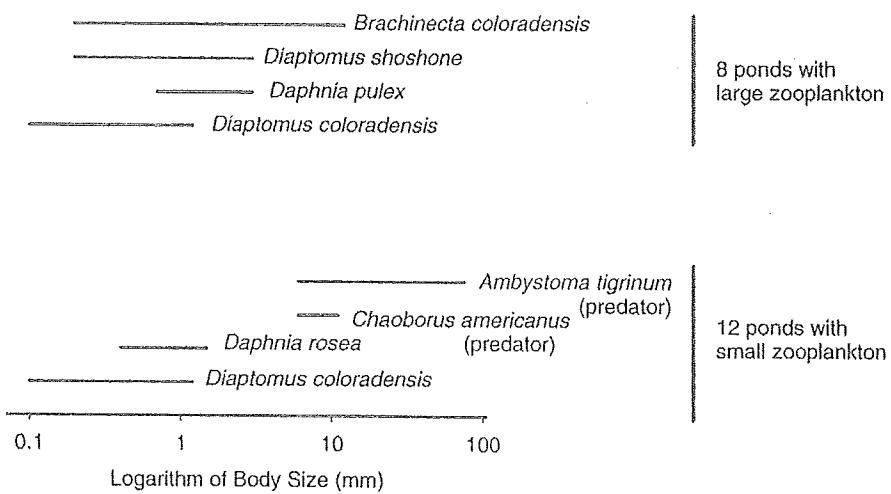
## INDIRECT MUTUALISM AND INDIRECT COMMENSALISM

Although some indirect effects have net negative consequences for the species on the receiving end of the interaction chain, other kinds of

positive effects, such as indirect mutualism (see Figure 8.2), are possible. Such indirect effects were suggested by a series of observations of alternate patterns of



Indirect positive interactions.



**FIGURE 8.5.** Alternate communities found in alpine ponds with vertebrate predators (the salamander *Ambystoma tigrinum*) or without vertebrate predators (Dodson 1970). Ponds with *Ambystoma* have zooplankton assemblages dominated by small species, whereas ponds without *Ambystoma* contain mostly large zooplankton species. The planktivorous midge *Chaoborus* can feed only on smaller zooplankton species, such as *Daphnia rosea*.

community composition made by Stanley Dodson (1970). Dodson noted that communities found in small alpine ponds in Colorado tended to fall into two groups (Figure 8.5). One series of ponds contained two predators, *Ambystoma* and *Chaoborus*, known to feed primarily on zooplankton with very different body sizes. Larval salamanders (*Ambystoma tigrinum*) feed primarily on larger zooplankton, including some large predatory copepods that can greatly reduce the abundance of smaller zooplankton species. Larvae of the phantom midge, *Chaoborus*, are restricted to feeding on smaller zooplankton species that usually do not coexist with larger species. In natural ponds, *Ambystoma* and *Chaoborus* are almost always found together, and *Chaoborus* usually does not occur in ponds without *Ambystoma*. Dodson explained this pattern as a consequence of *Ambystoma* maintaining the feeding niche provided by small-bodied prey consumed by *Chaoborus*. Presumably, the large-bodied zooplankton that predominate in ponds without *Ambystoma* are inappropriate prey for *Chaoborus*. An alternate hypothesis is that ponds without *Ambystoma* tend to freeze solid during the winter, and the same freezing that excludes *Ambystoma* may also eliminate *Chaoborus*.

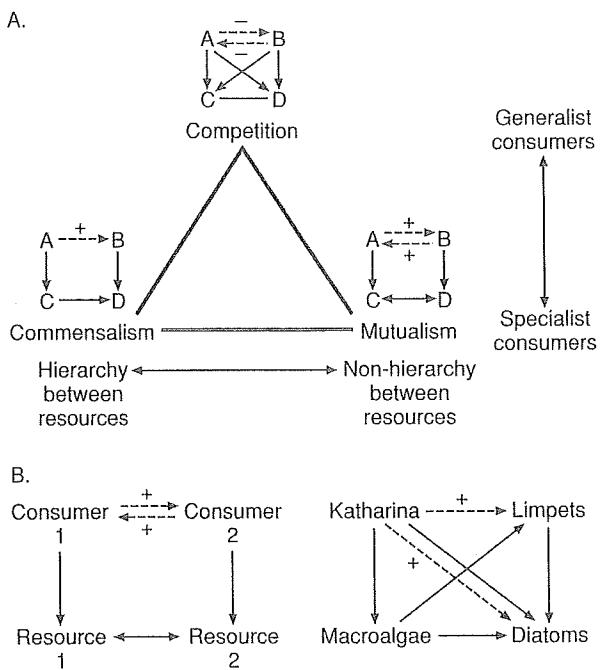
Although Dodson did not experimentally test the indirect mutualism hypothesis, Giguere (1979), working in a similar system, did find evidence that *Chaoborus* performs better in the presence of a different *Ambystoma* species. Although his experiment was unreplicated, Giguere was able to show that removal of *Ambystoma* from one pond shifted the body size distribution of zooplankton toward species of large size. The shift to larger zooplankton coincided with a decrease in the abundance of *Chaoborus*. Vandermeer (1980) subsequently explored a simple model of the indirect mutualism suggested by Dodson's observation. The model considers two predator species preying on two prey species. The kind of positive indirect effect suggested by Dodson is expected to occur when each predator is highly dependent on a different prey species and when the prey compete so strongly that one is likely to exclude the other in the absence of exploitation by its predator.

The kind of interaction outlined above really has more in common with a commensalism than a mutualism, since one predator indirectly facilitates the other, whereas no reciprocal interaction seems to occur. Dethier and Duggins (1984) describe another example of an indirect commensalism and also provide a conceptual framework to predict the conditions that influence whether interaction will lead to indirect mutualism, indirect commensalism, or simple consumptive competition. In their rocky intertidal system, *Katharina*, a chiton that consumes larger competitively dominant algae, positively affects the abundance of limpets, which graze on small diatoms that are competitively excluded by larger algae. The limpets have no reciprocal indirect effect on *Katharina*, which is what makes this interaction an indirect commensalism rather than a mutualism.

Dethier and Duggins (1984) suggest that the conditions favoring indirect mutualism or commensalism versus consumptive competition are predictable from the degree of resource specialization of the consumers (Figure 8.6). If the consumers are generalists that feed on both kinds of resources, the consumers will simply compete. If the consumers are sufficiently specialized so that each requires different sets of competing resources, then a positive indirect effect will result. Whether the effect is reciprocal (a mutualism) or asymmetric (a commensalism) depends on the extent to which the resource species compete in a hierarchical or asymmetric fashion. Asymmetric competition among the resource species should favor an indirect commensalism, whereas symmetric competition among the resources should lead to a more mutualistic interaction among highly specialized consumers.

## TROPHIC CASCADES, TRI-TROPHIC INTERACTIONS, AND BOTTOM-UP EFFECTS

Robert Paine (1980) coined the term **trophic cascade** to describe how the top-down effects of predators could influence the abundances of species in



**FIGURE 8.6.** (A) Conceptual model relating the extent of consumer specialization and the asymmetry (hierarchy) of competition among resources to the kinds of indirect interactions expected among consumer species (Dethier and Duggins 1984). (B) The kinds of interactions that result in an indirect commensalism between Katharina and limpets. (Adapted from Dethier and Duggins, 1984, with permission of the University of Chicago Press.)

 Indirect effects involving three trophic levels.

lower trophic levels. Others have focused on indirect effects that propagate from the bottom up through multiple trophic levels, called **tri-trophic effects** when the

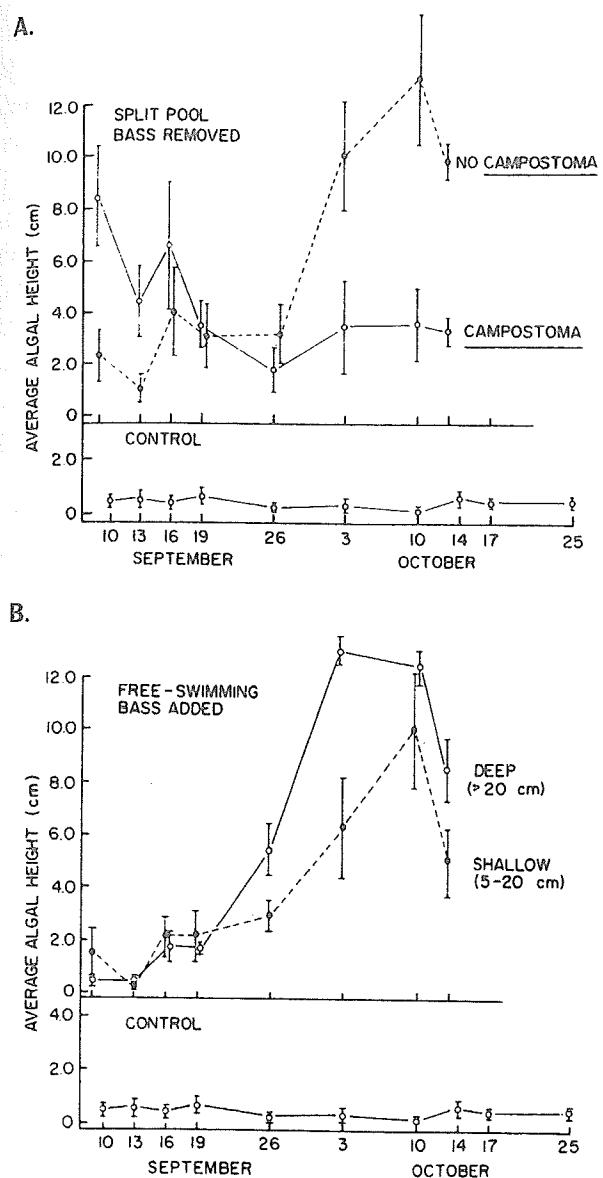
interaction involves three trophic levels (Price et al. 1980). Regardless of the direction of transmission, once an effect proceeds beyond the adjacent trophic level, it becomes indirect. Hairston et al. (1960) and Fretwell (1977) clearly invoke the trophic cascade phenomenon in their writings about population regulation; although they did not call the process by this particular name. Evidence for top-down trophic cascades is surprisingly scarce, and comes primarily from aquatic systems (Strong 1992). There is at least one convincing terrestrial example (Marquis and Whelan 1994). It has been suggested that the scarcity of trophic cascades in terrestrial systems represents a real difference in the structure of terrestrial and aquatic food webs. Strong (1992) suggests that aquatic food webs may tend to be more linear than terrestrial ones. Trophic cascades might be likely to develop in linear food

chains, in which effects of one trophic level are readily passed on to other levels. In contrast, in reticulate food webs, distinctions between trophic levels are blurred and effects of one species are likely to diffuse over many adjacent species.

Studies of stream communities provide some of the best examples of trophic cascades. Power et al. (1985) showed that a top predator, in this case largemouth bass, had strong indirect effects that cascaded down through the food web to influence the abundance of benthic algae in prairie streams. The system is best caricatured as a simple three-level food chain, running from algae (mostly *Spirogyra*) to herbivorous minnows (*Campostoma* sp.) to bass (*Micropterus* sp.). The prairie streams typically experience periods of low water flow, during which the streams become series of isolated pools connected by shallow riffles. At such times, two categories of pools become obvious: bass pools with bass and luxuriant algae, and minnow pools with abundant herbivorous minnows but without bass or much algae. The pattern suggests a cascading effect of bass, which prey on minnows and could thereby promote algal growth by eliminating an important herbivore.

To test this idea, Power et al. selected three pools for observation and experimental manipulations. The manipulations consisted of the addition of bass to a minnow pool and the removal of bass from a bass pool, which was then divided in half. One half of the pool received minnows; the other half remained minnow free. A third minnow pool remained unmanipulated as a control. The response of interest was the height of filamentous algae in the pools over time. After bass removal, *Campostoma* greatly reduced algal abundance to low, heavily grazed levels similar to those observed in a natural control pool with abundant minnows (Figure 8.7). Addition of bass to a minnow pool resulted in a rapid increase in algal abundance, whereas algae remained scarce in the control pool without bass. These results are consistent with a cascading indirect effect of bass transmitted through minnows to the algae. The actual mechanism involved appears to be largely a behavioral avoidance of bass by minnows. Minnows leave pools with bass, and, when confined with bass, limit their foraging to shallow water where the risk of bass predation is least.

Similar kinds of trophic cascades may occur in lakes (Carpenter et al. 1985; McQueen et al. 1989) and have been proposed as a possible way to control nuisance blooms of algae in eutrophic waters. Trophic cascades are less dramatic in lakes than in prairie streams, and the influence of top predators generally fails to propagate all the way down to the algae. In lakes, the basic food chain (ignoring the microbial loop) runs from algae to zooplankton to planktivorous fish to piscivorous fish. Where strong trophic cascades occur, lakes with abundant piscivorous fish should have less algae than lakes in which planktivorous fish form the top trophic level, since zooplankton



**FIGURE 8.7.** (A) Direct negative effects of herbivorous minnows, *Campostoma*, on algal abundance in a stream pool. Removal of minnows leads to an increase in algal height, whereas algal height stays unchanged in a control pool with minnows and without bass. (B) Indirect positive effect of bass on algal abundance, a trophic cascade, contrasted with the same control pool shown in (A). (Reprinted from Power et al., 1985, with permission of the Ecological Society of America.)

should be more abundant and should reduce phytoplankton to lower levels. However, the predicted cascading effects seldom appear as decreased phytoplankton abundance (Carpenter et al. 1987). One reason is that the phytoplankton consists of an array of species that differ in their vulnerability to grazing by zooplankton, and differences in zooplankton grazing pressure simply select for complementary communities of algae that differ in grazer resistance. This situation has been modeled by Mathew Leibold (1989). When zooplankton are abundant, the phytoplankton is dominated by grazer-resistant species. When zooplankton are less abundant, the phytoplankton is dominated by competitively superior species that are vulnerable to grazing. Phytoplankton remains abundant, but is dominated by different sets of species. Consequently, the prospects for manipulating fish populations to control the abundance of nuisance algae seem limited.

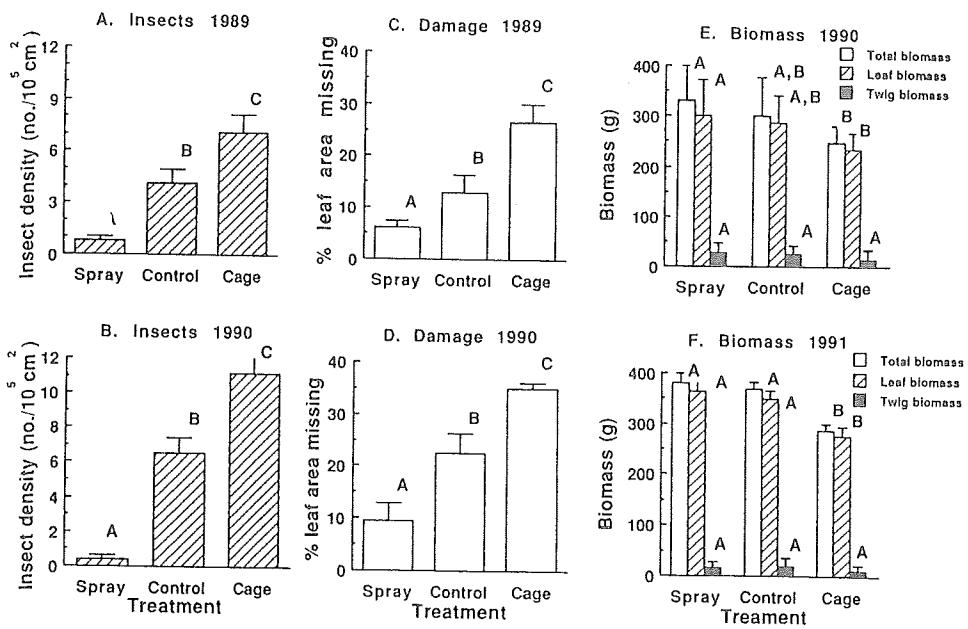
The best example of a terrestrial trophic cascade comes from a study by Robert Marquis and Christopher Whelan (1994). They found strong effects of insectivorous birds that were transmitted through herbivorous insects to white oak trees. Birds were excluded from some trees by netting (cage treatment), while other trees remained available to the birds (control treatment). Birds significantly reduced the abundance of herbivorous insects on the oaks. In turn, oaks with birds and reduced herbivorous insects had less leaf damage from insects and subsequently attained a higher biomass (Figure 8.8). The effect of birds on insects was further corroborated by including an insect removal treatment (spray treatment) consisting of applications of a spray insecticide combined with the hand removal of remaining insects.

Strong experimental evidence for **bottom-up indirect effects** also comes from manipulations of stream communities. Wootton and Power (1993) manipulated the amount of light available to algae by differentially shading small portions of a natural stream. They then measured how these manipulations affected the abundance of algae, herbivores, and carnivores. Increases in light created increases in algal abundance and increases in carnivore abundance, while herbivore abundance remained unchanged (Figure 8.9). These results are generally consistent with the models of Rosenzweig (1973) and Oksanen et al. (1981), which suggest that an increase in productivity in a three-level food chain should create an increase in the abundance of plants and carnivores, whereas the abundance of herbivores should not show much of an increase.

For example, consider the following simple model of a three-level food chain:

$$\frac{dn_1}{dt} = rn_1 - an_1n_2 - (r(n_1)^2)/k \quad (8.1)$$

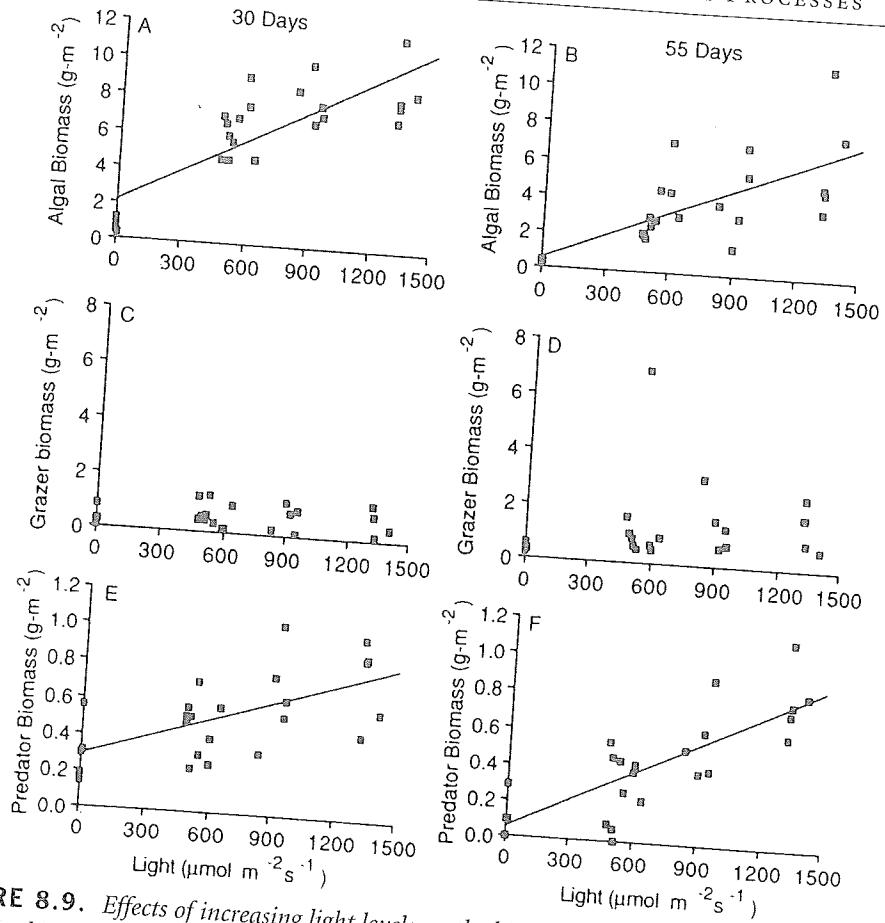
$$\frac{dn_2}{dt} = ean_1n_2 - xn_2 - cn_2n_3 \quad (8.2)$$



**FIGURE 8.8.** Indirect effects of bird exclusion on leaf damage and biomass of small oak trees in two consecutive years. The indirect effect of birds is mediated through the reduction of herbivorous insects on trees where birds forage. Treatments labeled "Cage" excluded insectivorous birds. Spray treatments used insecticide to remove insects. Controls were uncaged and contained natural densities of herbivorous insects maintained at low levels by birds. Bars with identical letters did not differ significantly. (Reprinted from Marquis and Whelan, 1994, with permission of the Ecological Society of America.)

$$dn_3/dt = gcn_2n_3 - yn_3 \quad (8.3)$$

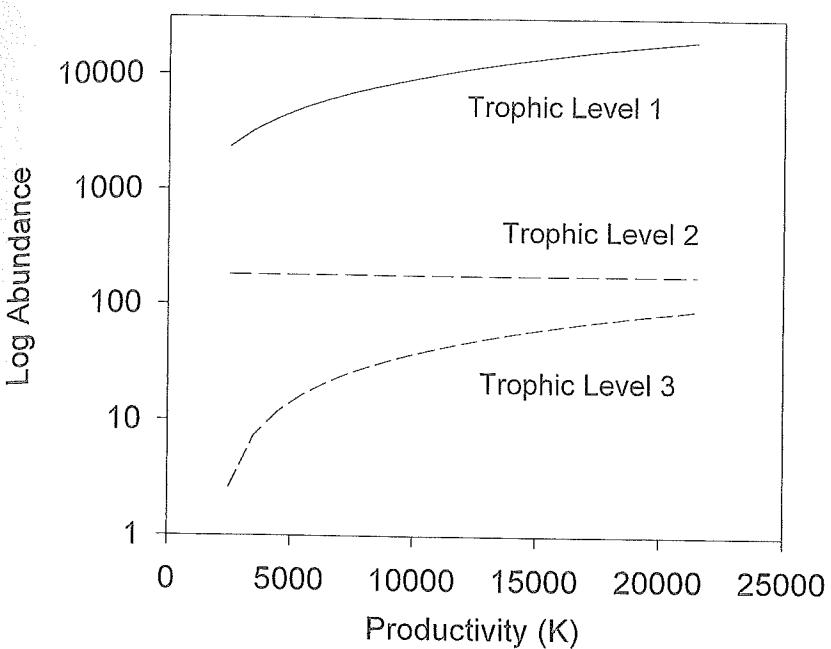
Here,  $n_1$ ,  $n_2$ , and  $n_3$  refer to the abundances of species on trophic levels 1, 2, and 3. Trophic level 1 has a carrying capacity of  $k$  and a rate of increase  $r$ . Trophic level 2 consumes trophic level 1 at a rate given by  $an_1n_2$ , the simple linear functional response of the Lotka-Volterra predator-prey equations. Consumption of trophic level 1 is transformed into new individuals of trophic level 2 at some efficiency,  $e$ , yielding  $ean_1n_2$  as the rate of birth of trophic level 2. Individuals on trophic level 2 die at a constant rate  $x$  in the absence of trophic level 3, and at a rate of  $cn_2n_3$  when consumed by trophic level 3. Individuals on the third trophic level are born at a rate of  $gcn_2n_3$ , assuming that consumed individuals of trophic level 2 are converted into new predators on trophic level 3 with some efficiency  $g$ . Predators on the top trophic level also die at some rate,  $y$ . This model is simpler than the one used by Oksanen et al. with respect to details of the functional responses of the predators to prey, but it makes roughly comparable predictions about how the



**FIGURE 8.9.** Effects of increasing light levels on the biomass of primary producers (algae), herbivores (grazers), and predators in streams. In these three-level food chains, species on odd-numbered levels increase with increasing productivity, whereas species on the even-numbered level remain constant, as suggested by Fretwell (1977) and Oksanen et al. (1981). (Reprinted from Wootton and Power, 1993. © 1993 National Academy of Sciences, U.S.A.)

abundance of each trophic level at equilibrium will change as  $K$ , a measure of productivity, changes (Figure 8.10).

Peter Abrams (1993) has used models to explore how different arrangements of interacting species in simple three-level food chains would affect the likelihood of bottom-up effects like those observed by Wootton and Power (1993). His theoretical results suggest that bottom-up effects will depend strongly on the amount of heterogeneity among species in their responses to species on other trophic levels. Three situations involving rather minor departures from a simple linear three-level food chain can prevent bottom-up effects (Figure 8.11). Competition among multiple species on the top trophic level may create situations in which the decline in one competitor is not offset



**FIGURE 8.10.** Relations between abundance at equilibrium and primary productivity ( $k$ ), using the model described in Equations 8.1 to 8.3. Parameter values are as follows:  $r = 2.5$ ,  $a = 0.001$ ,  $e = 0.05$ ,  $x = 0.09$ ,  $c = 0.01$ ,  $g = 0.5$ , and  $k$  varies between 2500 and 21,500.

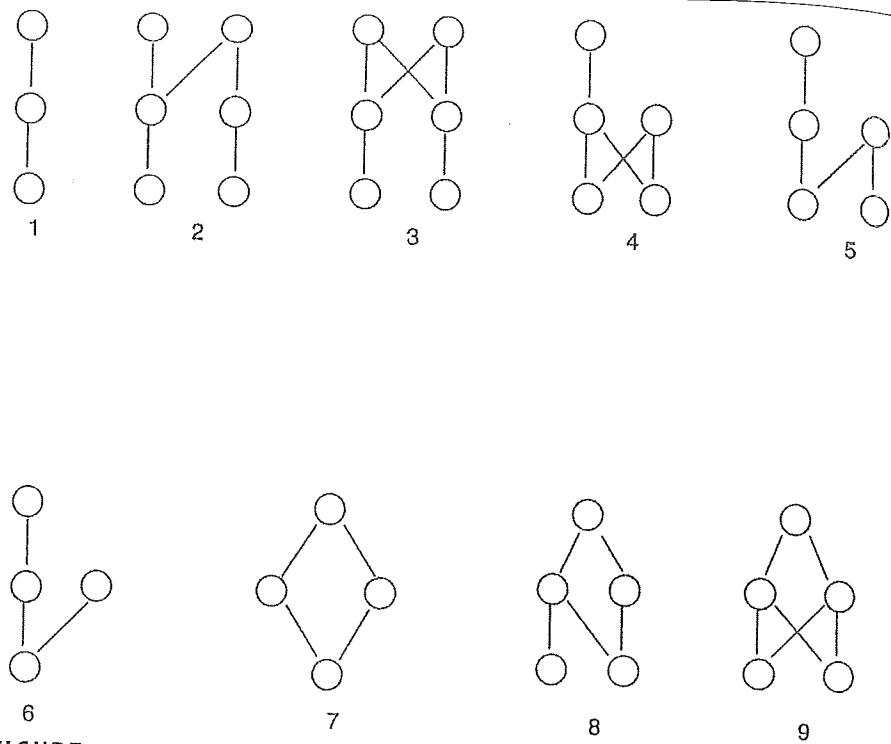
by the increase in another. In other situations, the presence of an invulnerable species on the intermediate trophic level may divert increases in productivity from reaching the top trophic level. Alternately, if species on the intermediate trophic level share the same prey and predators, then increases in productivity simply cause a shift toward more predator-resistant species, with no net effect on the abundance of the top trophic level.

## INTERACTION MODIFICATIONS: HIGHER-ORDER INTERACTIONS AND NONADDITIVE EFFECTS

Interaction modifications have attracted the attention of ecologists for many years because their existence gravely complicates the prediction of interactions in complex communities from

 Some indirect effects involve changes in the ways that species interact. knowledge of pairwise interactions in simple communities. For example, the multispecies formulation for the dynamics of a set of Lotka-Volterra competitors

depends on the assumption that per capita competitive effects are immutable properties of pairs of species (the competition coefficients) that do not



**FIGURE 8.11.** Departures from simple linear three-level food chains (web 1) that can prevent bottom-up (trickle-up) positive effects of enhanced productivity on top predators (Abrams 1993). Webs 2 and 3 incorporate competition among top predators. Webs 4, 5, and 6 have an invulnerable prey on the intermediate trophic level. Webs 7, 8, and 9 have intermediate species that share predators and prey.

change as other species in the community come or go. If the per capita effects of competitors do change with species composition, then phenomena often referred to as **higher-order interactions**, or **nonadditive interactions**, become a real concern. Higher-order interactions are a subset of the kind of indirect effects called interaction modifications. Unfortunately, both of these terms emphasize the ways in which observed interactions depart from statistical or analytical models of interactions rather than emphasizing the biological basis of indirect effects that involve interaction modifications (Abrams 1987). Typically we abstract the way in which a pair of species will interact as a coefficient, such as a competition coefficient or as an attack rate in a functional response term. The usual assumption is that those coefficients are properties of the particular pair of interacting species. However, those interactions, and the coefficients that describe them, may depend on the mix of

TABLE 8-1. Competition coefficients ( $\alpha_{ij}$ ) estimated for crustaceans interacting in combinations of two or three species. Changes in the coefficients measured for pairs or trios of species mean that competitive interactions among pairs of species (shown to the left of the slash) are changed by the presence of additional species (shown to the right of the slash), a kind of interaction modification.

Species <i>i</i>	Species <i>j</i>			
	<i>Alonella</i>	<i>Ceriodaphnia</i>	<i>Simocephalus</i>	<i>Hyalella</i>
<i>Alonella</i>	1	1.08/0.79	0.06/0.91	9.16/11.08
<i>Ceriodaphnia</i>	0/0	1	0.37/0.84	3.38/5.40
<i>Simocephalus</i>	0/0	0.13/0.12	1	4.30/4.40
<i>Hyalella</i>	0/0	0/0	0/0	1

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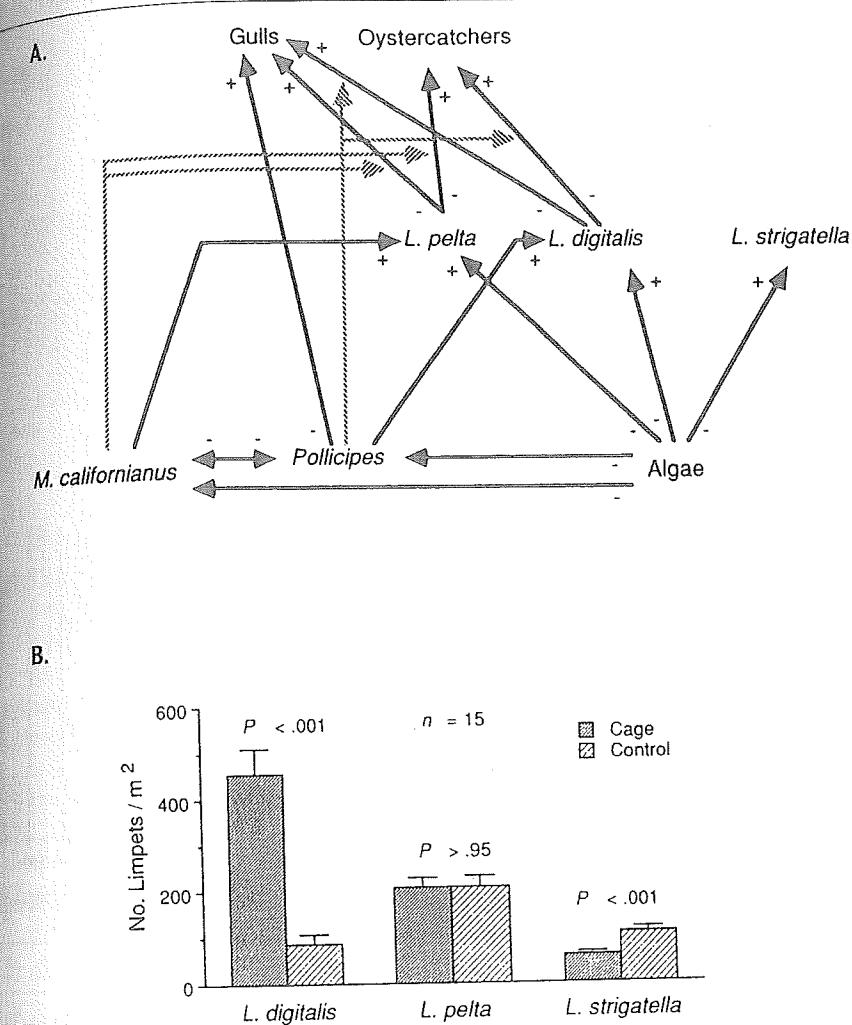
other species present when the interactions are measured because additional species can modify the ways in which the focal pair of species interact. Additional competitors can change the ways that species compete. Additional predators or prey can alter the way a given predator interacts with a particular prey. If these interaction modifications are important, it is difficult to predict the outcome of interactions among large sets of species from information about interactions between isolated pairs of species. In a sense, every interaction becomes a special case, the outcome of which depends on the particular features of the biotic and abiotic environment where the interaction occurs.

The kind of information needed to demonstrate the existence of interaction modifications is difficult to obtain (Billick and Case 1994; Wootton 1994a; Adler and Morris 1994). There are a few convincing cases, though. One of the first efforts was by William Neill (1974). Neill showed that the competition coefficients measured for interactions among four species of small crustaceans in aquatic microcosms changed with the number of species present in the system (Table 8-1). This result means that if one wanted to predict the outcome of competition among three or four species by summing up all the pairwise competitive interactions among species, errors would arise. Neill's study has been criticized on methodological grounds because it is very difficult to measure sets of competition coefficients accurately from experimental data (Pomerantz 1981). Nonetheless, the study has few equals, and it raises important questions about the validity of assumptions used to create multispecies Lotka-Volterra models of competing species.

Case and Bender (1981) have been critical of much of the evidence presented for interaction modifications. They outline an approach to the study of interaction modifications that circumvents the problem of estimating interaction coefficients by focusing on how initial population growth rates change in different combinations of one, two, or three species. They have shown that in simple laboratory systems of one to three species of *Hydra*, population growth rates in two-species communities are significantly greater than expected from growth rates observed in single-species and in three-species communities. They suggest that some sort of mutualistic interaction occurs at low densities in two-species communities that does not materialize in three-species communities.

Other evidence for interaction modifications comes from Tim Wootton's (1992, 1993, 1994b) studies of interactions among predatory birds, limpets, mussels, and gooseneck barnacles in the rocky intertidal zone. Important direct and indirect interactions in this system are outlined in Figure 8.12. Predatory birds change the abundance of two sessile species, *Mytilus californianus* and *Pollicipes polymerus*, which in turn are the preferred substrates of two different limpet species. *Lottia digitalis* is light in color and is cryptic on light-colored *Pollicipes*. *Lottia pelta* is dark in color and is cryptic on *Mytilus*. Birds selectively reduce the abundance of *Pollicipes*, favoring *Mytilus*. In turn, *Lottia pelta* becomes more abundant, since the presence of *Mytilus* makes it more difficult for visually foraging birds to locate the limpet that is cryptic on *Mytilus*.

Other kinds of interaction modifications materialize in terrestrial communities. In some cases, species can indirectly affect others either after death (Bergelson 1990) or through the effects of nonliving material such as dead leaves and other forms of plant litter (Facelli 1994). Jose Facelli found that leaf litter produced by forest trees fundamentally changed the interactions between tree seedlings and herbaceous competitors in open fields. Where litter is abundant, seedlings of herbaceous plants have a reduced competitive impact on seedlings of the tree *Ailanthus altissima*. Although litter creates a more favorable microclimate by increasing soil moisture, it also tends to shade out herb seedlings, making them weaker per capita competitors. The effects of litter on herbivores are even more complex. Although seedlings benefit from reduced competition from herbs, they suffer increased damage from herbivorous insects. The favorable microclimate provided by plant litter leads to increased insect abundance, which can cause increased damage to a variety of plant seedlings. The net result is that plant litter has multiple indirect effects on *Ailanthus* seedlings, some positive and some negative (Figure 8.13). Facelli was able to dissect these effects by factorial manipulations of herbaceous competitors, litter, and insecticide in a field experiment conducted under natural conditions.



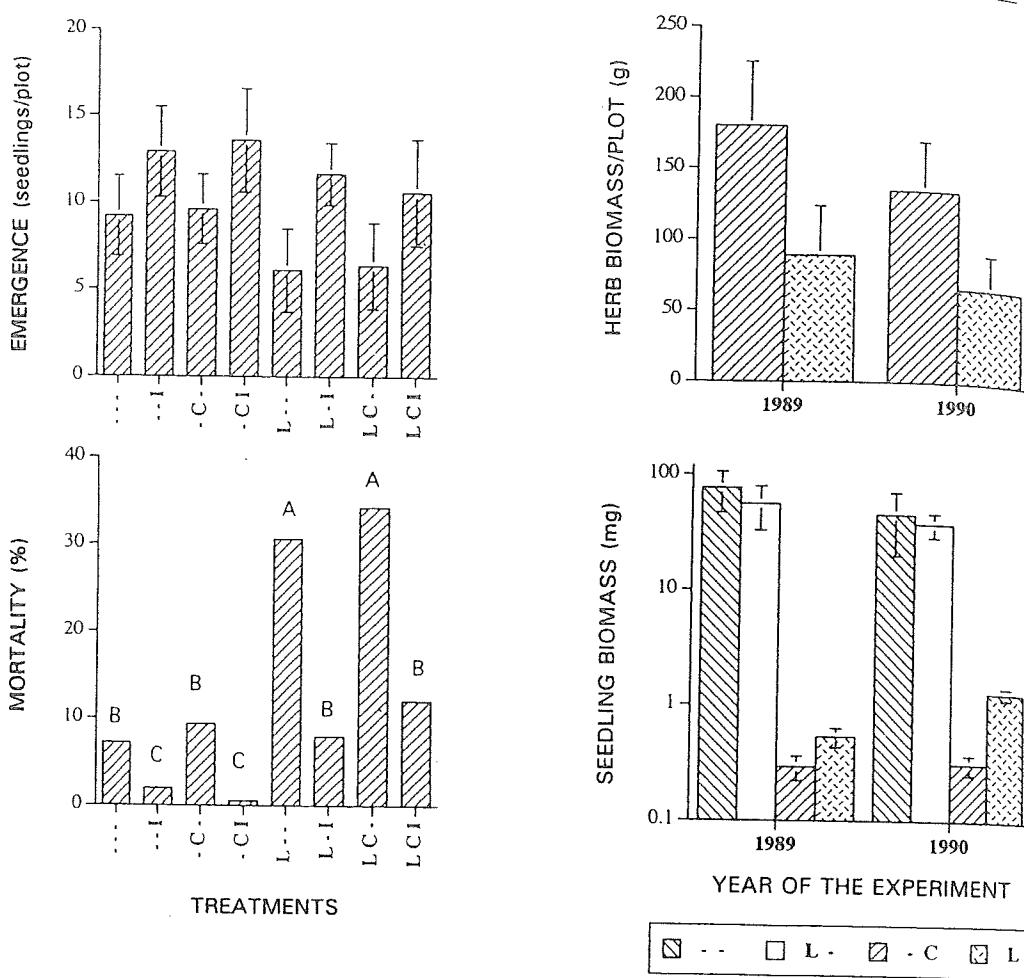
**FIGURE 8.12.** (A) Direct and indirect interactions affecting the abundance of three limpet species. Solid arrows indicate direct effects; dashed arrows indicate indirect effects resulting from the modification of direct interactions between pairs of species. (B) Results of bird exclusion (cage) on the abundance of three limpet species. *L. digitalis* increases because its favored substrate, *Pollicipes*, increases when birds are excluded. (Reprinted from Wootton, 1992, with permission of the Ecological Society of America.)

## INDIRECT EFFECTS AND THE INTERPRETATION OF MANIPULATIVE COMMUNITY STUDIES

Indirect effects can complicate the interpretation of ecological experiments. Bender et al. (1984) have pointed out that, depending on the kind of experimental manipulation that is performed,

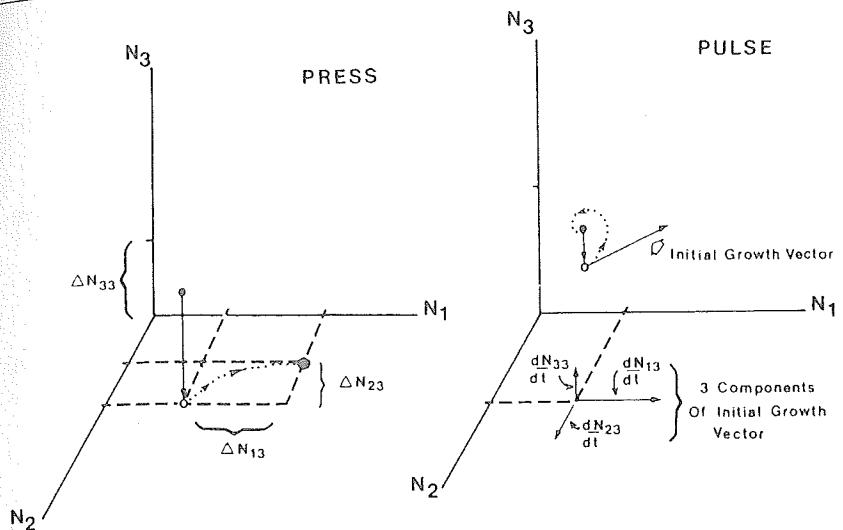
 Indirect effects complicate the interpretation of ecological experiments.

responses can include a mixture of indirect and direct effects or just direct effects. Bender et al. recognize two kinds



**FIGURE 8.13.** Effects of plant litter (*L*), herbaceous competitors (*C*), and insecticide (*I*) on the emergence, mortality, and biomass of seedlings of the tree *Ailanthus altissima*. Litter indirectly increases seedling mortality by increasing the abundance of herbivorous arthropods. However, litter indirectly enhances the biomass of surviving seedlings by reducing the biomass of competing herbs. (Reprinted from Facelli, 1994, with permission of the Ecological Society of America.)

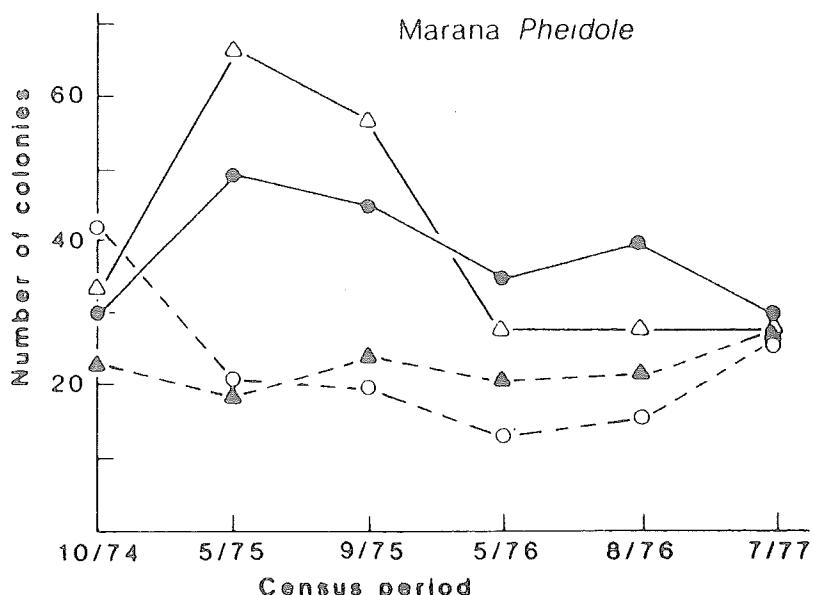
of experimental manipulations: press experiments, in which the density of a species is permanently changed, and pulse experiments, in which the density of a species is altered and then allowed to return to its previous state (Figure 8.14). Additions or removals of species correspond to press experiments, the most common kinds of manipulations done by ecologists. Pulse experiments would correspond to a one-time increase or decrease in density of a species already present in the community, without adding or removing a species from the community or maintaining the altered density at a particular level. Bender et al. argue on theoretical grounds that responses to



**FIGURE 8.14.** Phase space representation of the difference between press and pulse experiments. The axes  $N_1$ ,  $N_2$ , and  $N_3$  refer to the abundances of species 1, 2, and 3. In a press experiment, species 3 is eliminated, and the responses of species 1 and 2 are shown by the dashed line on the  $N_1$ - $N_2$  plane. In the corresponding pulse experiment, species 3 is reduced in abundance but not eliminated, and all three species can change in abundance over time. The initial growth vector can be decomposed into the responses of each species to a reduction in the density of species 3. (Reprinted from Bender et al., 1984, with permission of the Ecological Society of America.)

press experiments include direct and indirect effects, which makes them difficult to interpret. In contrast, pulse experiments should highlight only direct effects.

The theoretical arguments used to make this distinction rely on some assumptions that may be difficult to justify in natural systems, such as the existence of a stable equilibrium to which the community tends to return following a pulse perturbation. Also, the approach is limited in utility to those species that reproduce with sufficient rapidity so that responses are likely to be seen in a reasonable amount of time, say a few years. There is also the very real practical problem of engineering pulse perturbations that will be strong enough to elicit a detectable set of responses. Most press perturbations arise from the consequences of being able to either add or delete species from communities, either by additions or deletions of free-ranging organisms or by selective barriers such as cages. Species additions or deletions are often easy to engineer and yield detectable responses, important considerations for experimental ecologists. The point that press experiments must be interpreted carefully is well taken, and subsequent studies have shown that long-term press experiments often show changing patterns that can be attributed to the influence of indirect effects.



**FIGURE 8.15.** Initial and long-term responses of granivorous ants, *Pheidole* sp., to removal of granivorous rodents (solid lines). Controls with rodents are shown by the dashed line. Initial increases in ant density gradually return to control levels, as small-seeded plants that are preferred by ants are replaced by competitively superior large-seeded plants (Reprinted from Davidson et al., 1984, with permission of the Ecological Society of America.)

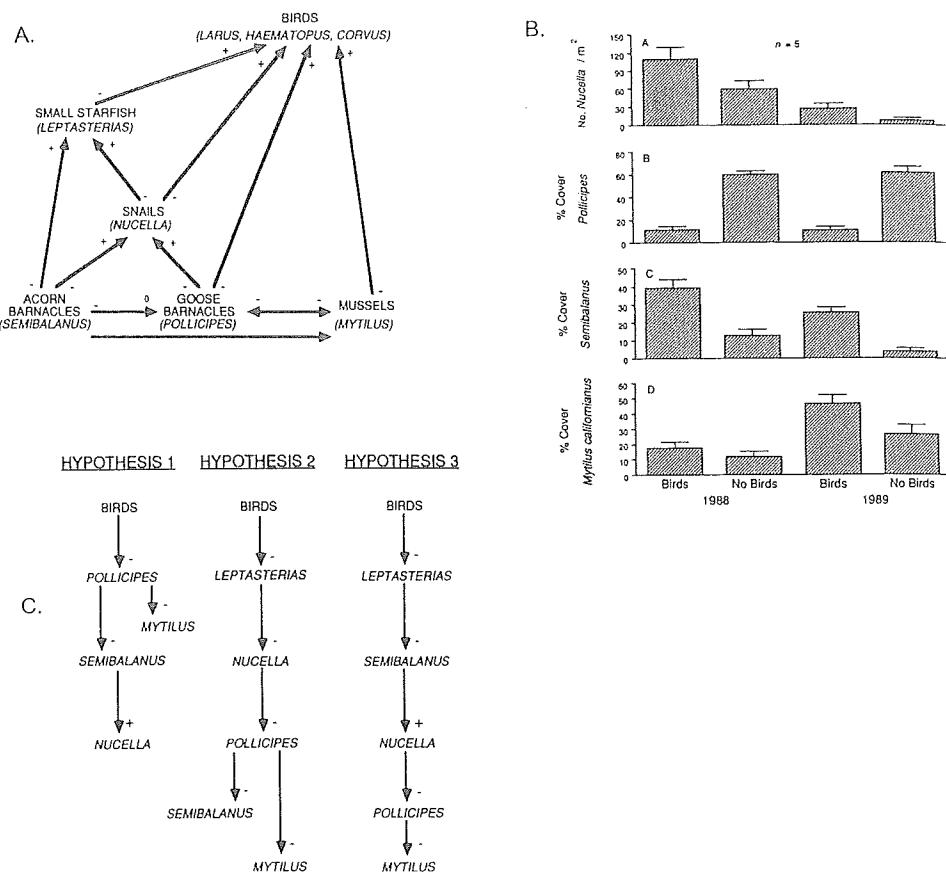
One field experiment showing the influence of unanticipated indirect effects involves a study of interactions between granivorous rodents, ants, and the plants that produce the seeds that these granivores eat. Davidson et al. (1984) initially found strong negative competitive effects of rodents on ants in an array of large field exclosures where seed-eating rodents were present at natural densities or excluded. Positive effects of rodent removals on ants were strong early in the experiment but then gradually disappeared over time despite the fact that rodent removals continued (Figure 8.15). The gradual decline in ant abundance was due to an indirect effect of rodent removal on the small-seeded plants that are selectively consumed by ants. Rodents prefer to eat the seeds of large-seeded plants, which tend to competitively displace small-seeded plants when rodent predation fails to keep the large-seeded plants in check. Although these indirect effects eventually led to a rather different pattern than would be expected from the initial responses to rodent removal, their cause is easily interpreted. The indirect effects also took several years to become pronounced. This suggests that although caution is called for in interpreting any long-term field experiment, initial strong responses probably reflect direct effects even when indirect effects may eventually become important.

Other studies (e.g., Wootton 1994b) have shown that reliable statistical tools, such as path analysis, can be used to tease apart and identify indirect effects. In any complex community there may be many possible causal pathways of interactions among species, which collectively form an interaction web. Wootton (1994b) has used path analysis to identify some of the more likely causal relations in complex communities. Path analysis can be used to make predictions about how changes in the abundance of key species will affect the abundance of other species in the community. To the extent that these predictions differ among proposed chains of interactions, it is possible to test which scenario, or interaction web, is most likely. Path analysis has limitations. It is no more than a descriptive technique that can summarize the ways in which temporal or spatial variation in abundance is correlated among species. Nonetheless, it can be used to generate testable hypotheses.

Wootton noted four important changes in the abundance of different intertidal organisms in response to the experimental exclusion of birds (Figure 8.16). At least three different interaction chains could have produced these differences. Fortunately, the different interaction chains made different predictions about how particular species would respond to additional experimental manipulations (Table 8-2). When those manipulations were done, the results were consistent with the simplest, shortest, interaction chain, which was also the scenario favored by the path analysis. The power of this approach is that it allows the generation of alternate hypotheses, which can then be tested by field experiments. Path analysis is a descriptive technique that by itself cannot determine whether a particular interaction chain is responsible for a particular pattern. It can, however, indicate whether certain chains are more plausible than others.

## CONCLUSIONS: FACTORS CONTRIBUTING TO THE IMPORTANCE OF INDIRECT EFFECTS

We still know very little about why indirect effects occur in some settings and not in others. A few tentative generalizations seem appropriate, if only to encourage further research. Strong direct effects are probably required to produce noticeable indirect effects; weakly interacting species are not likely to generate sufficient changes in abundance or behavior of transmitter species for those effects to appear in receivers. The impact of simple versus complex food chain structure on the transmission of indirect effects requires much further study. Strong indirect effects clearly materialize in systems with complex reticulate chains of interacting species, such as rocky intertidal communities (Wootton 1994b), as well as in systems with relatively linear food chains, such as the stream communities studied by Power et al. (1985). Where cascading effects fail to materialize, as in some large lakes, the failure may be



**FIGURE 8.16.** (A) Pathways of potential interactions among a group of species found in the rocky intertidal zone of Washington. Horizontal arrows indicate competition; other arrows indicate predator-prey links. (B) Responses of four species to bird removal. (C) Three alternate sets of causal links (pathways) that could account for the responses of species to bird removal. The shortest path, hypothesis 1, is most consistent with the result of experiments designed to distinguish among these alternate pathways. (Reprinted from Wootton, 1994b, with permission of the Ecological Society of America.)

due to compensatory changes in the abundances of species within trophic levels that differ in their resistance to consumers, as suggested by Leibold (1989) and Abrams (1993). Although most of the examples described here involve indirect effects among chains of three or four species, it is unclear whether this represents a limit to the transmission of indirect effects in natural communities or whether longer chains of interactions occur. McQueen et al. (1989) suggest that both top-down and bottom-up indirect effects are transmitted for very limited distances before they become undetectable. Thus, bottom-up effects would be most likely to be seen low in food chains, whereas top-down effects would be stronger for species high in food chains.

TABLE 8-2. Predicted responses to experimental manipulations of intertidal organisms that could be used to distinguish among the three alternate interaction pathways that might explain the indirect effects of birds (see Figure 8.16).

Manipulation and Target Species	Predictions		
	Hypothesis 1	Hypothesis 2	Hypothesis 3
<i>Reduce Nucella</i>			
1. <i>Pollicipes</i>	0	+	+
2. <i>Semibalanus</i>	0	-	0
3. <i>Mytilus</i>	0	-	-
Reduce <i>Semibalanus</i> independently of birds, <i>Pollicipes</i> , and <i>Mytilus</i>			
4. <i>Nucella</i>	-	0	-
Reduce <i>Pollicipes</i> independently of birds			
5. <i>Semibalanus</i>	+	+	0
6. <i>Mytilus</i>	+	+	+
7. <i>Nucella</i>	+	0	0
Reduce birds independently of <i>Pollicipes</i>			
8. <i>Semibalanus</i>	0	0	-
9. <i>Mytilus</i>	0	0	0
10. <i>Nucella</i>	0	-	-
11. <i>Leptasterias</i>	None	+	+

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Ultimately, we need to know the extent to which the dynamics of species in complex webs are tightly or loosely connected in order to understand whether indirect effects will propagate widely through the community or rapidly peter out. A useful analogy is to consider a web of interactions among species, in which the functional connections between species can be thought of as mechanical connections, like rigid rods or very flexible springs. Where species are linked by rigid rods, the case for tight connections among species, a force applied to any one species will be transmitted to many others. Where species are loosely connected by flexible springs, a force applied to a species may leave most others unaffected. The question is, in real communities, how many connections are rigid and how many are flexible?

