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# Indirect effects in complex ecosystems: recent progress and future challenges

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## Abstract

Indirect effects are fundamental to the biocomplexity of ecological systems, and provide severe challenges to predicting the impacts of environmental change. Interest in indirect effects has expanded exponentially over the past 20 years. Indirect effects arise when direct interactions mediated by changes in density share a species, when species change the interaction between individuals of other species, or both. Past work, including many studies of marine food webs, has primarily documented the existence of indirect effects and how particular examples arise. Future challenges include (1) developing methods for the systematic detection of indirect effects, (2) documenting the functions describing different classes of interaction modifications, (3) exploring methods to predict indirect effects, including measurement of interaction strengths among species, (4) integrating time-scale differences into the theory of indirect effects, and (5) linking indirect effects and environmental variability. Ecologists are not alone in dealing with complex systems. Consequently, progress may be facilitated by exploring approaches developed in other scientific disciplines oriented toward complex systems.

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## 1. Introduction

Throughout biology, there has been a growing realisation of the need to understand the dynamical interactions among multiple biological components, or biocomplexity (Mervis, 1999). Ecosystems are some of the most obvious complex systems in biology. A fundamental cause of ecosystem complexity is indirect effects, effects of one species on another that only arise in the presence of other species (e. g., Andewartha and Birch, 1984). Consequently, understanding and predicting the behaviour of ecosystems

depends on our ability to effectively identify and deal with indirect effects. In this paper, I review some of the recent advances in the study of indirect effects, and outline the future challenges facing studies of indirect effects.

Although the possibility of indirect effects has long been recognized (Darwin, 1859; Camerano, 1880; Forbes, 1887; Elton, 1927), interest in them has grown recently because of the widespread application of field experimental methods in ecology. When done in the context of complex natural communities, experiments have often yielded unanticipated results compared to predictions based on pairwise interactions (Sih et al., 1985), and these results are usually most easily

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explained by indirect effects. The increasing interest in indirect effects can be visualised by the patterns generated by an analysis of ecological papers in the Biological Abstracts database which address indirect effects and related concepts (Fig. 1). Over the past 20 years, the number and fraction of ecological papers on indirect effects have been increasing exponentially,

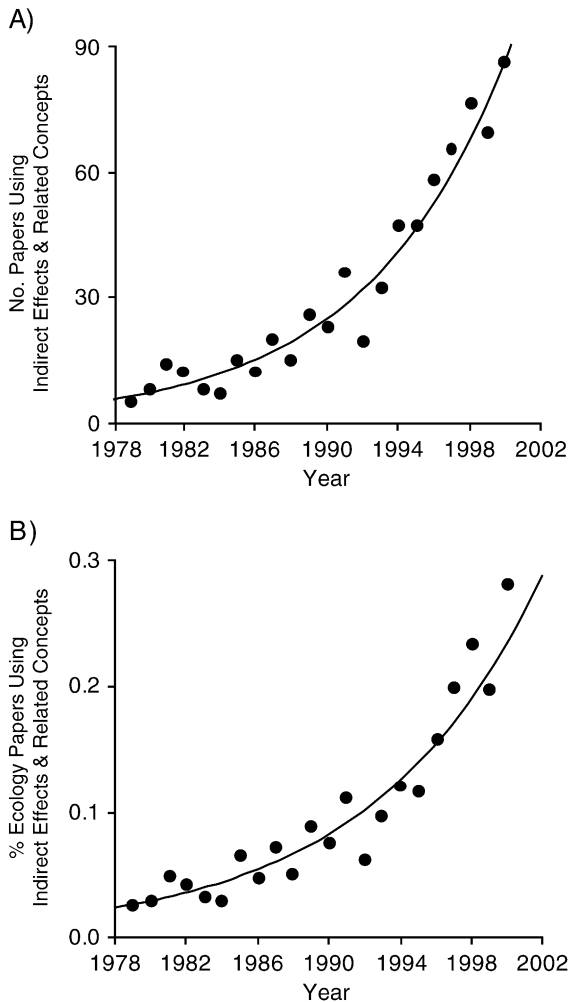


Fig. 1. Citations in Biological Abstracts using indirect effects/interactions or related concepts (apparent competition, higher order interaction, indirect mutualism, interaction modification, keystone predation/species, trophic cascade, trait-mediated indirect effect) in their title, abstract or keywords. A) Numbers of citations by year. B) Fraction of citations by year, relative to the total number of ecological citations in the database. Exponential curves of best fit generated by linear regression on log-transformed citation data.

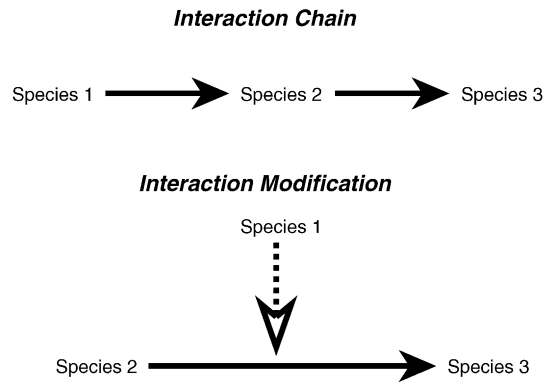


Fig. 2. Diagram outlining the two fundamentally different types of indirect effects. Top: interaction chains/density-mediated indirect effects. Bottom: interaction modification (after Wootton, 1993).

suggesting that this topic has become an important one in ecological research.

Indirect effects can have important implications for ecological study. First, their potential existence complicates experimental interpretation, because multiple pathways of causation are possible (e.g., Connell, 1983; Wootton, 1992). Second, they make implementing conservation and management strategies difficult because the effects of a species loss or an environmental perturbation become difficult to predict a priori (Yodzis, 1988; for some compelling empirical examples, see Estes and Palmisano, 1974; Thrupp, 1990). Therefore, a greater understanding of when they arise, which mechanisms are involved, and how their effects can be predicted is highly desirable.

## 2. Terminology

The terminology used in discussing indirect effects has been in a state of flux, as investigators have sought to develop the most useful categorisations and distinctions among these complex interactions (Vandermeer, 1969; Miller and Kerfoot, 1987; Wootton, 1993; Menge, 1995; Abrams et al., 1996). A distinction has been made between two basic types of simple indirect effects (Vandermeer, 1969; Wootton, 1993; Abrams et al., 1996). First, indirect effects can arise by linking two (or more) direct effects together via a species involved in both interactions (Fig. 2). Direct effects are defined as the effect of one species on another that does not

involve another species (i.e. they would occur if the species pair was in isolation). This type of indirect effect has been termed an ‘interaction chain’ (Wootton, 1993). Because ecologists often focus on the densities or abundances of species, linked direct effects usually imply that densities of the intermediary species change; hence these interactions have also been described as ‘density-mediated indirect interactions’ (Abrams et al., 1996). The first type of indirect effect is relatively straightforward to model and predict, once the direct interactions between species pairs are described (MacArthur and Levins, 1967; Levins, 1968; May, 1973; Yodzis, 1988). Several configurations of these indirect effects have been described sufficiently often that they have been given their own names (see Menge, 1995 for a recent review), among them keystone predation, trophic cascades, apparent competition, indirect mutualism or commensalism, and exploitative competition, although the latter is often not acknowledged as an indirect effect.

The second type of indirect effect arises when a species modifies the interaction between individuals of two other species. This type of indirect effect was first discussed under the term ‘higher order interactions’, because early investigators were interested in determining whether Lotka–Volterra equations with constant per-capita interaction coefficients estimated from two-species systems could predict the response of multi-species systems (Vandermeer, 1969; Wilbur, 1972; Neill, 1974). Where predictions were inadequate, higher-order (non-linear) terms would be required. Because such results could arise from non-linear direct effects (Case and Bender, 1981) and because designing experiments to estimate properly any higher order terms involving other species is tricky (Billick and Case, 1994; Wootton, 1994a), progress in evaluating the existence and importance of these effects on the basis of mathematical criteria has been slow.

As an alternative approach, a mechanistic perspective has been developed (Abrams, 1983; Wootton, 1993), where investigators observe the interactions among species pairs and ask whether they might change depending on the abundance of other species in the community. Such ‘interaction modifications’ (Wootton, 1993) could arise in two ways. First, one species can change the traits of individuals of a second species, and these altered traits can change how the second species interacts with a third species. Such

‘trait-mediated indirect interactions’ (Werner, 1992; Abrams et al., 1996) have been a topic of much recent interest. For example, predators may change the activity levels of their prey, which in turn may affect the prey’s foraging rate (Werner, 1992; Wissinger and McGrady, 1993; Peacor and Werner, 1997; Fryxell and Lundberg, 1998; Schmitz, 1998; Brown et al., 1999; Trussel et al., 2002) or susceptibility to other predators (Soluk and Collins, 1988; Flach and De Bruin, 1994). For example, fish nip off the tips of clam siphons, forcing clams to move toward the sediment surface to feed, where they become easier prey for birds (De Goeij et al., 2001). Second, one species can change the environmental context in which two other species interact, thereby modifying the interaction. In this case, the traits (i.e. the properties of individual organisms) do not change. Such ‘environment-mediated interaction modifications’ would include macrophytes reducing predation pressure on prey by providing hiding places (Crowder and Cooper, 1982; Gaines and Roughgarden, 1987; Norkko, 1998; Anderson, 2001; Hori and Noda, 2001), epibiota deterring attacks of prey by consumers by chemically or physically disguising them (Wahl et al., 1997), algal canopies ameliorating physical stress on predators, thereby facilitating attacks on prey (Leonard, 2000), or sessile invertebrates of different colours altering the degree to which limpets are cryptic to predatory birds (Wootton, 1992, 1993). For example, in the latter case, the traits of the species involved in the predator–prey interaction (colours of limpets, visual capabilities of birds) do not change with a change in sessile species. Instead, the environment (i.e. the background colour) provided by sessile species affects the rate at which birds with particular visual capabilities are able to detect limpets with a particular shell coloration. An alternative terminology has also been proposed, dependent on the modality by which the indirect effects are transmitted (Miller and Kerfoot, 1987): behavioural, chemical response and trophic-linkage. These identified modes of transmission are not exhaustive; one can imagine further categories such as morphological (Raimondi et al., 2000), interference-linkage, or direct mutualist linkage. All can be categorised as either density-mediated indirect effects or interaction modifications.

The two basic types of indirect effects have different implications for modelling and predicting the behav-

ior of ecological systems. Interaction chains can be predicted from reductionist studies by establishing how pairs of species interact and then linking them together in models to build a multi-species system. Plausibly, such indirect effects arising from the introduction of exotic species to a system could also be anticipated. In contrast, interaction modifications are generally only apparent when all species are present together, and therefore require a more holistic approach to their study. Additionally, the types of models applied to a system may need to be rather different from the differential equations usually applied to interaction chains (e.g., Levine, 1976; Bender et al., 1984; Yodzis, 1988), particularly if interaction modifications arise from changes in traits of individuals. Under such circumstances, state-structured models, individual-based models or spatially-explicit models may be better suited to anticipate the effects of changes in traits on the outcome of species interactions. Per-capita interaction functions which are dependent on other members of the community may suffice, however, for environment-mediated interaction modifications.

The type of indirect effects a species exerts on the community may have implications for whether results from small-scale empirical studies can be extrapolated successfully to larger scales. In particular, altering species composition of a community could change immigration and emigration rates from a local area. At a local scale, this would appear to be a density-mediated response because local density is affected by a combination of movement rates, survival and reproduction (e.g., Turner and Mittelbach, 1990). At a larger scale, however, densities will not have changed, but the spatial distribution of organisms will be different. In such a case, extrapolating local scale responses will not be straightforward. In contrast, changes arising from changes in survivorship, fecundity or growth are more likely to be applicable to larger areas. Therefore, documenting the mechanisms by which indirect effects arise can be quite important.

The distinction between interaction chains and interaction modifications may lose meaning under several circumstances. First, when more than three species are involved, indirect effects might result from a mixture of the two types of interactions (e.g., Wootton, 1992). Similarly, indirect effects of one species on another may simultaneously occur through different mechanisms, including both interaction chains and

interaction modifications (Underwood, 1999). For example, a predator may affect plant populations simultaneously through a trophic cascade, and by changing the activity levels of an herbivore (Turner and Mittelbach, 1990; He et al., 1993). Second, models which explicitly account for densities of individuals of the same species with different traits could convert trait-mediated indirect effects into an interaction chain framework. Whether such a conversion would also be possible for environment-mediated interaction modifications is less clear because the organisms themselves do not change. Perhaps models which account for populations of a species in space would resolve the problem. Both of these approaches need to be explored more fully both theoretically and empirically.

Finally, Anderson (1999) argued strongly that distinguishing the two types of indirect effects is irrelevant, because factorial experiments can be used profitably to investigate both. The basis of this argument is dubious, however, on two counts. First, the value of the distinction is derived from its implications for modelling and *predicting* the dynamics of ecosystems. Experiments do not make predictions, they test predictions. Therefore any similarity in experimental designs has little to say about the benefits of the distinction. Second, a factorial experiment can be carried out in two fundamentally different ways: either with or without letting densities of the manipulated species vary during the experiment. Distinguishing the two types of indirect effects clarifies vividly the rarely-discussed implications of these two designs. Experiments with fixed densities necessarily preclude interaction chains among the manipulated species whereas experiments which allow varying densities of manipulated species cannot isolate interaction modifications (Billick and Case, 1994; Wootton, 1994a).

### 3. Recent results and future challenges

Among the increasing number of studies related to indirect effects (Fig. 1), the vast majority have largely been focused on investigating examples in different systems. Establishing many empirical examples is important to give a sense of the generality of indirect effects, and the range of ways in which they arise. Nevertheless, we will need to move beyond simply documenting indirect effects if substantial progress in

grappling with indirect effects is to be made. Therefore, rather than attempting to review the numerous recent studies documenting indirect effects, I will emphasise several important questions that need to be addressed in future work, and focus on selected recent studies which point in tantalising directions along these lines.

### 3.1. How can we efficiently and systematically detect indirect effects?

Indirect effects have often been identified by accident when experiments produce unanticipated results (Sih et al., 1985). Multi-factorial experiments manipulating the presence or absence of different species have shed some insight into the existence of indirect effects by exploring the interaction terms among manipulated variables in factorial experiments (e.g., Menge, 1995; Anderson, 1999), but this approach only reveals indirect effects among manipulated species; indirect effects involving unmanipulated species are not revealed. Furthermore, it is well known (e.g., Snedecor and Cochran, 1989; Sokal and Rohlf, 1995) that when interaction terms arise in analyses of factorial designs, the main effects are usually also influenced, which limits the inferences that can be made about the relative strengths of direct and indirect effects by comparing main effects with interaction terms. As the possibility of indirect effects has become more appreciated and as the architecture and implications of particular interaction ‘modules’ have become better studied (Abrams, 1993; Holt et al., 1994), some investigations have looked for expected linked changes in multiple species (e.g., the alternating increases and decreases of trophic levels in trophic cascades; reviewed in Brett and Goldman, 1997; Chase, 2000). Still, in natural, multi-species communities, multiple direct and indirect pathways are likely to be operating simultaneously, potentially reinforcing or canceling each others’ overall effects. Therefore, developing and empirically evaluating methods to more systematically identify important, simultaneously-occurring indirect effects in empirical studies would be very desirable.

One possible approach is structural equation modelling (Jöreskog, 1973; Hayduk, 1987), an extension of path analysis (Wright, 1934). This approach combines analyses of variance-covariance relationships

among multiple variables with a priori hypotheses of the structure of causal interactions among the variables (such as the ‘envirograms’ of Andewartha and Birch, 1984) to estimate relative strengths of possible, specified direct and indirect pathways. It also allows hypothesis tests to determine whether the overall structure of particular models fit the data adequately. Ideally, the approach should include alternative scenarios of interactions, and the results treated as hypotheses for further experimental test. Structural equation models have now been applied to several ecological situations, including arctic and wetland plant communities (Wesser and Armbruster, 1991; Grace and Pugesek, 1997), mammal assemblages (Smith et al., 1997; Palomares et al., 1998), agroecosystems (English-Loeb et al., 1993) and aquatic communities (Johnson et al., 1991; Wootton, 1994b, 1995; Kupferberg, 1997; Englund and Evander, 1999). For example, Grosholz et al. (2000) applied the approach to understand the multiple mechanisms by which invading green crabs (*Carcinus maenas*) affected marine soft-sediment communities. Applying the approach to ecological questions has generated some controversy (Petraitis et al., 1996; Smith et al., 1997; Grace and Pugesek, 1998; Pugesek and Grace, 1998). Ultimately, the value of structural equation models to studying interactions in complex ecological systems should be determined by testing experimentally how well the approach works. Although more tests are needed, structural equation models have been reasonably successful at predicting the results of subsequent experiments in several instances (Wesser and Armbruster, 1991; Wootton, 1994b; Grace and Pugesek, 1998; Englund and Evander, 1999; Gough and Grace, 1999).

The development of other possible approaches to systematically detecting indirect effects would be welcome. For example, one might start with a known direct functional relationship between a species pair and ask whether there is any deviation from its predicted effects when species composition is changed. A variant on this approach was used in a weedy plant community by Miller (1994), who proposed that general relationships exist between the biomass of individuals of a focal species and the total yield of other species in the environment. He then tested whether the observed response of the focal species to removing another species was different from that predicted by the general biomass-yield function to estimate the occurrence of



indirect effects. Whether such general relationships can be derived when the organisms of interest are quite different taxonomically, as is often the case in marine benthic communities, remains to be determined, but the approach is intriguing.

### 3.2. What are the functional forms by which species modify interactions?

Recent progress has been made in empirically documenting interaction modifications in natural ecosystems (e.g., Wilbur, 1972, 1987; Crowder and Cooper, 1982; Morin et al., 1988; Soluk and Collins, 1988; Werner, 1992; Wootton, 1992, 1993; Wissinger and McGrady, 1993; Wilbur and Fauth, 1994; Morin, 1995; Peacor and Werner, 1997; Fryxell and Lundberg, 1998; Schmitz, 1998; Brown et al., 1999). In order to understand their importance and implications, however, ecologists need to move beyond documenting their existence to exploring their functional forms. It is presently very difficult to generate general theories incorporating interaction modifications and to explore their behaviour because we have limited information on what functional forms these interactions take.

One might start from first principles and extend the mass-action premise of Lotka–Volterra type models, and model the effect as occurring when three or more species simultaneously encounter each other (i.e. introduce positive or negative terms which involve the product of all species involved), as Wilson (1992) did in his analysis demonstrating that interaction modifications can facilitate multi-species persistence. Other forms, however, are readily imagined from first principles. For example, resource species can modify the interaction between their consumers and other resource species through consumer satiation or increased handling time, such as Viitasalo and Rautio (1998) found in marine zooplankton. It is reasonable to imagine that this interaction could be modelled by extending the standard Type II functional response for a single consumer ( $P$ ) and resource ( $N_1$ ):

$$-c_1 N_1 P / (1 + h_1 N_1), \quad (1)$$

where  $c_1$  is the per capita consumption rate of resource 1 by the consumer and  $h_1$  is the ratio of handling time of one resource individual by the

consumer to the total time increment being modelled (Holling, 1965). Extension of this expression to a multi species Type II functional response incorporating one or more other resources ( $N_2$ ) would produce a function of the form (Murdoch, 1973):

$$-c_1 N_1 P / (1 + h_1 N_1 + h_2 N_2), \quad (2)$$

where  $h_2$  is the relative handling time by the consumer on an individual of species  $N_2$ . The shape of this function differs somewhat from a consumer-resource interaction modelled with the mass-action function (Fig. 3):

$$-c_1 (1 - c_2 N_2) N_1 P, \quad (3)$$

in which a damping effect of a second species on the consumption rate of resource 1 by the consumer would be represented by the three-species term  $-c_2 N_1 N_2 P$ , where  $-c_2$  is the per-capita negative effect of a second species. Therefore the choice of functional form might lead to quite different conclusions. For example the effects of consumers on a prey species will be strongly damped over a wide range of densities of a species modifying the interaction if (Eq. (2)) holds, whereas they will only be damped at very high densities of a modifying species if (Eq. (3)) holds. Similar results have been obtained in analyses involving optimal foraging under risk (Abrams, 1992). Furthermore, although some of the few empirical relationships follow these equations (Colton, 1987; Chesson, 1989), others suggest that interaction modifications may take quite different forms from those described above. For example, the effect of barnacles in modifying interactions between bird predators and limpet prey (Wootton, 1992) follows a quadratic form (Fig. 4) because two mechanisms operate simultaneously. In this case, barnacles provide a cryptic background for limpets, affording them protection, but at high densities they can also interfere with the ability of limpets to clamp to the substrate, making it easier for them to be dislodged by birds.

### 3.3. How can we predict the consequences of indirect effects?

The ultimate challenge of indirect effects is to successfully place complex natural ecosystems in a predictive framework in order to understand the

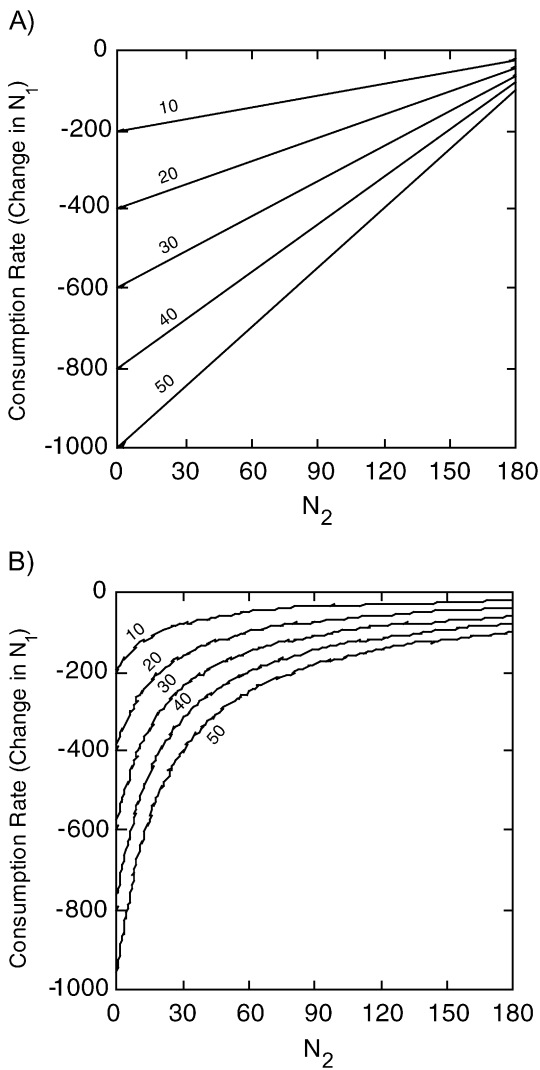


Fig. 3. Comparison of functional forms of interaction modifications involving a consumer species (P), its resource ( $N_1$ ) and a species ( $N_2$ ) which reduces the impact of the consumer on its resource. Plots compare the change in prey density caused by predation as a function of the density of modifying species (x-axis) and predators (different curves). Functions are derived from A) a negative mass-action term where all three species encounter each other simultaneously in order for the interaction modification to occur (e.g., Eq. (3)) and B) a multi-species type II functional response representing predator satiation by  $N_2$  (Eq. (2)). To make the functions comparable, parameters were scaled so that the relationships were the same for the two functions both at  $N_2 = 0$  and  $N_2 = 1800$ .

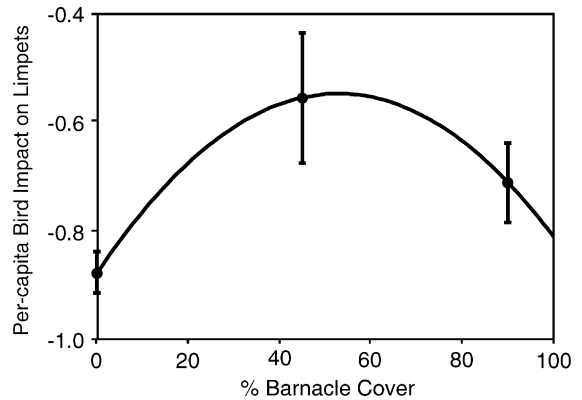


Fig. 4. Empirically-estimated functional form of an interaction modification involving bird predators, limpet prey and barnacles in a rocky intertidal habitat. Results from bird exclusion experiments with experimentally manipulated barnacle densities (data from Wootton, 1992). Mean impact of bird predators per individual limpet presented  $\pm 1$  s.e.,  $n = 12$ . Barnacles protect limpets from predation by providing a cryptic background, but interfere with limpet ability to clamp to the rocks and resist bird attacks at high densities.

impacts of environmental change and species extinction. At a basic level, we have a number of mathematical techniques that can provide insight into the relative roles of various direct and indirect effects in multi-species communities. For example, the inverse Jacobian matrix provides one method of estimating overall effects through both direct and indirect pathways (Levine, 1976; Lawlor, 1979; Vandermeer, 1980; Yodzis, 1988; Bender et al., 1984; Stone and Roberts, 1991; Higashi and Nakajima, 1995; Nakajima and Higashi, 1995), at least near equilibrium. Techniques still need to be worked out when non-linear systems are perturbed well away from equilibrium, but simulation studies of specific non-linear models, when available, minimally can be used to generate predictions in the face of indirect effects.

Before such theoretical methods can be employed, however, it is necessary to empirically derive parameters for these models from natural communities, and this need is currently the rate-limiting step. Such empirical studies are critical because theoretical work has clearly shown that predictions about the effects of species in complex ecosystems become indeterminate without parameter estimates to narrow the range of possible outcomes (Schaffer, 1981; Puccia and Levins, 1985; Yodzis, 1988, 1996). This need has generated much current interest in the estimation of interaction

strengths among species (MacArthur, 1972a; May, 1973; Paine, 1980, 1992). Because multiple concepts of interaction strength occur in the literature and imply different things (Laska and Wootton, 1998), investigators need to be precise in identifying what concept of interaction strength they are studying. Per-capita estimates of interaction strength are likely to be most useful for investigators evaluating interaction strength, because they can be directly inserted into standard dynamical models of multi-species systems.

Empirically estimating interaction strength is not straightforward (Bender et al., 1984; Laska and Wootton, 1998; Berlow et al., 1999). Several approaches have been taken to estimate interaction strength. The most popular approach is to experimentally manipulate numerous species and estimate the response of other members of the community (e.g., Paine, 1992; Fagan and Hurd, 1994; Raffaelli and Hall, 1996; Morin et al., 1988; Menge et al., 1994; Ruesink, 1998). For unambiguous answers, however, the densities of non-target species must be kept constant for the duration of the experiment, or the estimates will be affected by indirect effects (Bender et al., 1984; Laska and Wootton, 1998). This approach is also logistically daunting because of the large number of experiments that must be carried out. A second approach is to employ the PULSE methods of Bender et al. (1984), and estimate instantaneous responses of species to a small, temporary perturbation of a target species (e.g., Levitan, 1987; Schmitz, 1997). This approach can be difficult for statistical reasons (responses to small perturbations may be hard to detect above stochasticity in the system), and because of time-scale problems (e.g., Dungan, 1986; Abrams, 1995; see the discussion of time-scale issues below). The large number of experiments required is also a shortcoming. A third approach is to make observational measures of interaction strength (Goldwasser and Roughgarden, 1993; Wootton, 1997) or derive appropriate metrics from energy flow patterns (Moore et al., 1993; Raffaelli and Hall, 1996; Hall et al., 2000). This class of approach is limited because it is often difficult to observe some types of interactions directly, and because not all interactions are based on energy transfer (e.g., many interference and mutualistic interactions). A fourth approach has been to use allometric scaling and energetic considerations to estimate interaction strength (Yodzis and Innes, 1992). Again, a limitation

of the approach may be its lack of relevance for non-trophic interactions. A final approach is to use the dynamics of natural or experimentally-perturbed communities to fit multi-species models using time series analyses (Seifert and Seifert, 1976; Wootton, 1994c; Pfister, 1995; Elkinton et al., 1996; Laska and Wootton, 1998; Ives et al., 1999). This approach requires longer time periods to be successful, but relatively few experimental manipulations, particularly if the manipulations are chosen carefully to generate large dynamical responses.

These approaches are in their infancy and other methods may well be possible. An important goal of future work should be to experimentally evaluate these approaches. Several studies have done so (Levitan, 1987; Pfister, 1995; Raffaelli and Hall, 1996; Schmitz, 1997; Wootton, 1997) with modest success. Despite the relative paucity of studies to date, their results point to a surprisingly robust generality: that the distribution of interaction strengths tends to be highly skewed with many weak interactions and a few very strong interactions. Such a result may help in building and exploring multi-species models, and may also provide justification for focusing on a limited set of strong interactions empirically (Paine, 1980), if methods to efficiently identify them can be developed. Furthermore, the presence of many weak interactions has been suggested to stabilise ecological communities (McCann et al., 1998; Berlow, 1999).

Although the term ‘interaction strength’ may imply a particular number value, it is worth remembering that interaction strength may actually be a complex non-linear function of species abundance, particularly when species modify the interactions between other species (Abrams, 1995; Ruesink, 1998). Most current approaches assume that per capita interaction strength is constant, and even with this simplification, making estimates of interaction strength is still difficult (Bender et al., 1984; Laska and Wootton, 1998; Berlow et al., 1999). One justification from theoretical work is that near equilibrium, ‘sufficiently small’ perturbations should approximate linear functions, based on Taylor series expansion (May, 1973; Bender et al., 1984). Unfortunately, the ‘sufficiently small’ criterion is empirically useless. Consequently, methods to better understand and quantify ‘sufficiently small’ perturbations need to be developed. In the absence of such criteria, several approaches can be taken. Initial



approaches focusing on constant per-capita interaction strength may be justified by the argument that it makes sense to explore the simplest possibility first. Where substantial deviations from fits or predictions occur, follow-up studies can then more efficiently focus on situations where non-linearities probably are important. Additionally, investigators may choose to restrict their inference to the situation in the vicinity of equilibrium, although if the goal is to place indirect effects in a predictive framework, this scope may be very limiting. The alternative approach is to develop a good understanding of what non-linear functional forms are likely for particular types of interactions (see the previous section) and conduct more labour-intensive experiments or observational studies covering a range of fixed densities of interacting species. A final related issue is whether estimating non-linear interaction strength functions is worth the effort. Analyses of data generated by non-linear stochastic models suggest that models making linear approximations often provide better predictive ability of the original model than do non-linear models, even when the precise non-linear functional forms are known (Ives, 1995; Ives and Jansen, 1998). This result may occur because the error introduced by estimating more parameters offsets gains in precision from using a more realistic model (Ludwig and Walters, 1985).

In some situations, estimating interaction strengths may not be necessary, at least when perturbations to the system are not too large. Levins (Levins, 1975; Puccia and Levins, 1985) introduced loop analysis for investigating the net impact of direct and indirect interactions arising from environmental impacts. Rather than using a parameterised model, loop analysis provides a qualitative prediction of how species respond based on the pattern of interactions within and between species pairs and the sign of the interactions. The method is related to analysis of the Jacobian matrix, and assumes the system is sufficiently near equilibrium to be linearised. A major limitation to the application of loop analysis has been that, as discussed for other approaches, its predictions become indeterminate with large numbers of interactions unless interaction strength is known. Recently, Dambacher (Dambacher, 2001; Dambacher et al., 2002) has taken advantage of advances in computing power to extend loop analysis to more complex situations. Although predictions in complex situations

are not completely determined, Dambacher's analysis suggests that one can take a probabilistic approach to the problem. Certain outcomes are often much more likely than others, and these outcomes can be explored by evaluating the strength and prevalence of various opposing feedback loops. Furthermore, the effects of perturbations on some components of the system can be very predictable, even in complex systems, whereas others are more uncertain. Therefore, loop analysis may still be of value to make at least partial predictions in the face of indirect effects. This extension of loop analysis needs to be applied to empirical situations and experimentally tested.

Finally, it may be useful to explore methods which take a more abstract, less mechanistic approach to indirect effects. For example, several recent studies have developed multi-species Markov chain models based on transition probabilities that defined spatial locations shift among different ecological states, where states are defined as the species or species combination occupying particular points in space (Horn, 1975; Saila and Erzini, 1987; Pastor et al., 1993; Tanner et al., 1994; Wootton, 2001). These models have the advantage that they are relatively easy to parameterise empirically, but also have some clear limitations. For example, they provide only a crude idea of the specific role of indirect effects, because the transitions from one ecological state to another could arise from direct and/or indirect effects among species. Furthermore, it is tricky to incorporate the role of mobile species into these models (but see Saila and Erzini, 1987; Allen-Diaz and Bartolome, 1998; Wootton, 2001), or the consequences of changing some types of environmental conditions such as limiting nutrients or temperature. The Markov approach needs experimental testing to evaluate more fully its limitation. Still, the approach generally does an excellent job at recreating the composition of current communities (Horn, 1975; Wootton, 2001), and in the few instances to date where it has been challenged with novel conditions, it has performed remarkably well, given its apparent limitations (Wootton, 2001).

### *3.4. How do time-scale issues affect detection and understanding of indirect effects?*

For mathematical and conceptual convenience, the species and processes occurring in multi-species com-

munities are often assumed to operate at similar time scales in multi-species models (e.g., MacArthur and Levins, 1967; May, 1973; Yodzis, 1988; Schoener, 1993; Laska and Wootton, 1998). This perspective has strongly influenced suggestions about how indirect effects should be explored. Conceptually, when direct effects of species interactions operate at the same time scale, then one can separate direct from interaction chain indirect effects by taking advantage of the common time scale; direct effects should appear before indirect effects appear, so short-scale studies should reveal ‘pure’ direct effects whereas long-time scale studies will also involve indirect effects (Bender et al., 1984; Yodzis, 1988; Laska and Wootton, 1998).

Recent empirical evidence, however, raises doubts about the validity of this perspective. In experimental studies of rocky intertidal communities, indirect effects often are detected as fast or faster than direct effects (Dungan, 1986; Menge, 1997). Although these results are not well understood, several possible explanations come to mind. There may be statistical issues involved in which weak direct effects only produce a sufficiently strong signal to be detected above environmental noise after a long period of sustained experimental manipulation. But similar arguments can be made for indirect effects.

Alternatively, such results could arise because of mismatches in time-scale. For example, in aquatic communities, periphyton and phytoplankton have generation times on the order of days, grazing arthropods have generation times ranging from weeks to years, and fish have generation times of a year or more. Furthermore, different processes may produce results at quite different time scales. Predation and other mortality-causing events produce immediate changes in the population, as does displacement of one species by another in competition for space. In contrast, factors that influence birth rates may take longer to manifest themselves because reproduction is frequently episodic. Therefore, some direct effects may occur more quickly than others, raising the possibility that some indirect effects transmitted through fast-scale processes may arise before other direct effects can become apparent. Additionally, the perspective that short time scale changes reflect direct effects arises from a focus on interaction chain type indirect effects. Interaction modifications, however, often involve behavioural changes that can arise instantaneously; hence these

indirect effects can occur before some direct effects become apparent (Abrams, 1995).

The problem of time scale mismatching provides a rich opportunity for future work. Several solutions have been proposed. The most popular approach is to assume that organisms operating on faster time scales reach a temporary equilibrium over a single time step of slower species, and to use this equilibrium value in equations describing the dynamics of the slower species (MacArthur, 1972b; Schaffer, 1981). While this type of ecological abstraction is appealing, it is not clear that faster species react quickly enough to establish a short-term equilibrium in real communities. A second approach is to change the functions describing interactions among species to less-traditional, simple forms which qualitatively capture the expected effects of time scale mis-matching. This argument has been advanced as one reason for using ratio-dependent type models of predator-prey interactions (Arditi and Ginzburg, 1989). Of course, the proper approach is to integrate species responses across different time scales, but this can produce analytically awkward models even for systems with only a few species. For well-parameterised systems, simulation studies could circumvent some of these problems. On the empirical side, it may be profitable to generate data sets that document species dynamics over different time scales and ask whether accounting for time scale differences produces more accurate model predictions.

### *3.5. What is the interplay between indirect effects and physico-chemical factors?*

Most discussion of indirect effects has centred around interacting species. In many cases, species affect other species by changing the physico-chemical environment. In these circumstances, it will often be beneficial to treat certain environmental characteristics as dynamic variables, and in this sense, there is little difference with how species directly and indirectly affect each other. There has been much recent interest in consequences of species which alter the physical environment, termed ecosystem engineers (Jones et al., 1997). For example, in benthic marine habitats, numerous organisms can have profound effects on the physical environment by changing the sediment structure and topography, including

whales (Oliver and Slattery, 1985), sea otters (Kvitek et al., 1988), bivalves (Reise, 1983a; Flach, 1996; Widdows et al., 1998), crustaceans (Woodin, 1978, 1981; Posey et al., 1991), fish (Thrush et al., 1991) and polychaetes (Woodin, 1978, 1981; Reise, 1983b; Philippart, 1994). Beyond the issue of whether such interactions are considered as indirect effects by virtue of models incorporating the dynamics of the physical environment, ecosystem engineering is linked to classical indirect effects in several ways. Obviously, those species that respond to the altered environment could have subsequent indirect effects, such as salt marsh species that respond to the interplay of salinity stress and shifting mutualistic–competitive interactions (Hacker and Gaines, 1997). Furthermore, as noted previously, changing the physical environment can modify the interactions between other species (e.g., Woodin, 1981).

The benefits of incorporating the dynamics of the physico-chemical environment into a multi-species setting are perhaps most obvious when considering limiting nutrients. The dynamics of nutrients are often clearly linked to biological processes, and consequently they have been incorporated in much the same way as species in food web models (reviewed in DeAngelis, 1992). Incorporating nutrient dynamics has been helpful in elucidating two particular groups of interactions involving indirect effects. First, apparent trophic cascades may arise simultaneously through traditional top-down mechanisms and through nutrient recycling effects of species high in the food web (e.g. Vanni and Layne, 1997). Second, an emerging literature raises the possibility that, by recycling nutrients and energy contained in detritus, the microbial loop can provide a possible alternative to ‘classical’ food chains in fuelling species at higher positions in the food web (Pomeroy, 1974; Azam et al., 1983; Sherr and Sherr, 1988).

### 3.6. *What is the relationship between indirect effects, variability, and coexistence?*

An important unanswered question is what limits the length of significant indirect pathways. One suggestion is that environmental variability limits indirect effects (Schoener, 1993). Intuitively, because there are more species involved in indirect effects than in direct effects, one would expect them to be

more variable in their strength, and therefore they should be less detectable statistically. Statistical detectability is not equivalent to the average importance of an indirect pathway, however, and it is less clear whether environmental variability theoretically should affect the overall strength of indirect effects. Further theoretical investigations addressing this question would be useful.

A related question of recent interest is what role indirect effects play in affecting community variability and, ultimately, species coexistence. Recent work has developed methods of evaluating the role of biotic interactions in transmitting environmental variation in multi-species systems, and suggests that such stochasticity may be either amplified or damped, depending on the configuration and strength of direct and indirect effects (Ives, 1995). Estimates of interaction strength will be required to evaluate the role that indirect effects play in transmitting or damping environmental variation in real ecosystems.

The interplay between indirect effects and environmental variability may also play a role in promoting species diversity. A recent experimental study of intertidal organisms noted inter-annual variability in the total impact of species removal, which depended on variation in recruitment of species involved in an indirect effect (Berlow, 1999). In this situation, the direct effects of the manipulated species, a predatory snail, were consistently strong, but the net effects of the snail varied because of fluctuations in the strength of the indirect effect. Because indirect effects have more components which might be impacted by environmental variation, Berlow suggested that they might play important roles in maintaining species coexistence by introducing heterogeneity in space and time.

Recent theoretical work has also suggested that interaction modifications can have important impacts of species coexistence. Wilson (1992) did a simulation study on randomly constructed communities that included simple interaction modifications and spatial structure with varying recruitment to local communities. He found that increased complexity via introducing both spatial structure and interaction modifications promoted species coexistence because local variations in initial conditions and species composition shifted the short-term outcome of species interactions via interaction modifications, giving species that would be excluded from a single population a spatio-temporal

refuge. Similarly, McCann et al. (1998) showed that when omnivory and interaction modifications from joint consumer satiation are included in simple food web models, the community tends to fluctuate less and species coexistence is enhanced. Although this work emphasised the strength of the species interactions, the presence of the interaction modification is critical to the result, because joint consumer satiation produces frequency dependence that tends to protect rarer species from extinction, as envisioned by MacArthur (1955). These studies, which contradict results of linear multi-species models that suggested reduced stability with increasing complexity (May, 1973), clearly imply that further analyses incorporating non-linearities introduced by interaction modifications could yield interesting results.

### 3.7. *What can we learn from other disciplines studying complex systems?*

Ecologists are not alone in dealing with complex systems, and there may be much to gain by examining approaches developed in other fields. For example, as genetics moves from a descriptive phase to attempting to understand how gene products translate into organismal function, problems similar to indirect effects will emerge. Epistatic gene interactions, conceptually similar to interaction modifications, can potentially have important effects in organism function and evolution (e.g., Palopoli and Wu, 1994; Wolf et al., 1998), and alternative approaches to study such complex interactions may emerge. Possible parallels between complex economic and ecological problems have not gone unnoticed (e.g., Stevens and Krebs, 1986), and workers studying neural networks, computer systems and social sciences face similar challenges as ecologists. Exchanging methods and perspective among fields may lead to more efficient discoveries of how to deal with indirect effects. For example, structural equation modeling began with the development of path analysis in genetics (Wright, 1934) and is commonly used in the social sciences (Jöreskog, 1973; Hayduk, 1987), but has only recently begun to be explored in ecology. Similarly, research on self-organisation of complex systems spans such fields as physics, geology, social science, evolution, neurobiology, and ecology (Bak, 1996). As ecologists work toward understanding and predicting the behaviour of indirect effects in complex

ecosystems, taking a broader perspective on complex systems may be very valuable.

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