The qualitative approach in investigating the role of species interactions on stability of natural communities

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Community models with competition and mutualism are qualitatively analyzed using the methodology of loop analysis combined with computer stochastic simulation. The concept of "moving equilibrium" in the growth rate of the species is discussed in 14 "tables of predictions", presented as analytical tools that can help to shed light on controversial ecological issues such as direct versus indirect interaction and positive feedback effects on stability. While the stochastic simulation shows that only little or no difference exists in probability of stability between models with competition and models with mutualism, the related tables of predictions show that the networks among links are able to activate indirect interactions, with both negative and positive effects, between any pair of species. This phenomenon makes it difficult to determine how much stability is related to the direct interactions.

Keywords: Community analysis; Competition; Direct and indirect relations; Loop analysis; Moving equilibrium; Mutualism; Positive feedback.

Introduction

A common and controversial theme of modern ecological research is the role of intra- and interspecific processes. It has been widely accepted (May, 1976; Thompson, 1982) that the regulatory mechanisms underlying these aspects form the basis of the functioning of natural populations, and therefore of entire ecosystems.

Most investigations documented in the literature that deal with relationships between species (Fig. 1) have been oriented to the study of predation and competition phenomena (Berryman, 1981; Connell, 1983; Schoener, 1983), even though renewed interest in other forms of interactions is arising.

The influence of competition and mutualism on the stability of natural systems is challenging theoretical ecology, and mutualism, in particular, has been the subject of recent studies (Boucher, 1985; Wolin, 1985; DeAngelis et al., 1986).
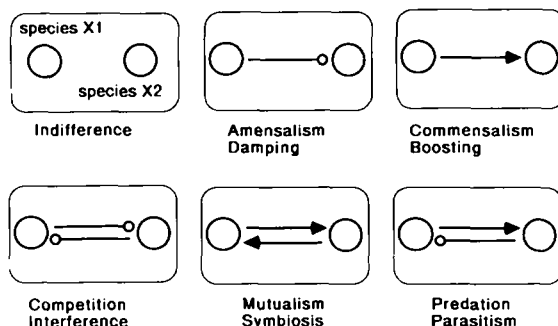

Fig. 1. Different kinds of interaction between species, and loop analysis symbology.

Some models of mutualism (Vandermeer and Boucher, 1978; Goh, 1979; Travis and Post, 1979; Pierce and Young, 1986) are based on modified Lotka-Volterra equations for two competitor systems. Since both the competitive and the mutualistic associations express positive feedbacks, the Lotka-Volterra type models prove to be unstable, and stability seems to be assured only by the presence of

particular controlling factors; for example by fairly strong intraspecific self damping, or by extremely efficient predators (Takeuchi, 1983).

If mutualism leads to instability, why is it so widespread (Boucher, 1982) in nature? In search of key-solutions for the paradox, different theoretical approaches have been developed.

Several authors (Sutherland, 1981, Pilette et al., 1987), in their investigations on community stability, pointed out the necessity of investigating system frameworks as wholes, because of the variety of roles played in them by the many components involved. In this line, we feel it is useful to analyze the effects produced by competitors and mutualists within natural communities. In doing so, two aspects require special attention.

First, the problem terms need to be clearly defined (see Addicott, 1981). The generic definition of mutualism, for instance, does not distinguish: (i) the type of association between species, which can be symbiotic or not; (ii) the mechanisms by which interactions, direct or indirect, are produced; (iii) the degree of dependence shown by species able to practice either obligatory or periodic forms of mutualism.

Second, complexity needs to be considered. Increased realism in models is sought by including several competitive and mutualistic species (Post et al., 1985), and species that influence the dynamics of the system, although they are not directly involved in those associations (Heithaus et al., 1980; Addicott and Freedman, 1984).

Methods

The investigations were carried out by means of analytical extensions of the loop analysis methodology and stochastic simulation. Specifically, the responses of equilibrium levels to changes in the growth rate of the species are determined. These responses are presented as "tables of predictions" for the moving equilibria. We use the phrase "moving equilibrium" as found in Levins

(1974): when the c parameters, assumed as constants in the system equation $dx_i/dt = f_i$ $(x_1, x_2, ..., x_n; c_1, c_2, ..., c_p)$, change at a rate slower than that of the x variable parameters, we are dealing with a system in moving equilibrium. The tables become tools for understanding (i) direct interaction versus indirect interaction (Lane, 1985) and (ii) interspecific processes with respect to stability.

It is possible to extend the qualitative analysis (details on the loop analysis principles are in the appendix) to predict how the system will behave in response to a variation of one or more components. Every model presents as many alteration entries as are the components belonging to it. The outcomes altogether form a table of predictions, that shows how "inputs" on variables' dynamical changes (growth rate increases) eventually affect the equilibrium values of all the components.

The table entries derive from the analysis of model's paths and feedbacks. A change in the equilibrium value of a generic jth component (∂X_j^* the star identifies the equilibrium value), produced by altering a parameter (∂c), is determined through the equation

$$\frac{\partial X_i^*}{\partial c} = \frac{\sum_i \sum_k \left[\frac{\partial f_i}{\partial c}\right] p_{ji}^{[k]} F_{n-k}^{[comp]}}{F_n}$$

applied $n \times n$ times (n is the number of model components) to give the elements of the table. The formula is interpreted as follows:

• The outer i-indexed summation is for all the functions f_i that include the altered parameter c ($\partial f_i/\partial c$).

• The inner k-indexed summation is for any open path $p_{ji}^{[k]}$ that leaves X_i towards the component X_j whose equilibrium value has to be computed. An open path is a circuit that connects two components without crossing any other component more than once. The length of the path is given by the k crossed components minus one ($k - 1$). The summation is necessary because, depending on the model, several paths might

exist of the same length, referring to the same pair of components.

- Each path is multiplied by the corresponding complementary feedback $F_{(n-k)}$. To evaluate a complementary feedback of a given open path, it is examined the subsystem of $n - k$ components with interconnections not included into the previous path.
- The resulting quantity is divided by the overall feedback F_n, computed only once for the whole system of n components.

In many instances, the calculation of feedback levels based on the algebraic signs of the loops remains indeterminate, as occurs for F_3 in the example described in the Appendix. In these cases, no conclusions can be reached regarding the stability of a system. What can be calculated, at most, are the conditions to which the coefficients involved must be subjected, so that stability will be assured.

The real values of a_{ij} must be known if these ambiguities are to be resolved, but this is difficult, because models of communities are often set up hypothetically, or express interactions hardly quantifiable. As a remedy, one might utilize stochastic simulations (Giavelli et al., 1988), in which the intensities of interactions between all the pairs of species in a given model are assigned values casually chosen from a prefixed conventional interval. In the models presented here, the values of coefficients a_{ij} refer to interval [0,1].

The stochastic process handles the links between variables in a totally independent way, and the assigned values are not constrained by the relative position of links and variables connected. This assumption might be somehow too aspecific, because it is expected that pairs of relations be correlated to some degree: a_{ij} shares with a_{ik}, and a_{ij} with a_{kj} the species i and j, respectively, while a_{ij} and a_{ji} share both. In an unknown system, however, with no references for the actual species involved, it would be quite subjective to trace back such dependencies, and consequently to weight values before assignment.

The computer procedure, repeated 10^5 times for each model, creates a large number of matrices, and analysis may be carried out on each one of them. The calculation of the percentage of cases found to be stable thus permits "measurement" of the probability of stability for the system under examination.

Results

The results are presented in Figures 2, 3 and 4. A total of 14 models were developed and their corresponding tables of predictions obtained. The stochastic simulation routine was applied to each model; the resulting probabilities of stability are reported in the figures.

The tables of predictions for each model are also shown; they give the direction of change of abundance of each species in a model. Every species has a row and column position: the row position designates the location of an external change ("positive input": a change in a parameter, e.g. fecundity or mortality) in such a way as to increase (+) the growth rate of the species abundance.

The symbols allocated within the tables denote the change in abundances for all the column-species of the system: (+) predicts an increase, (−) denotes a decrease, (0) expresses no change in the equilibrium level, (?) marks unpredictable results. Symbols between parentheses indicate that some uncertainties occur in those predictions, and the outcomes have to be considered on a chance basis.

It is important not to confound the damping/enhancing action of a species toward another species or itself (expressed by links in the graphs) from the network effects occurring to species, due to actions from outside upon each species (expressed by signs in the tables of predictions). It is not contradictory, for instance, that the diagonal of many tables has no negative signs, whereas the corresponding species are self-damped.

Details on loop analysis are in the appendix; Puccia and Levins (1985) give a complete description of the method.

Discussion

Direct and indirect relationships

The direct/indirect state characterizes relationships in models as well as in nature. One could easily justify the insertion of intermediate variables between any pair, or, by deliberately omitting a common resource, turn for instance a pair of independent predators into competitors. The moving equilibrium results will not change, but stability will. One always assumes that the hypothetical models faithfully mirror the reality, but one should be aware of the above aspect when building models and linking entities, which certainly is the major obstacle ecologists have to face in field-testing theory.

Browsing the recent literature it becomes apparent that no agreement has been reached among authors on how to define a certain interspecific relation as direct or indirect. This is particularly true for mutualism, but could equally apply to competition (see Neill, 1974; Davidson, 1980). Consider mutualism. From an intuitive point of view, direct processes should involve only cases in which two partners benefit each other without the involvement of other species. Conversely, the presence of one or more intermediate species could be thought of as a form of indirect relation (Addicott, 1984). In natural systems, examples of the first kind ("direct") typically refer to nutrient exchange (Kleinfeldt, 1978) and energy transfer (Glynn, 1976). Examples of the second kind ("indirect") include: protection of a species from a predator through the action of one partner (Bloom, 1975; Berger, 1980), increased availability of prey (Mares and Rosenzweig, 1976; Vandermeer, 1980), decreased competition resulting from the action of a mutualist (Osman and Haugsness, 1981).

While we do think that the terms competition and mutualism should be reserved only for species pairs directly interrelated, it is also true that agreement is still lacking on how to label the many forms of mediated negative/positive influence between species. In search of

a more precise definition of mutualism and its many varieties, DeAngelis et al. (1986, pp. 101–103) compiled a catalog of 46 positive dependencies, subdividing them into obligate, facultative, and indirect, involving intermediate agents. In addition, there are cases of species pairs without any connection at all between themselves (neither both nor one way) and yet referable to as "mutualists"; this happens through feedback among one or more of the remaining species.

Figure 2 compares three simple models with pairwise competition and mutualism. Schemes (2a)–(2d) refer to direct associations between species X1 and X2, whereas schemes (2e) and (2f) refer to indirect relations.

From the graphs of Fig. 2 (see the typologies of Fig. 1), X1 and X2 are competitors in models (2a), (2c), (2e), and mutualists in models (2b), (2d), (2f). With reference to these links, their tables of predictions (i) confirm the two way direct links shown in (2a) and (2b); (ii) clarify the links in (2c) and (2d) (in (2c) X2 damps X1 favoring its predator X3; in (2d) X2 defends the partner X1 from the assault of its predator X3); (iii) detect the hidden links in (2e) and (2f), where the two species are prediction-related, even though no connections appear to join them in any way. In these cases we say that X1 and X2 are indirectly associated, with competition in (2e), and mutualism in (2f).

It is interesting to note that X3 and X4, despite their appearing graphed links (mutualistic in (2e), competitive in (2f)), do not influence each other and themselves: a "positive input" on these entry rows produces no growth nor decrease in their equilibrium levels. The species are related in the models, but they result to be unrelated in the tables.

Another pair of "misleading" interactions is brought about by X2 and X3 in models (2c) and (2d): they turn out to be mutualist in (2c) and competitive in (2d). In fact one easily sees that table (2d) derives from the co-diagonal rotation of table (2c) as a direct consequence of the inverted roles played by X2 with respect to the other two species.

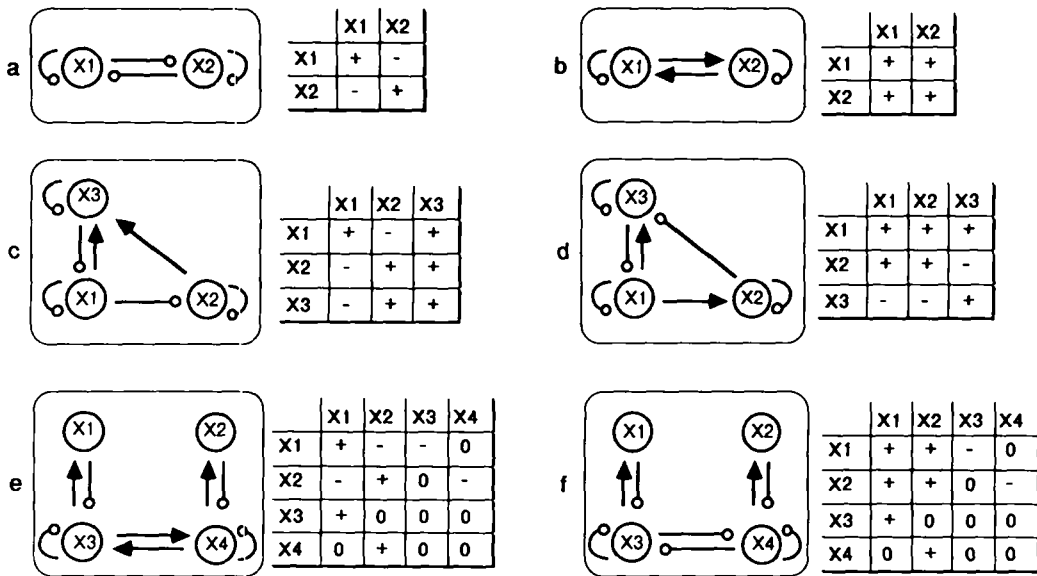A comparison among these six models and

Fig. 2. Models of simple communities with direct and indirect interactions between species X1 and X2. Direct, (a) and (c), and indirect (e) competition; direct, (b) and (d), and indirect (f), mutualism. On the right side of each model are the tables of predictions.

their tables of predictions demonstrates that greater complexity and connectivity yields relationships through feedbacks. These feedback-hidden relations alter our perception, based on well defined, directly observable interactions.

Competition and mutualism vs. stability

In ecology, one view of stability is the persistence of a community or ecosystem. This concept is not synonymous of static conditions or homeostasis: a system can be stable, in the sense of persistence, even if all of its components (species abundances, nutrient concentrations, etc.) and dynamics (predation rates, consumption rates, etc.) are changing, as long as none vanishes.

In two-species models, competition and mutualism seem to show the same properties of stability (Post et al., 1985), and theoretical studies do not explain why in nature cases of mutualism are so frequent (Heithaus et al., 1980).

The issue originally considered in the early stages of this study focused on the search for different stability properties between competition and mutualism in complex community models. Taking direct relationships into account, models were selected requiring only a single change to switch from competition to mutualism. We soon became aware that even with simple three-species models, altering a single relation did influence the entire model as a whole, according to the various combinations among feedbacks.

For example, we considered a community with two independent predators and one common self-damped prey species. Theoretical analyses carried out by Koch (1974) and Rescigno (1977) show that two predators of the same prey can coexist if the intensity of their use of the shared resource is identical: the model is stable only under particular circumstances. Our addition of competition between the predators caused the system to become unstable, while the substitution with

a — 48%

	X1	X2	X3	X4
X1	?	?	?	?
X2	?	0	0	0
X3	?	0	+	-
X4	?	0	-	+

c — 48%

	X1	X2	X3	X4	X5	X6
X1	(+)	(-)	?	?	-	+
X2	(-)	(+)	?	0	+	-
X3	?	?	0	0	0	0
X4	?	0	0	0	0	0
X5	-	+	0	0	+	-
X6	+	-	0	0	-	+

b — 50%

	X1	X2	X3	X4
X1	(+)	?	+	+
X2	?	0	0	0
X3	+	-	+	+
X4	+	0	+	+

d — 47%

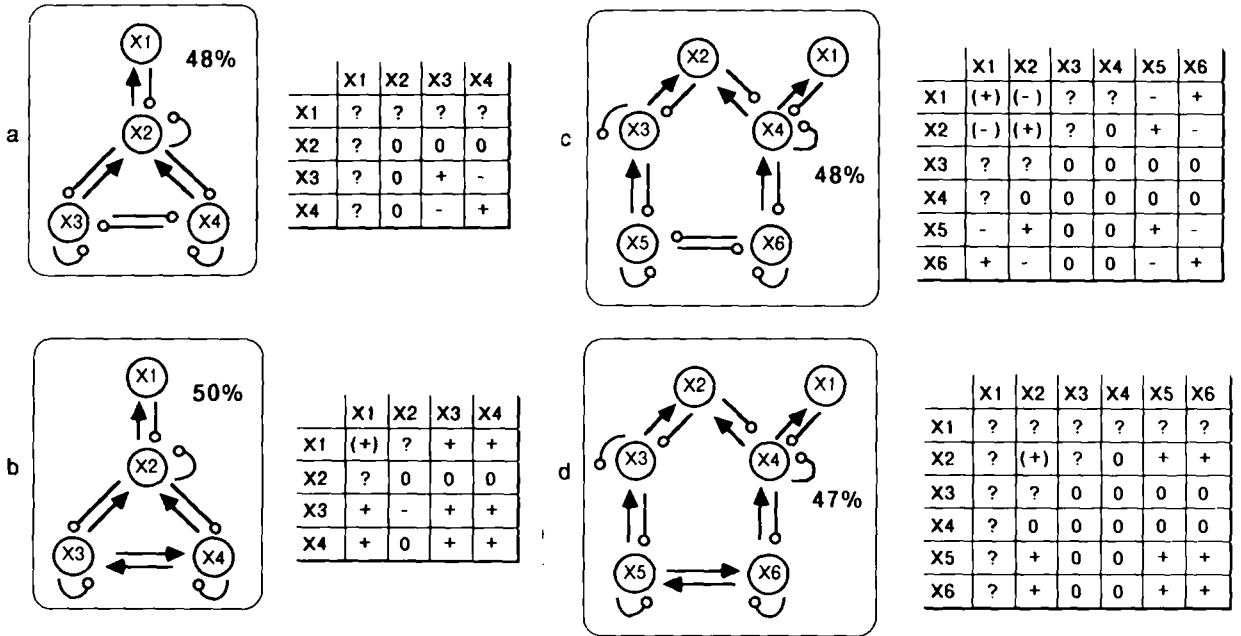|	X1	X2	X3	X4	X5	X6
X1	?	?	?	?	?	?
X2	?	(+)	?	0	+	+
X3	?	?	0	0	0	0
X4	?	0	0	0	0	0
X5	?	+	0	0	+	+
X6	?	+	0	0	+	+

Fig. 3. Models of mid-complex communities. Pair species X3-X4 and X5-X6 are "true competitors" in schemes (a) and (c), and "true mutualists" in schemes (b) and (d). The percentage of stability obtained with a stochastic algorithm is indicated within each model frame. The corresponding tables of predictions are also shown.

mutualism favored stability (from 0 to 36%). There was an explanation in terms of positive/ negative feedback balances, but the tables of predictions did not confirm the two prey species as mutualists. In this simple three-species system, no causation was deducible between mutualism and stability improvement.

In Fig. 3 two pairs of models with their associated tables of predictions are presented. These models represent mid-complex ecological communities and were chosen to exemplify how one small variation in the network can induce substantial changes in the tables of predictions without necessarily modifying stability.

Diagram (3a) shows a direct competitive interaction between X3 and X4, while in the analogous diagram (3b) the species are direct mutualists. Their tables of predictions confirm the competitive and mutualist relationships. Similarly, for the other two six-species models, X5 respectively competes (3c) or is a mutualist (3d) with X6. Their tables of predictions confirm

the relations drawn. For these four models the probability of stability ranges from 47% to 50% and thus does not reveal substantial differences between structures.

In (3a) species X3 competes with X4 and produces positive feedback at levels 2 and 3 (F_2 and F_3). In (3b) species X3 and X4 are mutualists and instability arises only in positive feedback at level 2 (F_2), while F_3 gains two negative feedback loops. Thus F_3 strengthens the first Routh-Hurwitz stability criterion (see the Appendix), but weakens the second, and stability depends on the balance of the relative strengths of the interactions, that is, the magnitude of the links. The simulation shows for model (3b) only a small, quite insignificant increment in the probability of stability.

The four-species models (and still more the six-species', with only a single interspecific link changed) produce ambiguous indirect relations. From the table for model (3a) species X1 enters in an indeterminate cause-effect relationship
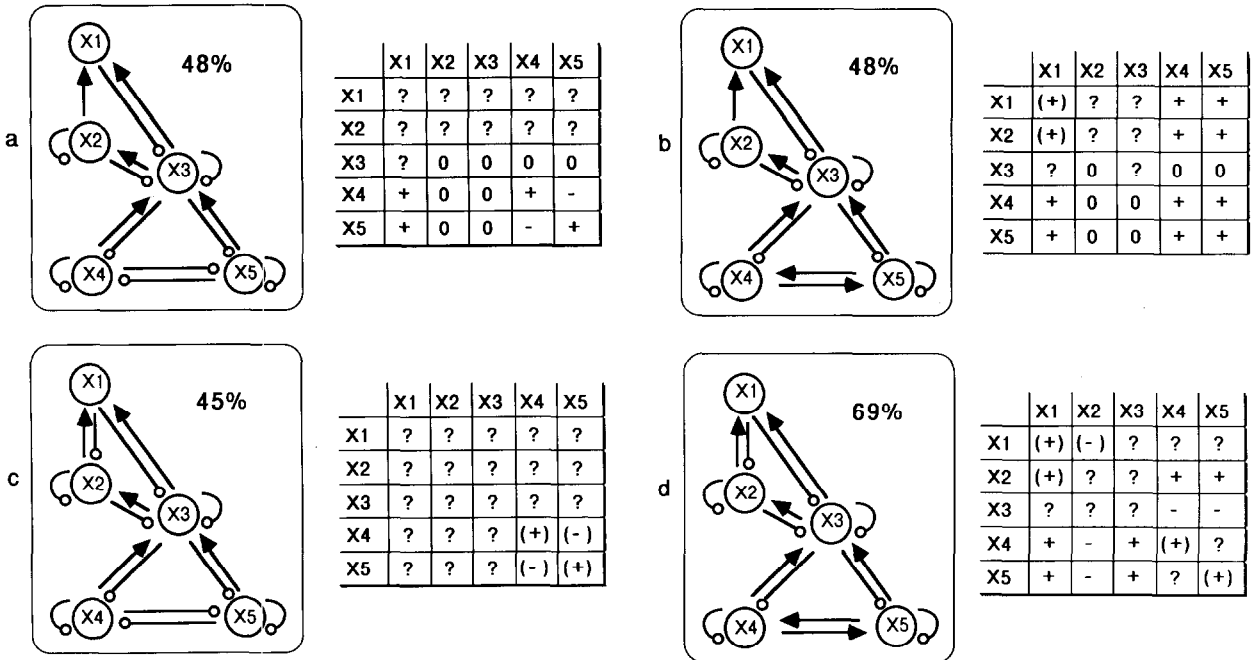
a   48%

	X1	X2	X3	X4	X5
X1	?	?	?	?	?
X2	?	?	?	?	?
X3	?	0	0	0	0
X4	+	0	0	+	-
X5	+	0	0	-	+

b   48%

	X1	X2	X3	X4	X5
X1	(+)	?	?	+	+
X2	(+)	?	?	+	+
X3	?	0	?	0	0
X4	+	0	0	+	+
X5	+	0	0	+	+

c   45%

	X1	X2	X3	X4	X5
X1	?	?	?	?	?
X2	?	?	?	?	?
X3	?	?	?	?	?
X4	?	?	?	(+)	(-)
X5	?	?	?	(-)	(+)

d   69%

	X1	X2	X3	X4	X5
X1	(+)	(-)	?	?	?
X2	(+)	?	?	+	+
X3	?	?	?	-	-
X4	+	-	+	(+)	?
X5	+	-	+	?	(+)

Fig. 4. Models of five-species communities. Species X4 and X5 are "true competitors" in scheme (a) and "true mutualists" in scheme (b), but, according to the predictions outcomes, only "possible competitors" in (c) and "possible mutualists" in (d). The probability of stability is indicated together with each structure.

with all the community species, including itself. The table for (3b) shows, instead, how X1 is a mutualist both with X3 and with X4. Such a community is characterized by one direct and two indirect mutualisms, but nevertheless its stability does not differ from that of (3a) where, according to the table of prediction, no mutualistic relationship can be demonstrated.

Also in (3c), characterized by a direct competition between X5 and X6, and in (3d) where these species are mutualists, the stochastic simulation reports no difference in stability probability. In model (3c) the table of prediction shows indirect mutualism in the couples X2-X5 and X1-X6, whereas the couples X2-X6 and X1-X5 are revealed to be indirect competitors. Furthermore in (3d) the X5-X6 mutualism, the counterpart to the competitive relation of (3c), determines two new indirect mutualisms in X2-X5 and in X2-X6, and the effect of an input on X1 towards all the community species becomes totally undetermined.

Typical multi-trophic communities are drawn in Fig. 4. Species X4 competes with X5 in model (4a) and is mutualist in (4b). The tables confirm these interactions, but reveal as many as 11 uncertainties in (4a) and only 5 in (4b) where an indirect mutualism can be found between X1 and X4 and between X1 and X5. The probabilities of stability are exactly the same. But with the other pair of models, which only differ in the presence of the damping effect of X1 over X2, stochastic simulation resulted in a probability of stability for model (4c), where species X4 and X5 compete, 24% lower than that of model (4d), where species X4 and X5 are depicted as mutualists.

A detailed analysis of the stability conditions for the two criteria shows that feedback F_3 is critical. Loops X3-X4-X5-X3 and X3-X5-X4-X3 provide potentially positive contributions in (4c), while the same loops become negative in (4d). Similarly, at the level of the second stability criterion, the same ambiguity of F_3 will render the positive conditions applied in this case

even more improbable. In fact, in expression $F_1^2 \cdot F_4 + F_1 \cdot F_5 - F_1 \cdot F_2 \cdot F_3 - F_3^2 > 0$, feedback F_3 is part of two negative sub-expressions. Excluding the quadratic element not affected by sign, it can be easily observed that $F_1 \cdot F_2 \cdot F_3$ will be negative if F_3 is also negative (in fact F_1 is always negative, while F_2 has only a few chances to be positive, because 5 two-species circuits out of 6 are negative). The only presence of this specific association between X4 and X5 gives negative loops in (4d) that contribute to satisfy the first as well as the second criterion for stability. We cannot however say X4 and X5 positively interrelated, because of ambiguities in the tables of predictions.

Conclusions

In order to investigate the effects on stability of direct competition and mutualism, three- to six-species models have been set up with observable interactions confirmed by the prediction tables. The stochastic simulations show that only little or no difference exists in probability of stability between models with competition and models with mutualism. The results would also confirm that these relations equally affect stability, as shown in two-species models' studies.

But in analysing the stability of complex communities, the "network effect" cannot be neglected.

First, community systems are characterized by links that generate indirect interactions (Levine, 1976; Vandermeer et al., 1985). In this context, changing, as we did, a single relationship in the same structure, activates different behaviors in terms of functional interactions among species, so that it becomes very difficult to ascribe stability properties of models to specific interactions. It does not seem possible to reach general conclusions, because (i) in models with both direct and indirect interactions, it is unclear if stability is related to the direct interactions only; (ii) if indirect interactions affect stability as well as direct interactions do, it remains undefined how much

stability belongs to each of these two functional mechanisms.

Second, models with species depicted as direct mutulists (and the same applies to direct competitors) lead to prediction tables that leave unknown in which way each partner affects the other (see model (4d)). There are, in fact, different paths, and different complementary feedbacks, that connect such variables. Some of these paths are characterized by negative effects, some others by positive effects: are the species to be considered mutualists?

Appendix

Loop analysis allows models be examined qualitatively, hence it is a tool for investigating cases where the magnitude of links between species is partially or completely unknown (difficulty of making measurements, unavailability of data, real interactions not suitable for quantifications, etc.).

Any system can be represented with a model. Its qualitative properties are represented in a diagram that graphically shows if and how each component is connected with the others. It is assumed that links "→" express favor relationships, while links "—o" denote contrast relationships. The models are based on links between variables that can be described by a set of linearizable equations.

In Fig. 1, the associations indicated by an arrow represent effects that favor the pointed entity (species), while those indicated by a circle represent inhibitory effects. The intensities of associations are expressed by means of coefficients a_{ij} *which indicate how much species "i" is* influenced by species "j". The entire group of coefficients forms the so-called "community matrix".

According to classical analysis, the study of the eigenvalues of the community matrix provides knowledge of the properties of stability, while loop analysis utilizes the concepts of positive and negative feedback. Positive feedback is set off when the compo-
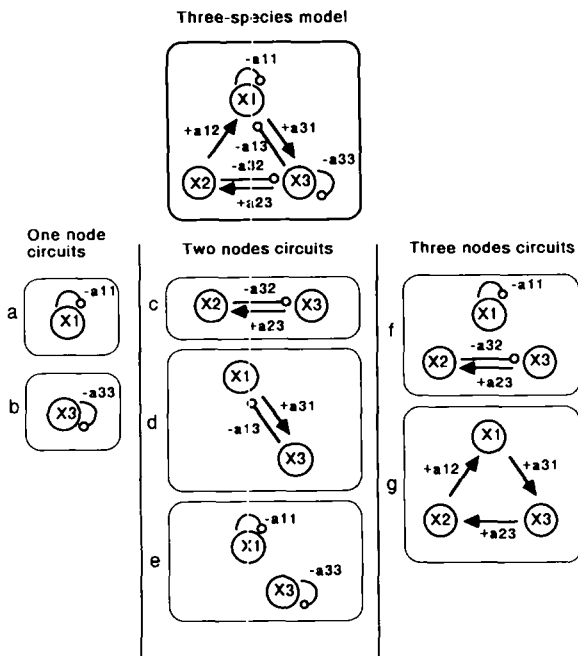
Fig. 5. A three-species model with all possible loops for positive and negative feedbacks. Schemes (a) and (b) are one-node loops that determine the overall feedback of first level F_1; schemes (c), (d) and (e) are two-node loops that determine the overall feedback at the second level F_2; schemes (f) and (g) are three-node loops that define F_3. Note that (e) and (f) are composed of two independent loops.

nents of a system interact so as to amplify the effects produced on the system by a perturbation; negative feedback, on the contrary, tends to moderate them. Since the stability of a given system is measured by its capacity to recover the equilibrium values of its variables after a displacement due to perturbation, we can deduce that a direct connection between negative feedback and stability exists. And since feedback effects are always associated with the presence of one or more functional loops linking the involved entities to the process of retroaction, loop analysis is able to reach conclusions on the stability of a system by examining it at the level of the loops that provoke internal feedback processes.

Fig. 5 illustrates a three-species model with all possible loops that determine both positive and negative feedbacks. In loop analysis, they are called closed loops which, following the direction of the interaction coefficients, return to the initial variable without crossing intermediate nodes more than once. The number of nodes making up a loop varies from 1 to N, N being the total number of components in a system.

In order to determine the stability of a given model, loop analysis utilizes circuits that are combinations of different unique paths: when the system complexity grows (i.e. more components and more links are implied in the model), the number of these circuits also goes up, and as a consequence the number of conditions to be met for the system be stable increases as well.

The model in Fig. 5 presents two one-node loops (5a), (5b) that determine the overall feedback of first level F_1, three two-node loops (5c), (5d), (5e) that determine the overall feedback at the second level F_2 and two three-node loops (5f), (5g) that define F_3. Rather than being closed circuits, (5e) and (5f) are composed of two independent loops: independent loops are loops that have no nodes in common; for example, in F_3 it would be incorrect to consider the one-node loop formed by species X3 and the two-nodes loop X2-X3, because they have X3 in common.

With respect to the feedback circuits, loop analysis dictates the conditions (or criteria) that must be satisfied in order to render the system stable.

The first criterion requires every feedback level be negative ($F_i < 0$, $i = 1,2..., N$). It is thus necessary to sum algebraically the products obtained from all loops that are part of a given F_i: the interaction coefficients a_{ij} are multiplied, a positive sign is given to the products obtained from the feedbacks formed by an odd number of independent loops (5a), (5b), (5c), (5d), (5g), and a negative sign is given to the products obtained from the feedbacks determined by an even number of loops, (5e),

(5f). On the basis of the example of Fig. 5, we have

$$F_1 = + [-a_{11}] + [-a_{33}] < 0$$

$$F_2 = + [a_{31} \cdot - a_{13}] + [a_{23} \cdot - a_{32}]$$
$$- [-a_{11} \cdot - a_{33}]$$
$$= - a_{31} \cdot a_{13} - a_{23} \cdot a_{32} - a_{11} \cdot a_{33} < 0$$

$$F_3 = + [a_{12} \cdot a_{31} \cdot a_{23}] - [-a_{32} \cdot a_{23} \cdot - a_{11}]$$
$$= a_{12} \cdot a_{31} \cdot a_{23} - a_{32} \cdot a_{23} \cdot a_{11} = ?$$

and since there is a three-node loop that generates positive feedback (5f), the sign of F_3 remains indeterminate: the system is stable only if the positive links intensity is lower than the negative links intensity that makes up level F_3.

The second criterion for stability states that the feedback intensity of the longer loops must not be too high with respect to that of the shorter loops. For a three-species system such as the one given in the example, this condition is expressed algebraically as $F_1 \cdot F_2 + F_3 > 0$. The same formula holds for a four-species system, while for systems with five or six variables the second criterion becomes $-(F_1 \cdot F_2 + F_3) \cdot F_3 + (F_1 \cdot F_4 + F_5) \cdot F_1 > 0$, or, after simplification, $F_1^2 \cdot F_4 + F_1 \cdot F_5 - F_1 \cdot F_2 \cdot F_3 - F_3^2 > 0$.

Acknowledgements

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