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The subtlety, complexity and importance of population interactions when more than two species are involved

La sutileza, complejidad e importancia de las interacciones poblacionales cuando más de dos especies están involucradas

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ABSTRACT

In my opinion, of the various subdisciplines in ecology, the study of communities is the most abstract and most tantalizing, most important and most urgent, but unfortunately also the most difficult. There is a great deal to be done in community ecology. We need to improve our understanding of how ecological systems behave. The traditional pair-wise approach to population interactions has proven to be totally inadequate. We must now attempt to understand indirect as well as direct interactions within complex *networks*. Properties of such networks themselves need to be evaluated. Topology and graph theory, while intriguing, require unrealistic assumptions, such as that all interactions are plus-minus and can be represented as either "on" or "off". Analogous, but more complex, approaches that incorporate mutualism and variable intensity in interactions need to be developed. Horizontal patterns of connectance within trophic levels should also be included and distinguished from the vertical ones that operate between trophic levels. Strong interactions may usually be more important than weak ones, but the cumulative effects of many weak interactions (as in diffuse competition and diffuse coevolution) could nevertheless be considerable. The extent to which indirect effects can and actually do balance direct effects needs to be ascertained, both in model systems and in the real world.

Key words: Indirect interactions, complex networks, multiple causality, normal science, community ecology.

RESUMEN

En mi opinión, de las varias subdisciplinas de la ecología, la que estudia las comunidades es la más abstracta, atractiva, importante y urgente, pero también la más difícil. Hay mucho por hacer en ecología de comunidades. Necesitamos mejorar nuestro conocimiento de cómo funcionan los sistemas ecológicos. El acercamiento tradicional a las interacciones entre pares de poblaciones ha probado ser totalmente inadecuado. Debemos ahora intentar comprender las interacciones tanto directas como indirectas dentro de las tramas complejas. Las propiedades de tales tramas necesitan ser evaluadas. Aunque la topología y teoría de gráficos son interesantes, requieren de suposiciones poco realistas, tales como el que todas las interacciones son del tipo "si" o "no" y que pueden ser representadas como situaciones más-menos. Acercamientos análogos, pero más complejos, que incorporen mutualismos e intensidades variables de interacción necesitan ser desarrollados. Los patrones horizontales de conectancia dentro de niveles tróficos también debieran ser incluidos y diferenciados de aquellos verticales que operan entre niveles tróficos. Las interacciones fuertes pueden usualmente ser más importantes que las débiles, pero los efectos acumulativos de muchas interacciones débiles (tales como competencia y coevolución difusa) podrían ser considerables. El grado en que los efectos indirectos pueden, y efectivamente balancean los efectos directos necesita ser evaluado, tanto en sistemas modelo como en el mundo real.

Palabras claves: Interacciones indirectas, tramas complejas, causalidad múltiple, ciencia normal, ecología de comunidades.

INTRODUCTION

North American ecology constitutes a vast subject matter. Most of the North American participants indicated that they experienced some difficulty reviewing their own subset of this extensive literature. If Jim Brown couldn't provide an overview of granivory studies in North America, how am I supposed to produce one over all these diffuse seminars and all of North American ecology? Entire volumes have been devoted to this effort. To my way of thinking, the most successful presen-

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tations were those that did not attempt to be reviews but rather adopted a more eclectic and conceptual approach. Hence I shall do the same in my "overview". I will emphasize phenomena that were *not* covered and examine some ideas that emerged from this conference that I find conceptuallly interesting. My contribution is a potpourri of ideas for further consideration rather than a summary of what took place at this conference. For those who are interested in the latter, I suggest a careful reading of this entire issue of *Revista Chilena de Historia Natural.*

First, I should call attention to two major gaps in our coverage: (1) we have ignored freshwater aquatic systems (fish, in particular, received almost no attention), and (2) very little was said about foliage-feeding insects, which include the preponderance of species on this planet. Hopefully these inconceivable omissions will not prove unduly disastrous!

Several subjects that were not mentioned, but certainly should have been, include aspect diversity, plant apparency, and crossovers between trophic levels (see below).

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STRONG INFERENCE AND MULTIPLE CAUSALITY

Most non-ecological biologists are content as long as they have reliable access to living organisms, even if these are captive, domesticated, or growing in pots in a greenhouse. The processes of interest can usually be studied by appropriate observations and experiments measured on a timescale of hours or days. Generally, the approach is reductionistic beginning with the organism and proceeding inwards to its component parts and processes.

In molecular biology, great advances were made quickly by formulating a logical framework of *mutually exclusive* falsifiable hypotheses that generate predictions one can examine by observation and experiment. This approach has been labelled "strong inference" by Platt (1964). Such a binary hierarchical structure allows rapid elimination of inadequate hypotheses and hence facilitates advancement of knowledge and understanding, but tends to lead to a very *specific* and narrow perspective.

The subject matter of an ecologist requires *wild* organisms in the context of relatively *pristine*[1] natural environments. Caged ones simply won't suffice. Ecologists are concerned with how organisms interface with, and conform to, their environments. Evolutionary ecologists are particularly concerned with adaptations that have arisen over millennia and which can be understood only in the context of a semi-natural environmental setting. Ecology looks *outwards* from the organism to the factors and forces that influence it. Ecology is thus much more holistic than other kinds of biology (some ecology can, of course, be reductionistic). In fact, the approach in ecology differs so fundamentally from the approach in other branches of biology that it is sometimes difficult to convince a hard-core mechanistic biologist that ecology is even scientific.

Indeed, ecologists often cannot even formulate mutually exclusive hypotheses – *multiple causality* is rampant and widespread. The subject is innately multidimensional. Some people are uncomfortable with so much complexity, but others, myself included, find it most tantalizing. Multiple causality constitutes a major dilemma in ecology today. We must find better ways of dealing with it.

"NORMAL SCIENCE" AND INDUCTIVE GENIUS

The vast majority of scientific endeavor is, of course, quite ordinary. Thus the research projects in which we engage ourselves are relatively pedestrian, constituting little more than building blocks for major advances. Such "normal" science is, of course, absolutely essential in that it provides the raw empirical material for progress in understanding. Periodically an extraordinary event occurs that enables a novel breakthrough. Occasionally, this may be just a serendipitous discovery by a more-or-less "ordinary" scientist[2]. But, more often than not, major new directions are charted by rare individuals with incredible intellectual prowess. Population biology has attracted a few of these extra-

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[1] This conference has made me begin to wonder if there really are any!

[2] Provided, of course, that someone has the wisdom to appreciate the true significance of the discovery and the creativity to develop it.

ordinary people in the past, and ecology today stands poised, awaiting another such inductive genius.

Cataloging pattern(s) within and between ecological systems is certainly of vital importance, but ultimately, as Paine noted, "we need to generalize, even if our generalizations are imperfect". Generalizations do not arise by normal deductive processes, but require a much rarer form of scientific inference. Because induction requires genius, it may well limit the rate of progress in science. To a certain extent, we may be able to simulate inductive genius by pooling our brainpower in think tanks (Pianka 1987). But time's a wasting – the very systems we seek to understand are being rapidly destroyed by the press of humanity. In the words of Rolston (1985), "destroying species is like tearing pages out of an unread book, written in a language that humans hardly know how to read". Just as ecologists are finally beginning to learn to read the "unread" (and rapidly disappearing) book, they are encountering governmental and public hostility and having serious difficulties atracting support. This backlash in response to rabid environmentalism is most unwise and must be changed.

In the meantime, we simply cannot afford to wait patiently for our next genius to emerge. The rest of us could benefit immeasurably from attempting to simulate inductive genius by means of think tanks. At this workshop, I was impressed with the very considerable insights that can arise from interactions between a relatively small number of ecologists with similar interests. Such "brainstorming" efforts effectively enhance our intellectual prowess. But we are too scattered around the country, too isolated from one another, to take fullest advantage of the possibilities. The duration of most meetings is far too short for interchanges to solidify into really lasting contributions. What is needed are more substantial blocks of time, say repeated meetings or meetings lasting from several months to a year, to continue bouncing ideas back and forth until they can be refined. This process would not only prove exhilarating for the participants concerned, but it would also greatly benefit the rest of the scientific community and ultimately everyone in the world.

As the human population continues to burgeon, we are increasingly finding that we need all the ecological understanding we can possibly marshal, particularly concerning the organization and function of ecosystems. However, as explained above, there is a great urgency to basic ecological research, particularly at the community level. We desperately need to improve our understanding of how ecological systems behave. We might even find that we are not collecting the right kinds of data.

In particular, the properties of complex networks must be evaluated. This will be a most challenging task, and one that will require considerable expertise in both the empirical and the theoretical dimensions, as well as a solid coupling between them. No one person is likely to be capable of doing it alone. We need to convince governments and the public that they cannot afford *not* to support ecological research. In particular, programs should be organized to support think tanks in ecology and we should begin using our capabilities to the fullest extent possible.

COMMUNITY ECOLOGY

For me, the most challenging kind of ecology is the study of communities. It is not only very abstract but remains in its infancy. Community ecology is also extremely promising and important, as well as exceedingly urgent. A great deal remains to be done. Major new insights lie just around the corner. But community ecology is not for the faint at heart: it is one of the most difficult of all sciences.

We are still in the process of developing a vocabulary in community ecology. Identification of appropriate aggregate variables or *macrodescriptors* (Orians 1980) is not only essential, but also constitutes a double-edged sword: macrodescriptors enable progress but simultaneously constrain the direction(s) we can pursue. At this early stage in community ecology, it is perhaps safest not to get overly "locked in" by words and concepts. Even the trophic level concept itself should not be inviolate (Kozlovsky 1968). For example, various workers have suggested and used the concept of a "trophic continuum" (Rigler 1975, Carney *et al.* 1981, Adams *et al.* 1983, Cousins 1985).

Many community-level properties are probably simply epiphenomena that arise from pooling component populations: examples would presumably include trophic levels, subwebs, and ecological pyramids. But, do communities also possess truly emergent properties that transcend those of mere collections of populations? For example, are patterns of resource utilization among coexisting species coadjusted so that they mesh together in a meaningful way? If so, truly emergent community-level properties arise as a result of orderly interactions among component populations. This fundamental question needs to be answered. Either way, transcendent phenomena or epiphenomena simply cannot be studied at the level of individuals or populations.

A major pitfall for community ecologists is that communities are not designed directly by natural selection (as are individual organisms). We must keep clearly in mind that natural selection operates by differential reproductive success of individual organisms. It is tempting, but dangerously misleading, to view ecosystems as "superorganisms" that have been "designed" for efficient and orderly function. However, antagonistic interactions at the level of individuals and populations (such as competition, predation, parasitism and even mutualisms) must frequently impair certain aspects of ecosystem performance. As a result, effective studies of community organization require a pluralism of approaches, including all of the following levels: individuals, family groups, populations, trophic levels, community networks, as well as historical and biogeographic studies. All these approaches have something useful to offer. The approach taken should be fitted to the questions asked as well as to the peculiarities of the system under study. For example, the experimental approach is relatively intractable for many terrestrial animals, but quite feasible with plants and intertidal sessile organisms. Of course, community-level studies are plagued by extremely difficult problems of scale in both space and time: patch size and dynamics, disturbance frequency, and dispersal ability are just some of the many factors that vary widely within and among systems, as well as over space from local to geographic areas and through time from the short-term to long-term.

Two brief examples follow that illustrate how repeated patterns in community-level properties can potentially be better understood in terms of natural selection operating at the level of individuals. A great deal more effort needs to be devoted towards attempts to connect community properties with those of individuals in populations.

Terrestrial succession

Although I am not aware of any direct evidence, it seems highly likely that a fast rate of photosynthesis and hence a rapid growth rate may well be incompatible with shade tolerance, and hence competitive ability in a light-limited situation. If so, these trade-offs at the level of individuals could very well dictate many of the sequential patterns of species replacement that characterize terrestrial succession.

Ecological efficiency versus community stability

Ecological energetics has thus far been concerned largely with rates of energy flow in ecological time – analysis of the evolution of such rates in terms of predator-prey interactions proves instructive. Natural selection operating by differential reproductive success of individual prey presumably favors escape ability, whereas selection acting on individual predators favors efficient capture of prey. Any given prey-predator pair has its own particular stand-off (stalemate?) between these conflicting selective pressures. Predator escape tactics of prey clearly reduce the rate at which materials and energy are transferred to higher trophic levels, thus reducing ecological efficiency. Prey escape abilities are also thought to confer stability on prey-predator systems (Rosenzweig & MacArthur 1963), hence presumably enhancing community stability. On the other hand, the efficiency with which predators capture and handle their prey enhances ecological efficiency but reduces the stability of the prey-predator system and hence presumably decreases community stability. These arguments suggest that a trade-off exists between ecological efficiency and community stability. Moreover, this trade-off of community-level properties has its roots in evolutionary interactions between predators and their prey.

A SPECTRUM OF INTERACTIONS

As a first attempt at summarizing some of this conference, I came up with a modification of what I could remember from part of a table presented by Dobson & Hudson (1986) with some major new entries. When I presented this preliminary table to the North Americans, serious issue was taken with certain entries in it. I now offer a modified, but unfortunately somewhat more equivocal, version again for consideration (Table 1). Notice that "marine" (rocky intertidal!) predation is placed next to herbivory (sessile prey), whereas granivory is put alongside terrestrial predation (prey diffuse and heterogeneously distributed in time and space).

The fraction of prey or hosts vulnerable to predators or parasites is of major importance: if most prey are protected, the interaction is what Pimm (1982) terms "donor controlled", and should be relatively stable (Smith 1972). An important way that prey can cope with predation is by means of prey refuges, such as safe sites, hiding places, or size thresholds above which prey can no longer be eaten by the largest predators. In the case of very intense predation on prey with little means of escape in time or space, high turnover rates of prey populations may also enable the prey to persist.

CROSSOVERS BETWEEN TROPHIC LEVELS

In a conference on interactions between trophic levels, I was quite surprised that no one mentioned "crossovers", in which some process or phenomenon alternates between trophic levels. For example, the now infamous arguments of Hairston, Smith, and Slobodkin (1960) asserted that most plants are not controlled by their herbivores, herbivore populations are thus limited by predators rather than by food, and carnivore populations must be food-limited by the availability of herbivores. Limiting factors would thus alternate between the herbivore and carnivore trophic levels.

Similiarly, Vandermeer (1980) proposed that competition and indirect mutualism might alternate as primary organizing forces as trophic structure is ascended. His reasoning is that primary producers have sunlight and nutrients as basic resources and therefore depend on resources that cannot "compete" among themselves. Hence, plants are likely to be competitors, given the absence of any direct mutualisms. Competition at the lowest trophic level in turn, implies that herbivores have the propensity to be indirect mutualists [for explanation of mechanisms, see section below on indirect interactions and Figure 1 (lower right)]. It also follows that con-

TABLE 1

Summary of the ways in which several factors vary along the parasite-predator spectrum.
Resumen de las maneras en que algunos factores varían a lo largo del espectro parásito-depredador.

Characteristic	Parasites	Parasitoids	Herbivory	Intertidal Predation	Granivory	Terrestrial Vertebrate Predators
Size	small	about same	can be small or large	slightly larger	much larger than seeds	larger than prey
Numbers	thousands per host	one to a few/host	variable usually many	many prey per predator	many seeds per granivore	many prey per predator
Mortality	hosts killed infrequently	hosts killed after exploited	some prey may survive	prey killed	most seeds eaten	prey killed instantly
Percentage of Prey/Hosts Vulnerable	most hosts vulnerable (immune response context)	density dependent, variable	variable depending on plant	most prey vulnerable	most (but variable)	variable (often low)

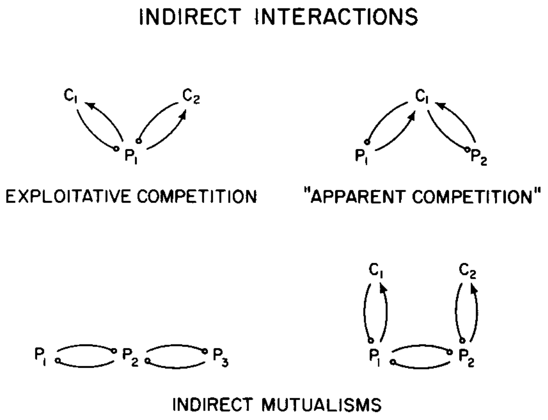

Fig. 1: Four different sorts of indirect interactions involving three or four different species' populations. Pointed arrows indicate beneficial effects whereas circle-headed "arrows" depict detrimental interactions. Upper left: Two consumers sharing a common prey may compete indirectly via classical "exploitation competition" (resource depression). Upper right: Two prey species may appear to compete because if either increases, a shared predator also increases, which operates to the detriment of the other prey population – Holt (1977) called this "apparent competition". Lower left: Three species' populations at the same trophic level, arranged so that one species (P_2) is sandwiched between two others. Populations P_1 and P_3 are indirect "mutualists" because each inhibits the other's competitor P_2. Such a situation can also arise even when P_1 and P_3 are actually weak competitors, so long as competitive interactions with P_2 are strong (this has been called "competitive mutualism" – Pianka 1981). Lower right: A four species system that results in an indirect "mutualism" (perhaps best termed "facilitation" – Vandermeer *et al.* 1985). In this case, populations C_1 and C_2, which do not interact directly but consume different prey species, interact indirectly because their prey compete: if consumer C_1 increases, its prey P_1 decreases, which in turn reduces the competition with P_2, hence allowing an increase in this second prey population (P_2) and providing more food for consumer C_2. Numerous other sorts of indirect interactions are also possible (for examples, see Lane 1985). I thank Jim Brown for generously allowing me to use this figure.

Cuatro diferentes tipos de interacciones involucrando tres o cuatro poblaciones de diferentes especies. Las flechas terminadas en punta indican efectos beneficiosos mientras que las terminadas en círculo indican efectos perjudiciales. Arriba a la izquierda: Dos consumidores que comparten una presa en común pueden competir indirectamente vía la clásica "competencia por explotación" (por depresión del recurso). Arriba a la derecha: Dos especies de presas pueden parecer compitiendo porque si una aumenta, un depredador compartido por ellas también aumenta, lo que opera en contra de la otra especie de presa, Holt (1977) llama a esto "competencia aparente". Abajo a la izquierda: Tres poblaciones de un mismo nivel trófico, ordenadas de tal manera que una (P_2) queda entre medio de las otras dos. Las poblaciones P_1 y P_3 son "mutualistas indirectos" porque cada una inhibe al competidor (P_2) de la otra. Tal situación puede darse aun cuando P_1 y P_3 sean competidores débiles, en la medida que las interacciones competitivas con P_2 sean más fuertes, Pianka (1981) llama a esto "mutualismo competitivo". Abajo a la derecha: Un sistema de cuatro especies que produce un mutualismo indirecto (quizás mejor llamado "facilitación"; véase Vandermeer *et al.* 1985). En este caso, las poblaciones C_1 y C_2, que no interactúan directamente entre sí, porque consumen presas diferentes, interactúan indirectamente porque tales presas compiten. Si el consumidor C_1 aumenta, su presa P_1 decrece, lo que, a su vez, reduce la competencia con P_2, así permitiendo un incremento de esta población de presas, proveyendo más alimento al consumidor C_2. Muchos otros tipos de interacciones indirectas son posibles (véanse ejemplos en Lane 1985). Agradezco a Jim Brown por permitirme usar esta figura.

sumers of herbivores, namely carnivores, would be likely to experience competition.

A better documented, but different, yet comparable sort of situation occurs in lacertid lizards of the southern Kalahari semidesert (Huey & Pianka 1981). Widely-foraging lizard species tend to consume relatively sedentary prey (particularly termites), whereas two other closely-related sit-and-wait species eat more active insects. Moreover, a sit-and-wait predator on these lacertid lizards, the horned adder *Bitis caudalis,* that hunts by ambush, consumes widely-foraging lizards; another lizard predator that forages more actively (the secretary bird *Sagittarius serpentarius*) eats more sit-and-wait lizards. These "crossovers" make immanent sense, since a sedentary predator will not encounter prey unless they move. Conversely, a moving predator has a higher likelihood of encountering non-moving prey species.

Identification and careful consideration of such "crossovers" between trophic levels may offer a useful way to enhance our understanding of interactions between levels.

INDIRECT INTERACTIONS

The traditional pair-wise approach to population interactions has proven to be inadequate (Lawlor 1979). Although exploitation competition is often considered along with direct pair-wise interactions, it actually represents an indirect interaction mediated through resource depression of shared prey. A wide variety of indirect interactions, including indirect or "apparent" competition and indirect mutualism (= "facilitation"), have now been catalogued by Holt (1977), Pianka (1981), Vandermeer *et al.* (1985), and Lane (1985), among others. Four major indirect interactions are summarized in Figure 1. Such indirect effects are by no means intuitively obvious and often require fairly circuitous thinking.

Indirect mutualism, or *facilitation,* occurs when the indirect effects as mediated via other members of a complex network, is +, +. This may arise in several different ways: 1) perhaps the simplest is when two nodes are two trophic levels apart connected by a pathway consisting of two negative interactions. 2) A more complex situation arises via four links traversing two intervening trophic levels before returning to the original level. 3) Also, indirect mutualisms may arise from paths traversing an odd number of trophic levels if interference competition minus-minus links occur between components on the same trophic level. Lane (1985) terms these three kinds of indirect mutualism type B, type A, and type C, respectively.

An indirect effect can be defined mathematically as the product of all the various direct effects along a series of links, or a *pathway,* in which no species node is passed through more than once (Lane 1985). Such a path product represents the indirect effect between two nodes which may also be connected by a direct effect. Typically, the longer the pathway by which an indirect effect is mediated, the longer is the time lag required for the effect to be transmitted from one node to another. Thus, indirect effects typically take longer to occur than direct effects [empirical evidence for this is given by Brown *et al.* (1986)]. Positive indirect effects can arise both by means of mutualistic links and by means of products of an *even* number of negative links. If, however, there are an *odd* number of negative links in a pathway, the overall indirect effect is negative. Because there are many more indirect effects than direct ones in a given system, the former may assume paramount importance (Patten 1983). Indirect effects can actually oppose the direct effects, and, if their overall effects are intense enough, the overall net effect on one population on another, termed the "community effect" by Lane (1985), can actually be reversed. Although this sort of double thinking seems complex at first glance, it may prove to be vital to understanding community organization: by moderating each other, opposing direct versus indirect interactions would leave a target species only weakly affected. Indeed, the interaction between any given pair of populations depends vitally on the exact complex network of other interactions within which the pair concerned is embedded. Indirect effects render interpretation of simple experiments and observations extremely difficult, if not impossible (Bender *et al.* 1984).

The complex interplay between indirect effects that are beneficial versus those that are detrimental can be illustrated with a very interesting four-species subsystem (Figure 2). Such a system can be modelled

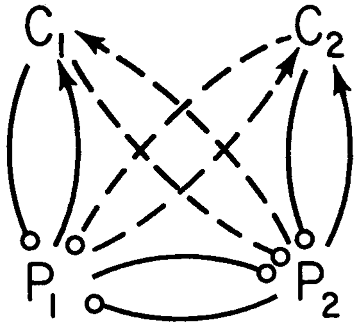

Fig. 2: A four-species subsystem that proves instructive in initial attempts at understanding the interacion(s) between beneficial versus detrimental indirect effects. In the absence of the dashed cross linkages, consumer species C_1 and C_2 are indirect mutualists as explained in Figure 1. However, if cross linkages are present and strong enough, these two consumer populations can experience a mutually detrimental indirect interaction (exploitation competition).

Un subsistema de cuatro especies que resulta esclarecedor para la comprensión de la interacción entre efectos indirectos beneficiosos versus perjudiciales. En ausencia de los eslabones en línea quebrada, las especies de consumidores C_1 y C_2 son mutualistas indirectos, tal como se explicó en la Figura 1. Sin embargo, si los eslabones están presentes y son suficientemente fuertes, estas dos poblaciones de consumidores pueden experimentar una interacción indirecta que les resulta mutuamente perjudicial (competencia por explotación).

mathematically (MacArthur 1968, 1972a; Levine 1976; Vandermeer 1980), as follows:

$$\frac{dC_1}{dt} = [z_1(a_{11}w_1P_1 + a_{12}w_2P_2 - T_1)]C_1 \qquad (1)$$

$$\frac{dC_2}{dt} = [z_2(a_{21}w_1P_1 + a_{22}w_2P_2 - T_2)]C_2 \qquad (2)$$

$$\frac{dP_1}{dt} = [\frac{r_1}{K_1}(K_1 - P_1 - \alpha_{12}P_2) - a_{11}C_1 - a_{21}C_2]P_1 \qquad (3)$$

$$\frac{dP_2}{dt} = [\frac{r_2}{K_2}(K_2 - P_2 - \alpha_{21}P_1) - a_{12}C_1 - a_{22}C_2]P_2 \qquad (4)$$

where a_{ij} is the probability that an individual of consumer species i will encounter and eat an individual prey of species j. P_1 and P_2 are the numbers of two prey resource species, which grow logistically with their own rates of increase (r_i) and carrying capacities (K_i). These two populations also can compete directly if the α_{ij}'s are positive. T_1 and T_2 are threshold amounts of food necessary for the consumer populations to maintain themselves, w_i are the average per capita weights of individual prey of type i, and z_1 and z_2 are factors governing conversion of food into new consumer individuals. Per capita rate of increase of the consumers is proportional to the excess of resource eaten over the resource needed for maintenance. Consumers are food-limited, but their populations can reach an equilibrium with those of the resource populations under certain parameter values.

If the dashed cross linkages are weak or absent (a_{12} and $a_{21} \approx$ zero), consumer species C_1 and C_2 are indirect mutualists as explained above (see also Levine 1976 and Vandermeer 1980). If, however, cross linkages are present and strong enough, these two consumer species can display a mutually detrimental indirect interaction (exploitation competition). In fact, the intensities of the various interactions can actually be adjusted so that the indirect beneficial effects exactly balance the indirect detrimental effects, leaving the two consumer populations essentially noninteractive! The direct minus-minus interaction between the two prey species P_1 and P_2 is pivotal: if this interaction is weak or non-existent, all other interactions become antagonistic, but if P_1-P_2 competition is strong, mutualistic indirect interactions become more likely. The intensity of the direct minus-minus interaction between P_1 and P_2 thus affects *both* types of indirect effects between C_1 and C_2 simultaneously, but in opposite ways. The overriding question is "how will natural selection operating on each of the four parties influence these various linkages?" A comprehensive analysis of this simple system is much needed and long overdue.

COMPLEX NETWORKS

Communities are so diverse and complex that they are difficult to comprehend even when little is known about their component species. The situation is greatly exacerbated when a lot is known. Recognition of trophic levels is one way to simplify communities, but it should not blind us to other approaches. We badly need to discover ways of representing community structure diagramatically such as with food webs and other simple pictures. For example, consider representing species as points[3] in a resource hypervolume (Pielou 1969). Two species can be plotted as points on a line with the distance between them being inversely proportional to their similarity in resource utilization. Similarly, three species can be represented accurately in two-space as the points of a triangle, four species as the vertices of a tetrahedron in three dimensions, and so on. But if consumer species are separated along several or many dimensions, even a relatively small system of only five species may require a four-dimensional space to depict accurately all the possible inter-

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[3] More realistically, these would be clouds of points or probability density distributions.

actions among its component species. Clearly, a community of a dozen species separated along multiple dimensions defies having its portrait painted!

Food webs have been the subject of considerable recent interest (Cohen 1978, Pimm 1982, Lane 1985) although existing data are crude and inadequate. Loop analysis, path analysis, as well as a variety of novel topological and graph theoretical approaches have been suggested as ways of depicting some of the structure of food webs (Levins 1975, Sugihara 1984, Lane 1985, Pimm 1986). While such innovations are certainly intriguing and should be pursued further, they often require unrealistic assumptions, such as that all interactions are plus-minus and either "on" or "off". Analogous, but more realistic, approaches need to be developed that allow for plus-plus mutualistic interactions, minus-minus horizontal interactions (such as interference competition), as well as variability in the intensity of interactions. The importance of interaction strength has been highlighted by both MacArthur (1972b) and Paine (1980). Strong interactions may well be more important than weak ones. However, the cumulative effects of numerous weak (both direct and indirect) interactions, such as in diffuse competition and diffuse coevolution, could nonetheless be rather considerable.

A few of the major ideas proposed by each of the North American ecologists are summarized in Table 2. About half involve networks directly, and most of the others involve networks indirectly. In Figure 3, interaction networks of several different kinds are portrayed. Although considerable discussion has centered around what constraints must exist in real ecological systems (May 1973, Lawlor 1978, Pimm 1982, Lane 1985, among others), we still await a definitive treatment of realistic complex networks. Even the relatively simple 7-species network with biologically realistic constraints (lower right, Figure 3) contains a rich mixture of indirect interactions, many of which are opposite in sign to the direct interactions. It will prove to be exceedingly interesting to examine in detail the behavior and stability of such networks as the magnitudes of the interaction intensities are varied.

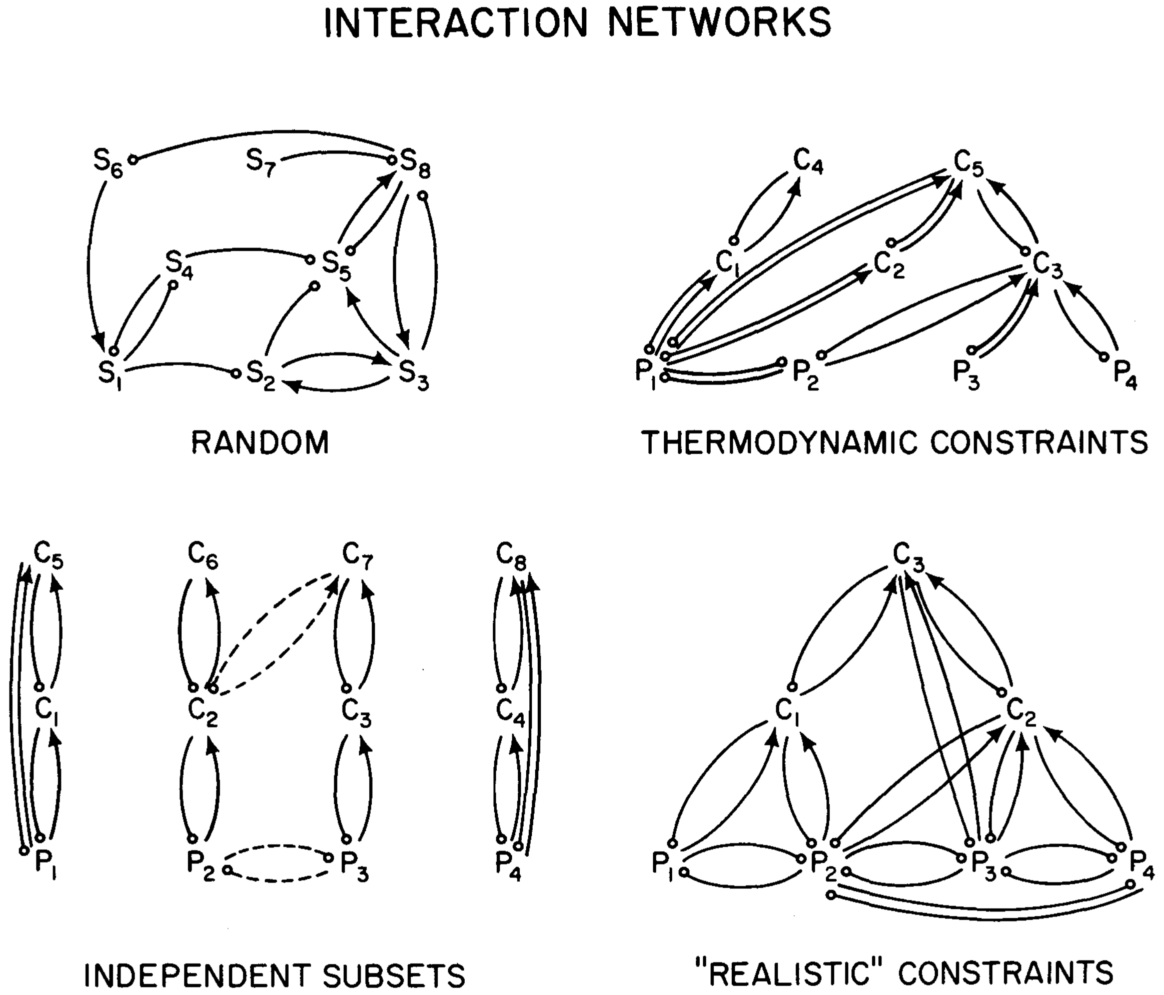
For me, perhaps the most interesting idea to emerge from this conference was Brown's suggestion that indirect effects in real systems might usually be opposite in sign to direct effects (see also Brown *et al.* 1986 and Brown's contribution to this volume). Although indirect effects may often be weaker than direct ones, there are considerably more of the former than the latter. If Brown is correct in his speculation that these two kinds of effects may often balance one another out, a given target population would effectively be in a position of relative *neutrality* in the context of its natural community. Presumably this would enhance prospects for persistence and coexistence, hence promoting both diversity and stability. Thus "May's paradox", that diversity begets instability (May 1973, Pimm 1984, Putman & Wratten 1984), may ultimately be resolved by a deeper appreciation of the importance of subtle indirect effects in complex networks.

TABLE 2

Some of the major ideas proposed by various North Americans.

Algunas de las ideas principales propuestas por los norteamericanos participantes.

Participant	Idea Proposed
Paine	Experimental effects can reverberate through a system (particularly via strong linkages).
Lubchenco	Environmental context is important – interactions are context dependent and can change from situation to situation.
Moore	Not obvious that parasites always cause harm or mortality; parasites may alter distribution and ecology of their hosts.
Marti	Predator escape tactics important, diverse, and complex.
Wagner	Precisely *which* node is perturbed in a network is of vital importance (competitive dominant versus others).
Feinsinger	There is a "conflict of interests" (asymmetry of costs and benefits) even in mutualistic interactions.
Brown	Indirect interactions may often balance direct ones.
Pianka	Properties of complex networks of interacting populations do not necessarily follow obviously from close scrutiny of pairwise interactions.



RANDOM

THERMODYNAMIC CONSTRAINTS

INDEPENDENT SUBSETS

"REALISTIC" CONSTRAINTS

Fig. 3: Four very different types of interaction (courtesy of Jim Brown). Upper left: A network of 8 species constructed randomly without reference to any constraints: 2 and 3 species food "loops" occur, as well as other biologically nonsensical interactions. Upper right: A somewhat more realistic network that obeys certain basic thermodynamic constraints: no loops are allowed, materials and energy flow from lower trophic levels to higher ones, predators impact negatively on their prey, there are fewer species at higher trophic levels, etc. Lower left: A network composed of four more or less distinct food chains, or independent subsets. In real systems, cross linkages (dashed arrows) usually occur, precluding such substructural compartmentation (Pimm 1982). Lower right: A seven species network that mimics biological reality with more-or-less "realistic" constraints (note that even this relatively simple system contains most of the indirect interactions catalogued in the text as well as many others). The behavior and stability of such a network needs to be assessed as the intensities of various interactions are allowed to change.

Cuatro tipos muy diferentes de tramas de interacción (cortesía de Jim Brown). Arriba a la izquierda: Una trama de ocho especies construida al azar, sin ninguna restricción, en que se encuentra eslabones tróficos bidireccionales que comprenden 2 ó 3 especies, además de otras interacciones biológicas sin sentido. Arriba a la derecha: Una trama algo más realista, que obedece restricciones termodinámicas: no hay eslabones bidireccionales, la materia y la energía fluyen desde los niveles tróficos bajos a los altos, los depredadores afectan negativamente a las presas, hay menos especies en los niveles tróficos altos, etc. Abajo a la izquierda: Una trama compuesta de cuatro o más cadenas tróficas distintas, que forman subconjuntos diferentes. En sistemas reales, usualmente hay eslabones entre las cadenas (flechas con líneas de segmento), impidiendo esta compartamentalización tan exagerada (Pimm 1982). Abajo a la derecha: Una trama con siete especies que se asimila mejor a la realidad biológica, con restricciones más o menos realistas (nótese que aún este sistema relativamente simple contiene la mayoría de las interacciones indirectas catalogadas en el texto, así como muchas otras). La conducta y estabilidad de tramas como ésta necesita ser evaluada, haciendo variar la intensidad de las diferentes interacciones.

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