

THE INDETERMINACY OF ECOLOGICAL INTERACTIONS AS PERCEIVED THROUGH PERTURBATION EXPERIMENTS¹

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Abstract. Press perturbation experiments, in which individuals of a particular species are continually added to or removed from an ecosystem and the responses of other species' densities are observed, are discussed in the context of whole systems. When the sizes of direct interactions are determined to within an order of magnitude, the long-term outcomes of press perturbations are highly indeterminate, in terms both of whether species densities increase or decrease and of which interactions have the largest effects. It is emphasized that short-term observations of systems subject to press perturbations (e.g., toxin additions to ecosystems, or experimental manipulations of species using exclosures) are not useful for estimating long-term impacts. The difference between long- and short-term responses is detailed, and a rule of thumb is given for what constitutes "long-term" in this context.

Key words: communities; ecosystems; environmental impacts; experiments; interspecific interactions; perturbations.

INTRODUCTION

Perturbation experiments, in which one or more species densities are altered and changes in density of other species in the community are observed, are important in ecology for a number of reasons. For one thing, they are widely viewed as a particularly meaningful probe for interspecific interactions (e.g., Connell 1983, Schoener 1983). For another, human impacts on ecosystems often amount to unwitting perturbation "experiments."

One can distinguish two distinct kinds of perturbation experiments. In one kind of experiment, termed "pulse" by Bender et al. (1984), one or more species densities are instantaneously changed, and then the system is observed as it returns to equilibrium (or some other attractor). In the second kind of experiment, termed "press" by Bender et al. (1984), one or more species densities are continually altered to a higher or lower level by means of a continual addition or removal of members of those species. Press experiments correspond to manipulations such as stocking or erecting exclusion cages or fences, or to persistent new mortality factors such as humanly produced toxins. I will consider press experiments here.

Press experiments involve both direct and indirect effects (e.g., Bender et al. 1984). The existence of indirect effects (where species A affects species C through a chain of intermediate species: species A affects species B₁, which affects species B₂, . . . , which affects species B_n, which affects species C) is well known in theory and to some extent has been documented in the field. Indeed, one of the most thoroughly studied of all interactions, pure exploitative or consumptive (Schoener 1983) competition, is an indirect one. Other, less ob-

vious, indirect effects have been studied in the field by Davidson et al. (1984) and Wilson (1986), among others.

I think it is fair to say that most ecologists, while aware that indirect effects are possible in principle, do not regard these effects (other than consumptive competition) as being of major importance. In order to assess this question, I have investigated press experiments in the context of plausible community matrices (Yodzis 1981) associated with observed food webs (Briand 1983) and have found that indirect effects are indeed of overwhelming importance in this context. More disturbingly, the long-term outcomes of these experiments exhibit a surprising degree of sensitivity to the values of the interaction parameters. In practical terms, given the difficulty of measuring these parameters and their considerable inherent variability, this means that the outcomes of press experiments are in significant measure indeterminate, in terms of the signs of the responses (whether a given density increases or decreases in response to the perturbation), and even in terms of the identities of those species that suffer the largest responses.

FOOD WEBS AND PLAUSIBLE COMMUNITY MATRICES

A "food web" for some set of species in some habitat is a listing of which of those species eat which others. Such a listing can take the form of a directed graph (Fig. 1). "Species" in this context refers to "tropho-species," by which is meant a lumping together of bio-species with similar feeding habits. Of course a shortcoming of existing food web data is the lack of a consistent usage for "similar" in this context; for the foreseeable future we are just going to have to live with this. A "community food web" is a food web that includes all species living in some given location. The

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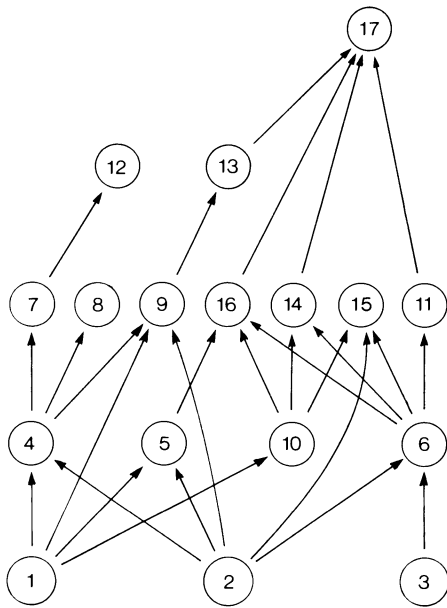


FIG. 1. Food web for Narragansett Bay, Rhode Island. Each vertex (circle) represents a species, and an arrow from vertex i to vertex j means that species j consumes species i .

web of Fig. 1 is a community food web for Narragansett Bay, Rhode Island (Briand 1983: Case 7).

I use here as empirical base the collection of community food webs culled from the published literature by Briand (1983). In each of these webs, I have lumped together species that, in Briand's (1983) original version, are listed as having exactly the same prey and predators. Briand has followed the same procedures in his later work (e.g., Briand and Cohen 1984, Cohen and Briand 1984).

I am going to assume that the dynamics of each community in the Briand collection can be described by a dynamical system of the form

$$dN_i/dt = f_i(N), \quad i = 1, 2, \dots, s, \quad (1)$$

where N_i is the density of species i , N represents the vector (N_1, N_2, \dots, N_s) of densities, and there are s species in the community. Biologically, this assumes that the instantaneous rate of growth f_i of any species i is a function of all the densities: any other quantities that may affect it are assumed not to vary significantly over the time periods of interest. Furthermore, I will assume the system (1) has an equilibrium at some point N_e in phase space. Then the stability of that equilibrium is determined by the eigenvalues of the "community matrix"

$$A_{ij} = (\partial f_i / \partial N_j)|_{N_e}, \quad (2)$$

as explicated, for instance, by May (1974).

It is not self-evident that such a simplistic descrip-

tion has any validity at all for such complex systems. I have, however, elsewhere offered quasi-empirical evidence in favor of its validity (Yodzis 1981, 1987), and will proceed on this basis here. In particular, for present purposes I neglect all interactions other than intraspecific interference and trophic interactions. Moreover, I assume that only basal species (those that feed on no other species) have significant intraspecific interference. The resulting community matrices are the simplest ones that could at all plausibly be associated with these food webs, in the sense of having the smallest possible number of direct interactions (matrix elements A_{ij} of A).

In this "simplest case," the only nonzero elements of the community matrix are as follows. (1) For all i , A_{ii} will be negative. However, if species i is not basal, the magnitude of A_{ii} will be negligibly small. (2) If species i is consumed by species j , then A_{ji} will be positive and A_{ij} will be negative. One can represent these matrix elements in graphical form as shown in Fig. 2, which corresponds to the food web of Fig. 1.

We could in this way associate a community matrix A with any real food web if we knew the magnitudes of the matrix elements A_{ij} . I determine those magnitudes as follows: the magnitude of each matrix element A_{ij} will be chosen at random from an interval $(B_{ij}/10, B_{ij})$. Thus each A_{ij} is determined to within an order of magnitude by B_{ij} . The bounds B_{ij} are obtained as fol-

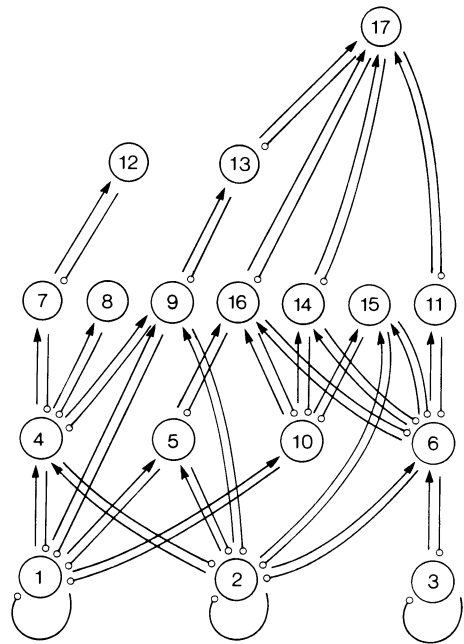


FIG. 2. Loop diagram for a simple family of community matrices associated with the food web of Fig. 1. Here each connective between two vertices represents a nonzero element of the community matrix. If a connection from vertex i to vertex j has an arrow [circle] at its vertex j end, this means species i has a positive [negative] direct effect on species j , so that $A_{ji} > 0$ [$A_{ji} < 0$].

TABLE 1. The Briand communities treated in this study. Citations of the original sources can be found in Briand (1983). S is species richness, the number of trophospecies in the community.

Case	Community	S
3	Long Island estuary	24
4	California salt marsh	13
5	Georgia salt marsh	6
7	Narragansett Bay	17
8	Bissel Cove marsh	15
9	Lough Ine rapids	9
10	Exposed intertidal (New England)	3
11	Protected intertidal (New England)	5
14	Mangrove swamp	8
15	Mangrove swamp	7
16	Pamlico River	14
25	Canadian Aspen communities	24
28	New Zealand salt meadow	32
29	Arctic seas	16
36	Mangrove swamp	19
40	Malaysian rain forest	11

lows. For all i such that species i is basal, the intra-specific interference bounds B_{ii} will be taken equal to 10. This corresponds to the assumption that they are all of the same order of magnitude, together with a choice of time units. For nonbasal species, B_{ii} is taken equal to 0.001.

To get the other bounds B_{ij} , I use the fact that A_{ij} is the per capita effect of species j on the growth rate of species i at equilibrium, which follows directly from statement 2. This enables one to make plausible guesses, based on the nature of the particular organisms involved, as to the relative magnitudes of the B_{ij} . For instance, if insects consume trees, then the per capita effect of insects on trees will be much smaller than the per capita effect of trees on insects.

I call a community matrix that is obtained in this way a "plausible community matrix." I have shown (Yodzis 1981) that plausible community matrices associated with the Briand food webs are far more likely to be stable than community matrices whose interaction strengths do not reflect the nature of the particular organisms in these food webs. It is difficult to see why this should be the case unless the simplistic formalism I have been discussing really does in some sense approximate the dynamics of these systems (Yodzis 1981, 1987).

The following analysis applies to stable equilibria. For practical reasons, I will treat only those Briand food webs for which the probability that a plausible community matrix, constructed as above, is stable exceeds 0.001. This is so for the 16 Briand food webs listed in Table 1.

PRESS PERTURBATION EXPERIMENTS

Suppose we continually add members of species j to the community, at a rate I_j members per unit area per unit time. How will this affect the equilibrium densities N_i ? Equation (1) is now

$$\begin{aligned} dN_i/dt &= f_i(\mathbf{N}) + I_j \\ dN_j/dt &= f_j(\mathbf{N}), \quad i \neq j. \end{aligned}$$

For sufficiently small I_j there will still be a stable equilibrium at some density $N_i(I_j)$, and at this equilibrium we will have

$$\begin{aligned} 0 &= f_i[N_i(I_j)] + I_j \\ 0 &= f_j[N_i(I_j)], \quad i \neq j. \end{aligned}$$

Differentiating this last set of equations with respect to I_j , we obtain easily

$$dN_{ci}/dI_j = -(\mathbf{A}^{-1})_{ij}, \quad (3)$$

where \mathbf{A}^{-1} is the matrix that is inverse to \mathbf{A} . Existence of the inverse matrix is guaranteed by stability of the matrix \mathbf{A} .

Thus: the inverse of the community matrix summarizes the outcomes of all possible press experiments. We can get an overview of the outcomes of press experiments in real whole communities by studying the inverses of stable plausible community matrices.

In the following, whenever I speak of the *effect* of species j on species i , I will mean it in the context of a press addition experiment. In numerical terms, such an effect is measured by dN_{ci}/dI_j (Eq. 3). Of course, the result of a press removal experiment will have the opposite sign to the result of a press addition experiment.

These effects are an expression of the complex of interactions among all species in the community. In principle, they are a complete expression of these interactions: by pressing each species in the community in turn, and measuring the effect on all species densities of each press, one could measure \mathbf{A}^{-1} , then recover \mathbf{A} by inversion. In practice, of course, this would be impossibly difficult.

DIRECTIONAL INDETERMINACY

The elements of plausible community matrices are determined only to within an order of magnitude. We expect that if, for some given real food web, we construct a number of different plausible community matrices (corresponding to different random choices within the intervals $[B_{ij}/10, B_{ij}]$), then there will be some variation in the matrix \mathbf{A}^{-1} as well. It could even be that the *signs* of those matrix elements will vary somewhat. Of course, the signs in \mathbf{A}^{-1} indicate the directions of the outcomes of press experiments: if $-(\mathbf{A}^{-1})_{ij} > 0$ [or < 0], adding members of species j will cause an increase (a decrease) in the equilibrium density of species i (recall Eq. 3).

I will say that the effect of species j on species i is *directionally determined* if the confidence level, in the statistical universe of plausible community matrices constructed as above, for the sign of $-(\mathbf{A}^{-1})_{ij}$ is at least 95%; otherwise I will call it *directionally undetermined*. For each food web in Table 1, I investigated these confidence levels as follows. Using a random number generator, I constructed 100 stable plausible commu-

nity matrices corresponding to the given food web, and computed the inverse matrix for each community matrix. Then for each given i and j , the effect of species j on species i was directionally determined if at least 95 of the resultant matrix elements $-(A^{-1})_{ij}$ had the same sign.

These computations required weeks of VAX 11/780 CPU cycles, so it would have been impracticable to increase the sample size much above 100. However, with this sample size the standard deviation of the fraction of matrix elements with a given sign, at the test value of 0.95, is $[(0.95)(0.05)/100]^{1/2} = 0.02$ (Campbell 1974:302). We are detecting the 95% confidence level to within $\approx 2\%$, so a larger sample size would very likely not make much difference in the results.

Table 2 summarizes the results, breaking effects down into several classes. A "self" effect is the effect of adding a given species on that same species' density. We expect such a manipulation to have a positive effect, but this is not always the case: of the 223 self effects in these food webs, 27% have a negative response in more than 5 of the 100 cases studied. But whenever the self effect is determined, it is always positive, as expected (last column of Table 2).

For a pair of species, one of which consumes the other, the "predator on prey" effect corresponds to adding predator individuals and observing the effect on the prey density (one expects a negative effect), and the "prey on predator" effect corresponds to adding prey individuals and observing the effect on the predator density (one expects a positive effect). For these effects, more than half are directionally undetermined, and in some cases where the effect is determined the more probable effect is the opposite of what we expect (Table 2).

Self effects and predator-prey effects involve both a direct component and an indirect component. For instance, in the Narragansett Bay system depicted in Fig. 2, species 4 has a direct effect on species 1, indicated by the directed link from vertex 4 to vertex 1 (the one with a little circle at the species 1 end, to indicate a negative effect), because species 4 eats species 1. But also, species 4 has an indirect effect on species 1 through the path of directed links in Fig. 2 from species 4 to species 9 to species 1; biologically, species 4 feeds species 9, which feeds on species 1. Species 4 also affects species 1 through the path species 4 to species 9 to species 13 to species 17 to species 16 to species 5 to species 1. Another indirect effect runs from species 4 to species 9 to species 2 to species 5 to species 1. The reader will easily find in Fig. 2 many other indirect pathways from species 4 to species 1.

The net effect of a self interaction or a predator-prey interaction is the sum of the direct effect plus all the individual indirect effects. It is this net effect that we observe in press perturbations, and which I am calling simply "the effect" here. The indeterminacy (and the "reverse determinacy") in these net effects (Table 2)

TABLE 2. Directional indeterminacy in plausible community matrices associated with the food webs of Table 1, categorized by type of effect on a species' density.

Type of effect	Number of effects*	Proportion directionally undetermined	Among determined, proportion showing reverse effect
Self	223	0.27	0
Predator on prey	317	0.52	0.11
Prey on predator	317	0.54	0.07
Indirect	3423	0.50	...
Competitive	566	0.58	0.29

* The total number of effects of each type, that is, the total number of pairs of species in each type category that occur in the 16 communities of Table 1.

can come about only if the direct component is "swamped" by a stronger indirect component. Because of this prevalence of indirect effects, even our most elementary expectations for press experiments (say, that adding predators will result in fewer prey) are not to be taken for granted.

Finally, Table 2 lists the effects that are purely indirect. For instance, in the Narragansett Bay system cf. Fig. 2, species 4 has no direct effect on species 15, because there is no link from species 4 to species 15. But there is an indirect effect of species 4 on species 15, through a number of pathways such as 4-2-15, 4-9-13-17-14-10-15, and so on. Not surprisingly, here, too, we find considerable indeterminacy. In particular, this is the case for competitive effects (in which the two species share a prey). For those competitive effects that are determined, 29% show the reverse of the expected effect (the expected effect being that the addition of members of a species will result in a decrease in the density of its competitors).

The species richness (total number of species) of these communities varies from 3 to 32 (Table 1). This variation is due mainly to differences among the investigators involved as to the extent of lumping of biospecies into trophospecies. Table 3 addresses the question of how this sort of lumping affects directional indeterminacy. Here, effects are categorized by the species richness of the community in which they are found. For the smallest communities (1-5 trophospecies), there is no indeterminacy, as one might well expect. For communities with 6-25 species there seems to be no significant variation in the proportion of effects that are undetermined. There is only one community larger than this, and it has less indeterminacy, but one is reluctant to ascribe significance to an effect that is based on only one community.

TOPOLOGICAL INDETERMINACY

Of the many effects in these systems, some will be weaker than others. One may object that Table 2 mixes big effects and little effects indiscriminately, so that possibly the biggest effects are highly deterministic,

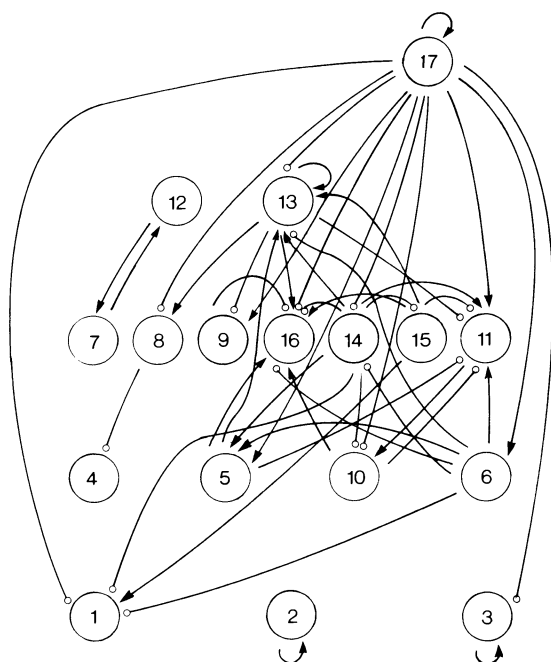


FIG. 3. Major effects on each species of the Narragansett Bay food web, obtained from a randomly generated plausible community matrix. Symbols here have the same meaning as in Fig. 2, except that here they are based on the inverse matrix A^{-1} rather than on the community matrix itself.

with most of the indeterminism in Table 2 confined to effects that are so weak as to be uninteresting.

There are also intrinsic reasons to single out the biggest effects. Sometimes, particularly in an applied context, what one really wants to know is which effects are the biggest. For example, one might want to know which species in a system are particularly sensitive to degradations elsewhere in the system, or one might want to know which other species in the system will be hardest hit (or experience the greatest benefits) by exploitation, or poisoning, or stocking of some species.

We can formulate these issues as follows. First, for any positive real number x , let $\text{mag}(x) = 10^N$, where N is the (unique) integer such that $10^N \leq x < 10^{N+1}$; $\text{mag}(x)$ is simply "the order of magnitude of x " in the

usual sense. For a given community matrix A , say that the effect of species j on species i is a *major effect on i* if, for all k ,

$$\text{mag} |(A^{-1})_{ij}| \geq \text{mag} |(A^{-1})_{ik}|,$$

and say that it is a *major effect of j* if, for all k ,

$$\text{mag} |(A^{-1})_{ij}| \geq \text{mag} |(A^{-1})_{kj}|.$$

Call the effect a *major effect* if either of the preceding two conditions is satisfied. These definitions simply identify the major effects as those that are biggest in order of magnitude.

In searching out major effects, we find a new indeterminacy: an indeterminacy in the very identity of major effects. For example, Fig. 3 and Fig. 4 depict, for two different plausible community matrices, the major effects on each species of the Narragansett Bay community of Fig. 1, using the conventions explained in connection with Fig. 2. However, the connections depicted in Figs. 3 and 4 are derived from the negative inverse matrix $-A^{-1}$ rather than from the community matrix A itself as in Fig. 2.

I remind the reader that the plausible community matrices that I am using here are determined to within an order of magnitude. This rather modest indeterminacy in A (due either to the shortcomings of our measurements, or to natural variation that is present whether we try to measure it or not) can result in considerable variation even in the topological structure of

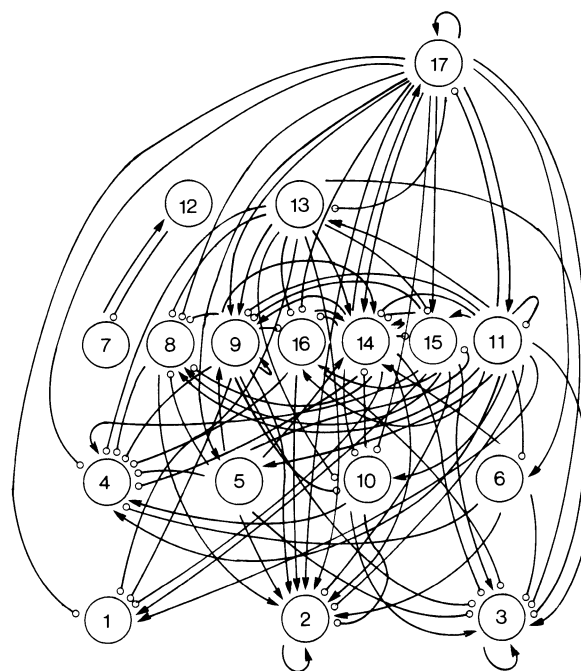


FIG. 4. Major effects on each species of the Narragansett Bay food web, obtained from another randomly generated plausible community matrix. Symbols here have the same meaning as in Fig. 2, except that here they are based on the inverse matrix A^{-1} rather than on the community matrix itself.

TABLE 3. Directional indeterminacy in plausible community matrices associated with the food webs of Table 1, categorized by S , the number of species in the community.

S	Number of communities	Number of effects	Proportion directionally undetermined
1-5	2	42	0
6-10	4	260	0.50
11-15	4	764	0.53
16-20	3	958	0.70
21-25	2	1200	0.56
26-30	0
31-35	1	1056	0.20

major effects. For instance, consider species 4. With the particular choice for interaction strengths corresponding to Fig. 3, by far the biggest effect on this species will come from pressing its predator (species 8): the only major effect is the link depicted in Fig. 3 from species 8 to species 4. But with the choice of interaction strengths corresponding to Fig. 4, fully 10 other species have about as large an effect (to within an order of magnitude) on species 4 as does its predator. In general, as we view the system through press perturbations, interspecific effects appear far more diffuse in the case of Fig. 4 than in that of Fig. 3. These two figures show that there can be tremendous variation even in the topological structure of major effects.

We can quantify the extent of this variation in the following way. Say that the effect of species j on species i is *unimportant* if, in a random sample of plausible community matrices constructed as above (Food Webs and Plausible Community Matrices), the probability for it to be a major effect is $<.05$, and call it *most important* if the probability for it to be major is $>.95$. If an effect is unimportant, we can be 95% confident that it will, in a given plausible community matrix, not be major; if an effect is most important, we can be 95% confident that it will, in a given plausible community matrix, be major. In practical terms, if the interaction strengths are known to within an order of magnitude in some real system, we can be 95% confident that unimportant effects are not major, and that most important effects are major, in that system. Effects that are neither unimportant nor most important are what I will call "topologically undetermined," since we cannot decide, at the 95% confidence level, whether those effects will be present or not in a graph, such as Fig. 3 or Fig. 4, of major effects.

Table 4 lists, for each food web in Table 1, the frac-

TABLE 4. Proportion of effects on plausible community matrices associated with the food webs of Table 1 that are unimportant, most important, and topologically undetermined.

Case	S (species richness)	Unimportant	Most important	Topologically undetermined
3	24	0.727	0.002	0.271
4	13	0.118	0.018	0.864
5	6	0.556	0	0.444
7	17	0.581	0	0.419
8	15	0.573	0.004	0.423
9	9	0.049	0.012	0.939
10	3	0.444	0	0.556
11	5	0.520	0	0.480
14	8	0.578	0.031	0.391
15	7	0.531	0	0.469
16	14	0.577	0.005	0.418
25	24	0.760	0.002	0.238
28	32	0.901	0.002	0.097
29	16	0.598	0.008	0.394
36	19	0.332	0.008	0.660
40	11	0.579	0.017	0.404

TABLE 5. Directional indeterminacy of important effects in plausible community matrices associated with the food webs of Table 1, categorized by type of effect.

Type of effect	Number of effects*	Proportion directionally undetermined	Among determined, proportion showing reverse effect
Self	167	0.33	0
Predator on prey	208	0.55	0.10
Prey on predator	208	0.58	0.02
Indirect	2468	0.53	...
Competitive	365	0.64	0.31

* As in Table 2, but restricted to important effects.

tion of effects in these three categories. There is a high degree of indeterminacy in the topology of major effects. However, there seems to be a trend for this indeterminacy to be less pronounced in more finely differentiated food webs (Fig. 5). Lumping biospecies very coarsely into trophospecies (resulting in smaller species richness S) results in more topological indeterminacy.

Finally, let us return to the question of determinacy of the direction of effects. Table 2 shows a high degree of indeterminacy if we consider all effects. Does this indeterminacy reside mainly in weak effects? The answer can be seen in Tables 5 (where attention is restricted to *important* effects, i.e., those that are not unimportant) and 6 (where attention is restricted to most important effects). Even the most important effects have still a high degree of directional indeterminacy.

DISCUSSION

The communities considered here represent a wide variety of habitats, geographical locations, and researchers. What they have in common is a very high degree of indeterminacy, both in direction and in topology, of interactions as viewed through press experiments, at least, within the context of equilibrium dynamics in deterministic models of the form of Eq. 1.

Admittedly, many ecologists are skeptical of this kind

TABLE 6. Directional indeterminacy of most important effects in plausible community matrices associated with the food webs of Table 1, categorized by type of effect.

Type of effect	Number of effects*	Proportion directionally undetermined	Among determined, proportion showing reverse effect
Self	44	0.07	0
Predator on prey	55	0.31	0
Prey on predator	55	0.33	0
Indirect	769	0.30	...
Competitive	28	0.39	0.35

* As in Table 2, but restricted to most important effects.

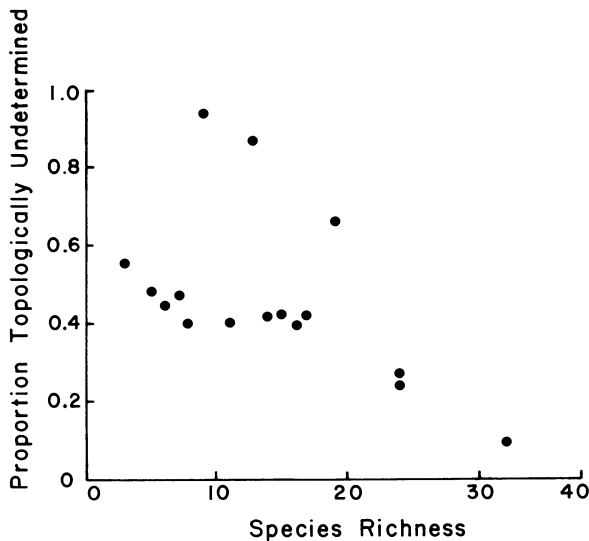


FIG. 5. Topological indeterminacy vs. species richness for the 16 food webs of Table 1.

of model, thinking it overly simplified. However the only attempt that I am aware of specifically to test in a quasi-empirical fashion the appropriateness of this whole theoretical framework (Yodzis 1981, 1987) tends to support it. In any case, the point I am making here is that even these simple models behave in a very complicated way with respect to press perturbations. It would be quite astonishing if more realistic, hence more complex, models (or, for that matter, nature itself) behaved more simply than these models, so I expect that the basic message of these results will be extremely robust with respect to the underlying assumptions.

A similar remark applies to the troublesome problem of what to assume about the intraspecific interactions A_{ii} . Pimm (1982 and elsewhere) argues, unconvincingly to my mind, that these interactions are negligible for all but basal species. This assumption is crucial in certain applications, for instance the work of Pimm and Lawton (1977) on food chain lengths. But it is not at all an important determinant of the results I am reporting here. I have adopted Pimm's assumption here, not because I believe it justified, but because, again, this is the simplest possible assumption one can make. Dropping this simplifying assumption would hardly be expected to yield simpler behavior in press experiments. Preliminary calculations indicate that, indeed, this is not a crucial assumption in the present context.

Another major simplifying assumption may not be so harmless. As indicated above the "species" that are the fundamental building blocks of currently available food web data are not individual species in the biological sense, but trophospecific aggregates of biospecies. In applying models of the form Eq. 1 to these data, we tacitly assume that such trophospecies behave

dynamically as do normal populations. There seems to be some indication, in the case of topological indeterminacy, that the indeterminacy is less severe in food webs that are more finely differentiated in the identification of trophospecies (Fig. 5). This raises the possibility that topological indeterminacy might be in part an artifact of aggregated models. But Fig. 5 can only be regarded as raising this possibility; more work is required to substantiate it.

Figs. 3 and 4, which indicate the typical topology of major effects, may be relevant to the current controversy over the importance of competition in nature (for instance, Connell 1983, Schoener 1983), at least insofar as this process is manifest in press perturbations. Competitive effects will correspond to horizontal links in these diagrams. Inspection of Figs. 3 and 4 suggests that competition is seldom a major effect among herbivores, but it is frequently a major effect among carnivores.

This hints at a fascinating generalization about exploitative competition (remember that interference is not included in these models), but I would caution against asserting such a generalization at this time again because of the high degree of aggregation in these models. The competition that has traditionally been studied in ecology is among closely related species such as congeners; this is happening within the aggregated trophospecific categories rather than among them. Again, more work is called for.

Patten (1982) has argued for the importance of "indirect influences" in ecosystems. However, Patten's notion of indirect influence is thoroughly different from the indirect effects treated in the present work. As pointed out, correctly, by Wiegert and Kozłowski (1984), Patten's methodology does not yield a sensible measure of the strength of indirect effects.

It is important to understand that the effects considered here contrast equilibrium densities before a press has taken place with the new densities attained after the press has been operating for a sufficiently long time for the system to reach a new equilibrium. That is, these are *long-term* effects. The intervening "transient" behavior, and especially the short-term behavior, can easily be different (Bender et al. 1984). Specifically, one can show (Yodzis, *in press*) that the temporal behavior of the density of species i , in response to a press perturbation of sufficiently small size δ of the density of species j , commencing at time $t = 0$, is

$$N_i(t) = N_{ci} + \sum_{m=1}^{\infty} (t^m/m!)(A^{m-1})_{ij}\delta,$$

where N_{ci} is the density of species i before the press, and $(A^{m-1})_{ij}$ is the ij element of the matrix that is the $(m-1)^{\text{th}}$ power of the community matrix A .

At early times, the dominant term in the sum will be the nonzero term with the smallest value of m . In particular, if species j has a direct effect on species i ,

then at early times we will see that effect. For instance, if species j predaes species i (A_{ij} negative), and we remove members of species j from the system (δ negative), then at first species i will increase in abundance. (In this case the term with $m = 1$ in the sum is zero, and the term with $m = 2$ is positive.) There is no indeterminacy in this short-term behavior: it is exactly what we expect on elementary intuitive grounds. However, if we continue to remove members of predator j from the system for an extended time, then we are performing a press perturbation, and as we already know from Table 2, the abundance of its prey species i may eventually *decrease*, and it could easily wind up *less* than its initial value N_{i0} . (This is more easily seen using Eq. 3 than the above sum, since at large t we would have to deal with the whole infinite sum.) Brown et al. (1986) discuss field data that seem to demonstrate this sort of contrast between short-term and long-term behavior.

How long is "long term"; how long need we wait to be reasonably confident that the system has settled near its new equilibrium? I would suggest the following rule of thumb. Find all pathways in the loop diagram (such as Fig. 2) from the pressed species to any species whose response is of interest. For each pathway, add up the generation times of all species that occur in the pathway. Find the largest of these sums, and multiply it times 2.

For those doing practical work with environmental impacts, it is of crucial importance to understand that short-term observations of environmental impacts that can be viewed as press perturbations are close to useless for estimating probable long-term impacts. Moreover, as the present study makes clear, predicting those long-term effects not only requires data on the strengths of many interactions in the system, it requires very accurate data on many interaction strengths. This is a daunting prospect indeed.

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