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THE NATURE AND CONSEQUENCES OF INDIRECT EFFECTS IN ECOLOGICAL COMMUNITIES

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Abstract

Indirect effects occur when the impact of one species on another requires the presence of a third species. They can arise in two general ways: through linked chains of direct interactions, and when a species changes the interactions among species. Indirect effects have been uncovered largely by experimental studies that have monitored the response of many species and discovered "unexpected results," although some studies have looked for specific indirect effects predicted from simple models. The characteristics of such approaches make it likely that the many indirect effects remain uncovered, but the application of techniques such as path analysis may reduce this problem. Deterministic theory indicates that indirect effects should often be important, although stochastic models need exploration. Simulation models indicate that some indirect effects may stabilize multi-species assemblages. Five simple types of indirect effects have been regularly demonstrated in nature: exploitative competition, trophic cascades, apparent competition, indirect mutualism, and interaction modifications. Detailed experimental investigations of natural communities have yielded complicated effects. Indirect effects have the potential to affect evolutionary patterns, but empirical examples are limited. Future directions in the study of indirect effects include developing techniques to estimate interaction strength in dynamic models, deriving more efficient approaches to detecting indirect effects, evaluating the effectiveness of ap-

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proaches such as path analysis, and investigating mechanisms in which a species changes how other species interact.

INTRODUCTION

Ecologists have long been interested in determining the role that biotic interactions play in ecosystems. Many workers have suggested that biotic interactions between pairs of species play a major role in shaping the ecological and evolutionary patterns in natural and human-impacted systems. If true, then one should expect that species will also indirectly affect other species when a species is involved in several strong pair-wise interactions. Finding indirect effects thus indicates that biotic interactions are important to ecological systems, and that community-level phenomena must be incorporated to understand and predict the dynamics of natural systems. Aside from the basic interest in this question, the existence of indirect effects can have important implications for applied problems. If indirect effects are common, then environmental impacts such as species introductions and the reduction or extinction of species can have widespread effects on the rest of the system. Furthermore, because indirect effects can offset or exacerbate direct effects of the manipulation, the task of predicting the consequences of particular environmental manipulations becomes extremely complicated (88, 101, 140). In this paper, I review the nature and occurrence of indirect effects in natural systems, discuss methodological approaches to their investigation, and suggest several directions for future research.

TERMINOLOGY

To define indirect effects, one must first define direct effects. I consider direct effects to arise as a result of a physical interaction between two species. Therefore direct effects would occur between a pair of species both in isolation and within multi-species communities of varying composition. Common examples include one species consuming, interfering with, or physically benefiting another. Logically then, indirect effects are those effects of one species on another that are not direct effects. The key feature of indirect effects is that they require the presence of intermediary species in order to arise. Thus, they are a property arising in multi-species assemblages.

In some instances, indirect effects have also been considered to arise through a change in a physical or chemical variable in the environment as well as through another species (116). For example, fish foraging activity may change the sedimentation regime of a stream, which in turn may influence invertebrates and algae (37, 94, 96). Similarly, a species may affect the availability of inorganic nutrients in the system, which in turn affects the population dynamics of producers (9, 41, 123, 131). The major feature in such examples is that the physical or chemical variable of interest acts in a dynamic manner, much as another species would. Little is gained in debating whether or not such effects should be considered "indirect," as long as the underlying mechanisms are recognized and the dynamics of the physical or chemical variable are accounted for when necessary. For the purposes of this paper, I consider indirect effects to be only those mediated through other species.

Indirect effects arise in ecological systems through two general mechanisms (Figure 1; 74, 133, 136). First, varying the abundance of one species can indirectly affect the abundance of another by changing the abundance of an intermediary species that interacts with them both—an interaction chain. For example, one species can reduce the abundance of its prey, thereby reducing the food base of other consumers of the prey (i.e. exploitative competition). Second, varying the abundance of one species can indirectly affect the abundance of a second species by changing the interaction between the second species and a third species, an interaction modification. Thus, these indirect effects arise because the interactions between pairs of species are not independent of other species. For example, increasing vegetation density may indirectly increase the abundance of a prey species by allowing it to hide from its predator, thereby reducing the intensity of the predator-prey interaction. Distinguishing between the two types of indirect effects is important because they have different implications for predicting system responses to a perturbation. Indirect effects arising from interaction chains can be predicted readily, given a knowledge of how species pairs directly interact. In contrast, indirect effects arising from interaction modifications can be uncovered by identifying instances where one species might affect the interaction between two others. At our present level of understanding, however, the quantitative consequences of interaction modifications can only be determined by experimental manipulations within the context of the community of interest; they cannot be predicted ahead of time.

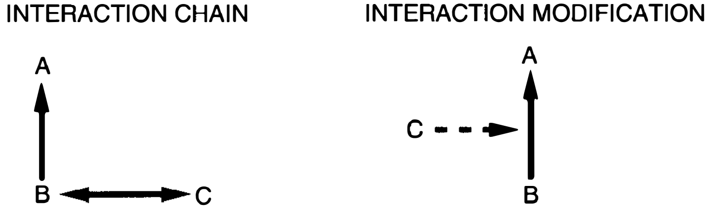

Figure 1 Two basic ways in which one species can indirectly affect another. Left, species C affects species A through a chain of direct interactions involving a change in the abundance of species B. Right, species C indirectly affects species A by modifying how species A interacts with species B. Adapted from (133).

The definition of indirect effects used here (see also 74, 116) is broader than the one advocated by Billick & Case (8), who suggest that it be applied only to interaction chains. Because "indirect" is the antonym to "direct," however, applying the term "indirect effects" only to a subset of the nondirect impacts of a species breeds confusion. Similarly, most discussion of interaction modifications has been carried out under the term "higher-order interactions." Much confusion has arisen in these studies, in part because higher-order interactions can also refer simply to nonlinear direct effects. Nonlinearities need not arise because one species changes how a species pair interacts (92). "Interaction modification" accurately describes the general mechanism by which this class of indirect effects arises, thereby drawing attention to the salient features to be investigated. Consequently empiricists need not be at the mercy of a mathematical description of a system in order to identify and study such indirect effects. Additional terminology (e.g. response, behavioral, morphological, and chemical indirect effects) has been proposed for specific mechanisms by which interactions are modified by other species (74, 116). This terminology can be useful in more precisely categorizing different types of indirect effects, but the recognition of interaction modifications as a general class of indirect effects is useful because they represent a fundamental difference in how such effects are modeled, yet provide a general mechanistic criterion to classify particular interactions identified from field observations.

THE DETECTION OF INDIRECT EFFECTS

Indirect effects have come to the attention of ecologists largely as a result of either experimental manipulations or large-scale (re-)introductions of species that have been placed in a multi-species context. Usually, they have been detected only when an experimental manipulation produces "unexpected results" on a target species (109). The reliance of ecologists on fortuitous results to identify indirect effects is a cause for concern, because such an approach is likely to give a biased or incomplete picture about the importance of indirect effects. This is particularly true when indirect effects have impacts in the same direction as those expected from more obvious direct interactions. Under such circumstances, the overall change observed between treatments usually is assumed to arise from the direct effect alone. This assumption is not always a safe or appropriate one to make. For example, removal experiments on birds that forage intertidally (132) have demonstrated a five-fold increase in the population of the limpet *Lottia digitalis,* consistent with a strong predator effect. A detailed examination of the results that accounted for changes in other members of the intertidal community showed, however, that the direct effects of predation actually caused only about a two-fold change in population size. The remaining change in population size of the limpet was attributable to negative indirect effects of birds on limpets arising from changes in the abundance of sessile species that comprise the habitat of the limpets.

Recently, indirect effects have been identified in studies that have looked explicitly for patterns of population changes predicted from a specified type of indirect effect (e.g. 14, 93, 102). Such studies still limit the identification of indirect effects, because predictions depend on the particular type of indirect effect under investigation. In these studies, other types of indirect effects continue to be detected only when results produce patterns that are unexpected both through the indirect interaction under study and through known direct interactions.

Aside from the disadvantages of current methodological protocols for uncovering indirect effects, an increasingly common statistical application would seem to bias against detecting indirect effects too. Multivariate analysis of variance (MANOVA) has commonly been applied to data sets involving multispecies response variables in order to control type I error rates (e.g. 77). Some ecologists may not appreciate that this technique factors out interdependencies between dependent variables. Such interdependencies are naturally present when indirect effects occur among the dependent variables, so this technique essentially excludes all variation in community structure due to indirect effects.

DEMONSTRATIONS OF INDIRECT EFFECTS IN NATURE

Despite the difficulty of identifying indirect effects, there is now a considerable amount of work showing that they can play an important role in natural systems. In this section, I review some of the common patterns of indirect effects found in field experiments or following the large-scale introduction or extinction of a species.

Exploitative Competition

Although often erroneously considered a type of direct interaction among species, exploitative competition is an indirect effect; one species indirectly reduces a second species by directly reducing the abundance of a shared resource (Figure 2a). This indirect effect has been the central focus of community-level studies for decades, and consequently there are numerous demonstrations of its importance in natural communities. Experimental studies of exploitative competition have been extensively reviewed by others (18, 21, 41, 103), so I do not do so here. In some cases, it is unclear whether the effects from experiments are the result of direct interference competition or indirect exploitative competition, because the mechanism of competition is often not investigated (120). It is important to emphasize that exploitative competition possesses no unique properties relative to other kinds of indirect effects. Thus, the extent to which exploitative competition has been demonstrated may pro-

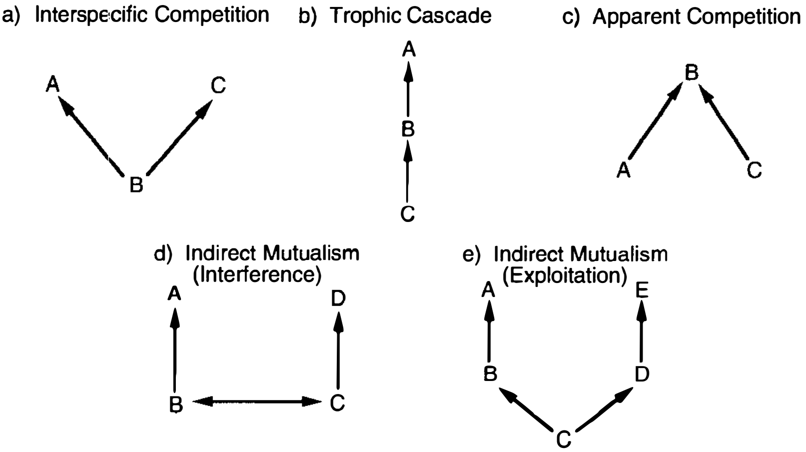

Figure 2 Five commonly investigated types of simple indirect effects. Horizontal arrows: interference competition (arrows show impacted species); vertical arrows: consumer-resource interactions (arrows determine direction of energy flow). Subfigures: (a) exploitative competition, (b) trophic cascade, (c) apparent competition, (d) indirect mutualism involving interference competition, (e) indirect mutualism involving exploitative competition.

vide an indication of the prevalence of other less-studied indirect effects. Furthermore, other types of indirect effects are just as likely as exploitative competition to have effects on the ecological and evolutionary dynamics of natural communities.

Trophic Cascades

Trophic cascades are indirect effects mediated through consumer-resource interactions (Figure 2b; 14, 82). Hairston et al's verbal theory of highly aggregated terrestrial food webs (45) clearly predicted their existence, and similar predictions have subsequently been made by many mathematical theories of food-chains (38, 78, 99, 112). Evidence from experiments and species invasions has now established that trophic cascades can occur in a variety of habitats.

In marine systems, the recovery of the sea otter (*Enhydra lutris*) in Alaska has been associated with large reductions in sea urchins (*Strongylocentrotus* spp.). In turn, reduced sea urchin grazing has led to increases in kelp cover, which has affected the structure of near-shore communities by changing both physical characteristics of the environment (e.g. water movement) and energy-flow patterns (via kelp detritus; 29, 30, 33, 34). Whelks (*Morula marginalba*), gulls (*Larus glaucescens*), and oystercatchers (*Haematopus bachmani*) in rocky intertidal systems also indirectly increase algal abundance by feeding on limpet grazers (*Lottia* spp.; 35, 132). In salt marshes, killifish (*Fundulus heteroclitus*) prey upon grass shrimp (*Palaemonetes pugio*), thereby indirectly enhancing the abundance of the anemone *Nematostella victensis* that the shrimp feed upon (56). Finally, human harvesting of grazing (*Fissurella* spp.) and of predatory gastropods (*Concholepas concholepas*) in Chile has led to increased abundances of algae (*Eridaea boryana*) and sessile invertebrates (*Perumytilus purpuratus*) that the gastropods consume (75, 76).

Examples of trophic cascades in freshwater systems are equally common. Experimental introductions of fish have caused reductions in the abundance of large zooplankton grazers and increases in phytoplankton biomass in the water column of lakes (14, 108), and small ponds (121). Similarly, removing fish has caused increases in snail grazers and declines in benthic algae in lakes (10, 68). Removing bass from Ozark streams has lead to an increase in grazing fish populations, which in turn has caused reductions in algae (95). In northern California rivers, however, removing steelhead has led to an increase in small predators, a decrease in grazers, and an increase in algae (93, 137).

Strong (117) has argued that, unlike aquatic habitats, trophic cascades are unimportant in terrestrial systems because of the compensatory effects of interspecific competition within trophic levels. Experimental manipulations of top consumers (particularly entire trophic levels), however, are much more difficult in terrestrial settings because the dominant species usually have much slower dynamics that operate over much larger spatial scales than those of aquatic systems. Thus, the relative scarcity of examples of trophic cascades from terrestrial systems may be a reflection of experimental limitations. Nevertheless, examples of trophic cascades do exist in terrestrial settings. In the East African savannah, the introduction of rinderpest caused reductions in grazers and browzers, leading to an increase in tree cover (110). On tropical islands, the removal of lizards caused an increase in phytophagus insects, and a subsequent increase in leaf damage (105, 114). Removal of spiders has caused an increase in grasshoppers and a decline in grassland vegetation (53). Exclusion of bird predators has caused increases in grazing insect abundance and a reduction in the biomass of oaks in Missouri (67). Along the Pacific coast of North America, the re-establishment of peregrine falcons (*Falco peregrinus*) has been associated with an increase in murres, cormorants, and oystercatchers, apparently as an indirect result of falcons feeding upon nest-robbing crows (84).

Apparent Competition

Apparent competition arises when two prey species share a common predator (Figure 2c; 50). In this case, an increase in one prey species may lead to an increase in the shared predator, causing a subsequent decline in the other prey species. Although examples are still scarce, some evidence of apparent competition exists in natural communities. In a subtidal marine community, increasing the abundance of bivalves leads to declines in the abundance of grazing gastropods because of increases in invertebrate predators (102). The introduction of the variegated leafhopper (*Erythroneura variabilis*) into the San Joaquin Valley of California causes reductions in the grape leafhopper (*Erythroneura elegantula*) by increasing the population of parasitic wasps (107). Increasing the abundance of the terrestrial isopod *Porcellio laevis* causes increases in the prevalence of an iridescent isopod virus, which in turn causes the reduction in a second isopod species, *Porcellio scaber* (44). More work needs to be done to determine the prevalence of this type of interaction in natural systems.

Indirect Mutualism and Commensalism

"Indirect mutualism" or "indirect commensalism," defined as indirect positive effects of one species on another (28, 71, 106, 122), can arise through a number of mechanisms. Typically, the indirect effect involves a consumer-resource interaction linked with either exploitative or interference competition (Figure 2d,e). In intertidal systems, adding starfish or snails indirectly increases the abundance of competitively inferior sessile species by reducing the abundance of mussels (*Mytilus*), the competitively dominant space-occupiers (66, 70, 80, 81). Intertidal bird predators indirectly increase the abundance of their snail prey (*Nucella* spp.) by consuming goose barnacles (*Pollicipes polymerus*), a competitively superior species to the snail's preferred prey, acorn barnacles (*Semibalanus cariosus*; 135). Birds also enhance the abundance of acorn barnacles by consuming limpets that "bulldoze" young individuals off the rocks while feeding (133). Grazing fish, molluscs, and crabs indirectly increase the abundance of crustose algae and diatoms by removing fleshy algae that shade and abrade shorter species (28, 72, 82). In some cases (28, 82) this shift in algal community structure has generated further indirect consequences by enhancing the abundance of grazers that specialize on crustose algae and diatoms. In the Gulf of California, adding predatory snails (*Acanthina angelica*) reduces the abundance of acorn barnacles (*Chthamalus anisopoma*), releasing algae (*Ralfsia* spp.) from competition for space, and enhancing the food supply of limpet grazers (*Lottia strongiana*). Likewise, limpets indirectly enhance snail abundance by reducing algal cover, thereby increasing the abundance of the snail's acorn barnacle prey through reduced competition for space (31, 32).

Similar patterns have been found in freshwater systems. For example, by feeding on competitively superior frog tadpoles, predatory salamanders indirectly increase the abundance of competitively inferior frog species in ponds (77, 127). Planktivorous fish, by preferentially feeding on large zooplankton, indirectly enhance the abundance of small zooplankton in lakes (11). Zooplankton prefer to feed upon green algae, thereby indirectly enhancing the abundance of blue-green algae in some lakes (59).

Several examples of indirect mutualisms and commensalisms exist in terrestrial systems. In the deserts of the southwestern United States, kangaroo rats (*Dipodomys* spp.) indirectly increase the abundance of small-seeded plant species by preferentially consuming large-seeded plants. As an indirect result, ants increase in abundance because they are only able to forage effectively on small seeds (26), and birds increase in local abundance apparently because after rodents reduce vegetation cover they can detect seeds more readily (119). In northern Europe, fieldfares (*Turdus pilarus*) aggressively defend their territories from avian predators, thereby indirectly enhancing the abundance of other avian species (111).

Indirect mutualisms and commensalisms may also play an important role in the dynamics of succession following disturbance (22). By removing rapidly invading, consumer-susceptible species, consumers may indirectly push the assemblage of sessile organisms of a system to a more consumer-resistant group of species by freeing them from preemptive interference competition. This mechanism of succession has been demonstrated frequently in experimentally manipulated marine systems. Intertidal snail and crab grazers remove early successional algal species, allowing grazer-resistant algae to become dominant (64, 65, 113). Subtidal starfish remove early successional species of bryzoans, allowing more resistant species to dominate (27). Intertidal bird and snail predators remove earlier successional blue mussels and goose barnacles, promoting the establishment of California mussels on rocky intertidal benches above tidal heights frequented by large starfish (130, 134). Evidence of consumer-driven succession also exists in lakes. By grazing on early-blooming algae, zooplankton shift the algal community over time to domination by cyanobacteria (100).

Because of the difficulties of performing experiments, there are few solid examples of consumer-driven succession in terrestrial settings. Ecologists have noticed patterns of late-succession plant species having higher levels of defenses against grazers, which suggests that this indirect effect may be important in terrestrial systems too (13, 16, 17, 40).

Interaction Modifications ("Higher-Order" Interactions)

As mentioned above (Figure 1, right), these indirect effects occur when one species modifies the interaction between two other species. Good examples of these indirect effects are limited because of difficulties in executing appropriate experiments and confusion about the mathematical criterion used in statistical tests (15, 92, 136). The strongest studies are those that can mechanistically identify how one species modifies the interactions between other pairs of species. Several mechanisms seem particularly likely to be important. Crypsis is one manifestation of an interaction modification. For example, sessile invertebrates indirectly affect limpet populations by making them harder for bird predators to discover, thereby changing the intensity of bird predation (73, 132, 133). Aquatic macrophytes may also reduce the intensity of predation by interfering with the detection of prey by fish predators (23, 125). Similarly, barnacles interfere with limpets grazing on algae (31, 36, 51).

Changes in behavior may also cause interaction modifications. For example, the activities of one predator species may flush out prey species, making them more susceptible to other predators. Alternatively, aggression among predators may reduce the consumption rate on the prey (129). Another possibility is that a predator is deterred from feeding in a patch by defended prey species, thereby reducing consumption of undefended prey species, an associational defense. For example, undefended plants perform better when associated with defended plants in the face of grazing (46, 90, 118). Some species may provide other species with defensive items, thereby indirectly reducing consumption rates. For example, the dinoflagellate *Protogonyaulax* spp. secretes a neurotoxin (the cause of paralytic shellfish poisoning or "red tide") that the butter clam *Saxidomus giganteus* can sequester in its body. The sequestered toxin deters gulls and other vertebrate predators from feeding on the clams (57). Furthermore, consumers may become satiated at high levels of prey availability. When several prey species are involved, a predator's consumption of one prey species may preclude the consumption of another prey species at the same time. Thus, a type II (49) functional response of a predator feeding on one prey (N1) when it also consumes another species (N2) should take the mathematical form:

$$c_1 N_1 / (1 + c_1 ht_1 N_1 + c_2 ht_2 N_2),$$

where c_x is the per-capita consumption rate of prey species x and ht_x represents the predator's handling time of an individual of species x. In this case, species 2 clearly reduces the predator's effect on species 1 (2). These mechanisms and others (1) indicate that interaction modifications may be common in natural systems, making community dynamics even more difficult to predict.

Overview

Indirect effects have commonly been observed in long-term experiments or observations of species introductions and deletions when ecologists have focused on the response of multiple members of the community, rather than on species pairs. For example, Menge's recent review of indirect effects in rocky intertidal communities (71) found exponential increases in the number of indirect effects detected with increases in the number of species considered. Indirect effects have been most commonly found in marine and freshwater systems but have also been detected in terrestrial systems, despite the above-mentioned logistical difficulties of doing so. Many indirect effects can be

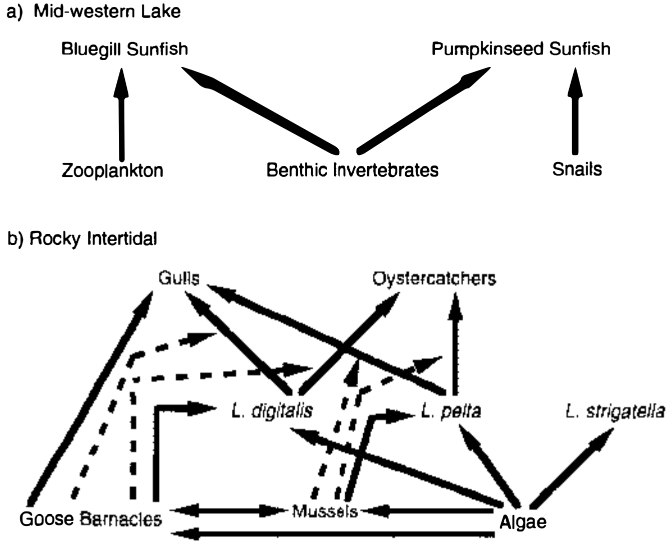

Figure 3 Examples of complex indirect effects in natural communities: (a) small lakes in Michigan (adapted from [79]), (b) a rocky intertidal community in Washington state (adapted from [132]). Vertical arrows: consumer-resource interactions, with arrow following the direction of energy flow. Arrows ending on horizontal: nonconsumptive direct interactions (interference competition, habitat preference) with arrows showing impacted species. Dashed arrows: modifications of consumer-resource interactions via crypsis.

ascribed to the simple types of interactions listed above (see also 71). However, there are often cases where the results do not fit such simple scenarios (71). For example, adding bluegill sunfish (*Lepomis gibbosus*) in Michigan lakes causes declines in zooplankton, declines in pumpkinseed sunfish (*Lepomis macrochirus*), and increases in snails through a combined effect of exploitative competition and apparent competition (Figure 3a; 79). Similarly, intertidal bird predators affect limpet grazers and algae through a morass of direct and indirect pathways (Figure 3b; 132). It is tempting to coin new terms to characterize such newly recognized patterns of interactions, but this type of enterprise would soon lead to a quagmire of new terminology. In characterizing indirect effects, it seems more appropriate simply to place them in the context of a functional web of interactions (71, 82) among species within a particular community.

In detailing the occurrence of indirect effects in the literature, it is also of interest to know whether direct effects are stronger than indirect effects. On the surface, one might expect direct effects to be stronger for a couple of reasons (106). First, because many indirect effects arise from chains of strong direct effects, strong direct effects are often required before even weak indirect effects can arise. Second, environmental variation may act independently on each species within an indirect pathway, thereby progressively weakening the strength of the effect relative to other sources of variation. Most arguments on the subject are verbal and deserve more rigorous theoretical investigation. Furthermore, the results of deterministic theory are at odds with these arguments: indirect effects in several theoretical studies can overwhelm direct effects in the absence of environmental variation (85, 140).

At present, empirical work on indirect effects seems too limited to merit strong generalizations on the relative importance of direct and indirect effects. In Schoener's literature analysis (106), selected direct effects tended to be stronger and to exhibit less variability than did indirect effects. This analysis, however, restricted its focus to direct effects that had been shown to be important, and it required assumptions in some cases about the whether an effect was predominantly direct or indirect when both could occur. The question may be better answered as techniques are developed to estimate simultaneously the strengths of various direct and indirect pathways that might affect a particular species, and when a better accounting of weak interactions is developed. For example, Menge (71) presented several possible approaches to assigning overall community variance due to direct versus indirect effects. In his analysis of a New England intertidal community, direct and indirect effects accounted for approximately equal amounts of community variation. Even if direct effects generally tend to be stronger than indirect effects, there are many examples where the direct effects of a manipulated species on a particular target species are much weaker than the indirect effects involved (e.g. 93, 132)

POSSIBLE EVOLUTIONARY CONSEQUENCES OF INDIRECT EFFECTS

Aside from the basic question of whether indirect effects exist, a related question of interest is whether indirect effects can play a role in evolutionary processes. Evidence bearing on this question is scarce, but several arguments can be made that indirect effects do affect the evolutionary trajectories of species. One would expect that if a species was negatively affected by another species, natural selection would favor the evolution of traits that either reduced the co-occurrence of the two species or reduced the impact of the indirect effects. This topic has been much discussed in relation to one indirect effect, exploitative competition. Arguments tracing back to Darwin (24) suggest that interspecific competition should lead to habitat separation between species or to character shifts that reduce competition between species pairs (12, 42). Although it is difficult to rigorously demonstrate such evolutionary changes in response to exploitative competition (20), there is some evidence that it occurs. For example, Grant (43) and his colleagues have mustered an enormous amount of observational support for the notion that competition for seeds has led to character divergence in Darwin's finches (*Geospiza* spp.). As mentioned above, there is nothing special about exploitative competition relative to other indirect effects, so one might predict similar evolutionary changes when a species is indirectly affected by another in a negative manner, regardless of the pathway.

Just as negative indirect effects should lead to traits favoring reduced coexistence or the minimization of the indirect effect, positive indirect effects should favor the evolution of traits that increase sympatry with the species involved and that maximize the effect of the indirect pathway. One possible example involves limpet habitat selection in the rocky intertidal communities of western North America (132). By making limpets more cryptic to bird predators, certain mussels and barnacles indirectly affect limpets by reducing the intensity of predation by birds. Corresponding with this indirect benefit, limpet species differentially select habitats that afford them the most protection from bird predation. Although the genetic basis of the behavior remains to be demonstrated, this scenario is consistent with positive indirect effects leading to the evolution of traits to maximize co-occurrence. There is some evidence that positive indirect effects may also affect morphological traits. For example, populations of the Caribbean tree lizard *Conocarpus erectus* have fewer trichomes on their leaves where high *Anolis* lizard densities reduce the abundance of grazing arthropods (104).

MECHANISMS PREVENTING INDIRECT EFFECTS

Although it is of great interest to know if and how indirect effects occur, it is also important to determine when and why indirect effects will not occur. Few studies have addressed the topic, although several causes have been proposed (106). The most obvious reason why indirect effects might not occur is because a system may be characterized by weak direct interactions between pairs of species. Even if direct effects are strong enough to be detected, they may be sufficiently weak that when linked together the effect of a perturbation becomes damped out. A second reason that indirect effects may not be important is if the system contains a great deal of environmental variation. For example, high rates of stress or disturbance might keep populations at sufficiently low levels that species do not interact strongly (5, 19). Similarly, if sufficient environmental noise affects the populations of each species in a chain of interactions, it may progressively swamp out the signal arising from the manipulation of a particular species at one end of the chain (106). Little theoretical work has been done on this topic (106), but in taking a path-analysis approach to analyzing indirect effects (described below), one can readily see how environmental stochasticity might weaken the importance of indirect effects.

A final reason that indirect effects might not be apparent is that other strong interactions may oppose the effect, yielding no net change. For example, birds that forage intertidally may have no net effect on some limpet species because positive indirect effects mediated through sessile habitat species may counteract the negative direct effects of predation (132). Under other circumstances, strong self-limitation may reduce interspecific effects (63, 135).

MATHEMATICAL ANALYSES AND PREDICTIONS OF INDIRECT EFFECTS

Theoretical Explorations

Theoretical analyses of multi-species models are critical to understanding and predicting the consequences of indirect effects; such analyses employ several different approaches. The most common approach uses dynamical models of multi-species systems. Because of the difficulty of analysis, these efforts have largely been restricted to linear equations taking the form of a standard Lotka-Volterra models. Methods have been developed to estimate indirect effects, based upon the per-capita effects of direct interactions among species pairs (58, 60, 101, 115). This approach has shown the potential for indirect effects to alter significantly the predicted relationships of species involved in either competition or consumer-resource interactions (25, 58, 60, 101, 106, 115, 122, 140). To date, this approach has not been particularly useful in predicting the consequences of changes to natural communities because of the difficulty in obtaining estimates of interaction coefficients in the field.

An early modification of this approach was loop analysis (61, 97). This technique, derived from the sort of linear models described above, allows qualitative predictions about how a system should respond to a perturbation, given that one knows the existence and the sign of interactions among the variables of interest. Because loop analysis does not require estimates of strengths of interaction among species, it has been more useful in making predictions. This approach is limited, however, to relatively simple community configurations; estimates of interaction strengths are required to make predictions in more complex webs.

The dynamic modeling approach has been extended to evaluate the consequences of adding nonlinear complexity. Work on models with nonlinear foraging effects (1–3) has shown a dizzying array of possible outcomes beyond those derived from linear models. Recent analyses have also started to incorporate spatial variation and higher-order terms representing interaction modifications (128). Although the complexity of the models precludes analytical results, simulation studies have come to the interesting conclusion that the higher-order terms promote the coexistence of species. If the result is general, then it would help answer the question of why natural communities can support so many species when simple mathematical models predict that they should be relatively unstable (69). Clearly more theoretical work is needed on these issues.

A second general theoretical approach has involved the analysis of networks of material flow through ecosystems (48, 85–87). In this approach, the amount of a material (e.g. carbon) residing in a particular compartment (e.g. within particular species, or within particular parts of the physical environment—sediments, for example) at a given point in time is divided fractionally between that which remains in the compartment and that which flows into other compartments at the next time interval. The method assumes that all compartments are at steady state, and that all flows (i.e. transition probabilities) are constant (48). Indirect effects are estimated by adding up all of the possible routes that a unit of material can travel from one compartment to another over an infinite time interval, compared to the magnitude of the direct exchange (48, 85–87). From these analyses, great importance has been placed upon the role of indirect effects in natural systems. This approach has spawned a lively controversy over methodological and interpretational issues (48, 62, 87, 91, 124). The network approach appears to have several drawbacks that may limit its utility in predicting the direct and indirect consequences of environmental impacts. The steady-state assumption would seem to make the method difficult to apply to a situation involving an environmental change (62), and it is hard to tell how nontrophic interactions (e.g. interference competition), which are known to be important components of indirect effects (e.g. 28, 64, 80, 81, 82, 113, 132, 134, 135), can be subsumed into this framework (62). Most importantly, the assumption that flows between compartments are independent of the states of the compartments seems particularly unrealistic. For example, most ecologists expect that higher numbers of predators should increase the total number of prey consumed, thereby increasing the flow from prey to predator compartments. Models taking the network approach have been parameterized for several systems and have been used in environmental impact assessments (87), but I know of no empirical tests of the approach. Experimental manipulations are clearly called for in these systems to determine the ability of this approach to predict the direct and indirect consequences of an impact on the environment.

Path Analysis

Another recent approach to the study of indirect effects is the application of path analysis (47, 138) to ecological systems. Path analysis is a statistical approach that estimates the degree to which changing a causal variable will affect a dependent variable through both direct and indirect pathways. Because this technique depends on the presence of variation in the system, the approach is strongest when applied to communities that are dynamic in space and time. Perhaps the best way to ensure this condition is to apply an experimental manipulation to the system and use the path analysis to follow the routes that the signal of the manipulation travels through other elements of the community (135).

Several kinds of information can be gleaned from a path analysis that make it a potentially important extension in the study of indirect effects. First, given several schemes of how variables are related to one another in a causal network, path analysis can be used to identify the most likely scenario (47, 135). This ability should promote a more frequent consideration of alternative causal hypotheses, particularly those that include multiple factors (98). Furthermore, because the technique deals with substantially more complex hypotheses than most statistical approaches, information on multiple variables is more likely to be obtained in empirical studies, thereby broadening our knowledge of possible impacts of a variable. Second, given a particular causal scheme, path analysis estimates the relative strength of direct and indirect pathways between pairs of variables. This represents a major improvement in the study of indirect effects, because the identification of important indirect effects is less tied to the discovery of "unanticipated results." Third, once a causal scheme and interaction strengths have been derived from path analysis, predictions can be made about the consequences of changing particular (previously unmanipulated) variables in the system. Obtaining such predictions of the direct and indirect consequences of an environmental impact has been and continues to be a basic goal of ecology.

The path-analysis approach has been applied in various forms to intertidal, freshwater, and terrestrial systems (6, 52, 126, 135). A key question is whether the technique works. Recently, experimental tests of path-analysis predictions have been carried out in a rocky intertidal community (135) and a steppe-boreal forest community (126). In both cases the predictions derived from path analysis have been supported, suggesting that the approach may indeed be useful. More applications and experimental tests of path analysis in different systems are clearly needed to evaluate its abilities to differentiate direct and indirect effects and predict their consequences.

There are several possible limitations of using path analysis that require further investigation. First, the results depend on the underlying causal scheme assumed. Therefore it is important for investigators to consider a variety of possible mechanisms by which an experimentally manipulated variable affects other variables of interest and to adjust their data collection accordingly. Second, the path analysis may do a poor job in systems near equilibrium, where little variation is available for the path analysis to work with. Third, although path analysis can incorporate reciprocal interactions (47, 139), its ability to do so has not been challenged to date in the ecological systems where it has been experimentally evaluated. Because path analysis is related to traditional linear regression techniques, which assume unidirectional causality, it is unclear whether it can adequately handle reciprocal effects. Fourth, interaction modifications are fairly tricky to handle in path analysis. They can be accommodated only if a specific higher-order functional form is assumed to describe the effect (e.g. the product of two causal variables). Finally, as the complexity of a causal model increases, sample sizes must increase too. This may limit the application of this approach in complex systems, unless those systems are organized to some extent into sub-modules of highly interacting species (82).

FUTURE DIRECTIONS

Evidence is now accumulating that indirect effects can play an important role in natural communities, indicating that they deserve further study. I foresee several directions to future research. First, experimental investigations of indirect effects will undoubtedly continue, given the rise of field experiments in ecology. It is critical that these experimental investigations monitor a variety of response variables and try to place these variables in the context of the entire community or ecosystem to better understand the mechanisms involved. Furthermore, techniques (e.g. path analysis) must be developed and applied to more accurately distinguish possible direct and indirect effects. Second, experiments will be of particular value if they are designed to test specific mechanistic models of community organization in order to evaluate predictive approaches in ecology. For example, several studies have experimentally investigated the degree to which simple food chain models predict the effects of adding or deleting top predators or varying productivity (14, 93, 121, 135, 137). Third, the development of theory for complex systems remains an important area of research. For example, Wilson's (128) simulations of systems incorporating higher-order interactions and spatial structure is one excellent starting point for further investigation into the consequences of complex interactions. Two other research directions seem particularly important and will likely lead to more extensive progress: the estimation of interaction strength in the field, and the determination and evaluation of mechanisms that modify interactions among species.

The development and testing of theory would be greatly facilitated by empirical measurements of interaction strength, because the predictions of many models change as interaction strength changes (97, 106, 140). An important initial consideration is what interaction strength means. To this end, it is critical to distinguish between interaction strength and effect strength. In theoretical treatments (69), interaction strength refers to the per-capita rates of

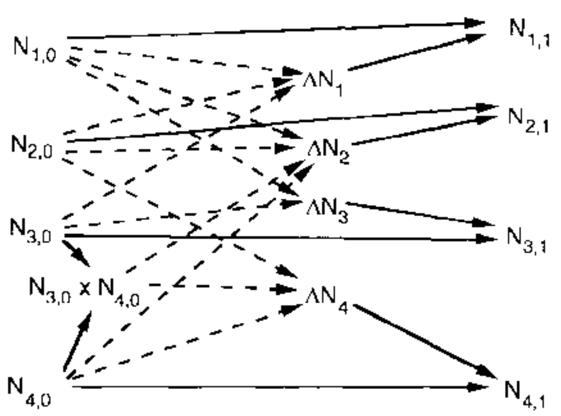

Figure 4 General structure of a path analysis designed to estimate interaction strength in dynamical models. $N_{y,0}$ represents abundance of species y at time $t = 0$; δN_y, represents the change in abundance from one census to the next ($t = 1$); $N_{y,1}$ represents abundance of species y at the subsequent census. Dashed arrows represent those terms yielding estimates of interaction strength to be incorporated into dynamical models. Arrows involving the term ($N_{3,0} \times N_{4,0}$) illustrate how an interaction modification can be incorporated into path analysis (here species 3 modifies the effect of species 4 on species 2).

change of one variable caused by the direct effects of another variable (e.g. the average effect of one predator individual on one prey individual). Effect strength is the total impact that one variable has on another (e.g. the effect of a predator species on a prey species). This latter quantity is measured most often in experimental manipulations. Effect strength differs from interaction strength in that a rare species with a high interaction strength may have the same total effect as a common species with a low interaction strength. Both quantities provide important information, but interaction strength is the quantity that belongs in models.

Several approaches seem possible to estimate interaction strength. One method is to manipulate the value of every variable in a system by a known amount and estimate the per-capita consequences on target species (7, 39, 83). In doing so, one must be careful to ensure that only direct effects are being measured. Although the experimental perturbation approach is powerful, it is logistically difficult, if not impossible, to apply to the entire system of interest. A second approach is to take observational data that directly reflect interaction strength in the models (i.e. per-capita rates). Many types of information have been used as indices of interaction strength (e.g. percent composition in a diet, energy flow rate), but frequently these measures correspond poorly to experimentally derived results (82). This situation is not surprising, because the units of the quantities being measured match the units neither of interaction strength nor of effect strength in the models. In contrast, measurements that have the proper units of interaction-and-effect strength can predict quite well the direct effects manipulations (130). A third approach is a synthetic framework that combines experimental manipulation, mathematical theory, and path analysis. A difficulty with previous applications of path analysis to ecological systems is that the path analyses were not structured in the same manner as the commonly used theoretical models. Most models examine rates of change in variables as a function of the states of other variables, whereas the path analyses to date have examined the state of one variable as a function of the states of other variables. Therefore the interaction strengths measured by path analysis and those required by the models are not equivalent. By defining the response variables in path analysis to match the structure of the models of interest (Figure 4), the two approaches could be linked, and the models could be more effectively developed. Furthermore, reciprocal interactions and nonlinearities are more easily handled in this format. A simplified version of this approach has been applied to communities of tide-pool sculpins, and the technique successfully predicted the consequences of experimental manipulations (89).

A final important area of future research on indirect effects is to identify the mechanisms by which interactions among species pairs are modified by other species. Past work addressing this question focused on quantitative evidence, but methodological, definitional, and theoretical difficulties have complicated the interpretations of this work (4, 8, 15, 92, 136). By considering instead how interaction modifications arise in natural systems, the identification of likely mechanisms should come more quickly, allowing novel experimental approaches to test their importance (e.g. 129), as well as focusing investigators' attention on the interactions to be studied most intensively.

CONCLUSION

In summary, the study of indirect effects remains an important area of investigation as ecologists worry about how abstract models can be while still yielding useful predictions about the consequences of an environmental change. If indirect effects are important, then models must account for community- and ecosystem-level phenomena in order to make useful predictions. Experimental demonstrations of indirect effects—both through chains of direct interactions and through one species modifying interactions between other species—are becoming increasingly common as experimentalists pay more attention to the responses of multiple variables. The relative importance of indirect effects remains uncertain because of methodological difficulties in determining their existence and strength, but recent applications of path analysis may improve the situation. Future progress is most likely to occur through the synthesis of experimental, statistical, and theoretical methods to derive estimates of interaction strength and the degree to which these strengths are modified by other ecological variables. Through this work, insight will be gained into whether the behavior of ecological systems can be decomposed into their component parts, and how predictable the consequences of human impacts are on the environment.

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