What is the role of predation on stability of natural communities? A theoretical investigation

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A basic question in ecology concerns the role of species interaction on dynamics of natural communities. In this framework, ecologists have considered predation, competition, mutualism, the three most important interactions, highlighting their specific effects on distribution and abundance of species, providing knowledge about phenomena like coexistence and extinction. This paper seeks to identify the effects of predation on stability of natural communities by mathematical models. Simple multispecies community models, organized in trophic levels, are analyzed by means of a qualitative technique, loop analysis, combined with a computer calculation procedure. Results do not support the hypothesis of predation as a stabilizing factor. Rather, the outcomes of the analysis suggest that predation may or may not stabilize a community. This depends on the predator's behaviour and on the network of the community.

Keywords: Stability; Feedback; Loop analysis; Simulation; Network; Lotka–Volterra systems.

Introduction

This article focuses on the stability of natural communities, one of the key concepts of community ecology. Both theoretical (May, 1973; Saunders and Bazin, 1975) and experimental (McNaughton, 1977; Lawlor, 1980) approaches have been used to investigate this theme. Most have been oriented toward the solution of the complexity-stability controversy, and, from a theoretical point of view, stability has been evaluated as a function of various parameters, the most common of which is the connectance (Gardner and Ashby, 1970; Somorjai and Goswami, 1972; Yodzis, 1980; Armstrong, 1982). Such an approach pays little attention to specific relations involving individual entities (Maertens, 1987) and how each contributes to the stability of the whole system.

By contrast, other ecological studies have emphasized the specific role of different types of interaction in affecting both structural and functional characteristics of natural communities. Considering the problem of coexistence, for example, several authors (Paine, 1966; Connell, 1975; Caswell, 1978) supported the idea of predation as a factor allowing coexistence; on the other hand studies centered on competition (Tilman, 1982) indicated that such interaction very often determines exclusion. More recently (DeAngelis et al., 1986), it has been suggested that even mutualism could play a peculiar and significant role in the development and organization of ecosystems.

In summary, it seems that each relationship behaves in a characteristic fashion with respect to some aspects of community ecology. Is this also true for stability? Do predation, competition and other species interactions contribute differently to the stability of a natural community?

This article examines the role of predation on stability using a theoretical approach. Other authors have addressed this issue. Levins (1975) stated that a predator (keystone predator) may

stabilize two competitors, and Yodzis (1976) showed that harvesting could alleviate competitive instabilities. In a previous work (Parrish and Saila, 1970; Cramer and May, 1971), however, a predator was only shown delaying extinction due to competitive instability. More recently, other theoretical evidence (Takeuchi, 1983; Takeuchi and Adachi, 1983) seems to confirm a possible stabilizing role of predators.

Looking at the dynamics of interacting populations in terms of feedback, predator-prey relationships produce negative feedbacks that should increase stability, unless the feedback is so strong and delayed that it produces time lag oscillations, but the question of stability of two species models versus multispecies community stability is far from being resolved.

Models presented here involve two, three and four species, organized in trophic levels. Such models are analyzed by a semi-quantitative procedure that combines loop analysis and a computer eigenvalue analysis.

Methods

Loop analysis (Levins, 1974) applies to communities at or near equilibrium. A loop model representing a natural community is a signed digraph in which vertices, that is the species, are connected by lines. Some of these lines end with an arrowhead, others with a circlehead. The former signifies positive or enhancing effect, while the latter indicates inhibition. A loop model of a predator-prey system shows two vertices connected by an arrowhead pointing to the predator and a small circlehead going from the predator to the prey, as shown in Fig. 1.

Associated with each link is a coefficient (a_{ij}), which is positive for an arrowhead and negative
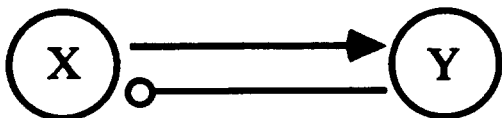
for a circlehead. These coefficients are obtained by linearizing near equilibrium the differential equations describing the rate of change of each species. A loop model is a pictorial representation of a Jacobian matrix (community matrix) whose eigenvalues determine the stability of the system. Eigenvalues are calculated by solving the characteristic equation $|A - \lambda I| = 0$, where A is the Jacobian matrix and I is the identity matrix.

Levins (1975) showed the correspondence between the coefficients of the characteristic equation and the feedbacks involved in the related signed digraph. Thus, stability analysis can be performed by evaluating all the feedbacks generated by loops connecting the variables of a model. Since not all loops involve the same number of variables, the analysis requires computation of different levels of feedback. The Routh–Hurwitz criteria translated in terms of feedback (Puccia and Levins, 1985) require that all the feedback levels must be negative for an equilibrium to be stable ($F_k < 0$, $k = 1,2,...,n$). Furthermore, negative feedbacks produced by longer loops must not be too strong when compared to those from shorter ones (for the models presented here this means $F_1F_2 + F_3 > 0$).

Pilette et al. (1987) utilized loop analysis to investigate the role played by various components of several natural systems with respect to stability of their model systems. They evaluated, in particular, the effects of entity removal on the stability of the remaining structure.

To examine the role of predation on community stability, a different strategy, based on the assigning of random values to matrix coefficients a_{ij} (Giavelli et al., 1988), is used in this work. For a given model 10^5 different combinations of values are assigned by the computer to the coefficients of the community matrix. Such values are conventionally chosen from within the standard interval [0 – 1]. Eigenvalue analysis is performed for each combination and the percentage of stable cases is assumed as the probability of stability for the given structure.

In addition, some of the models investigated were further examined, and the percentage of stable cases plotted as a function of the

Fig. 1. A signed digraph representing a predator-prey system (x = prey; y = predator).

magnitude of each single link involved in the structure itself. It was therefore possible to investigate the influence of the links' intensity on the stability of the entire model.

Results of this analysis are summarized in labelled diagrams shown in Figs. 2 – 4 below the graphs. Such diagrams display changes in probability of stability (scale from 0% to 100%) as a function of links values. The direction of the arrows express variation of link's intensity from 0 to 1. The diagrams were obtained in the following manner. For each link in a given model,
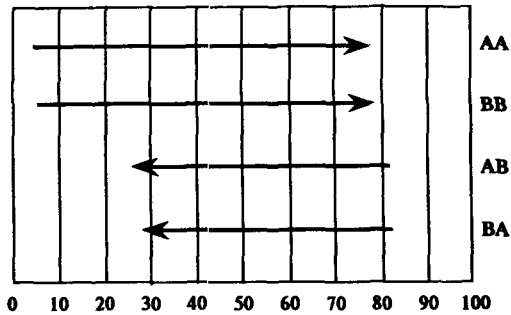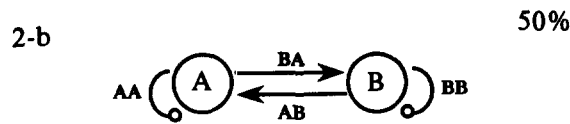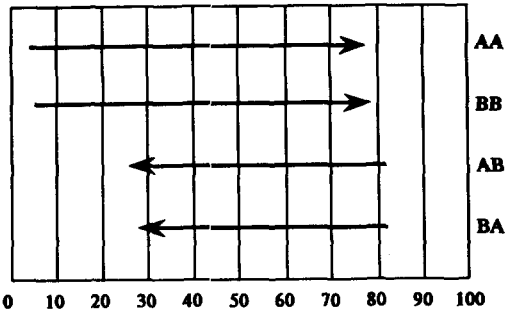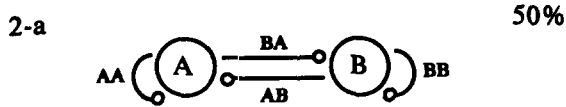
2-a 50%

2-b 50%

Fig. 2. Two species models: (2a) competition, (2b) mutualism and their percentage of stable cases. Diagrams below each model plot the probability of stability as a function of model links (see text for explanations).
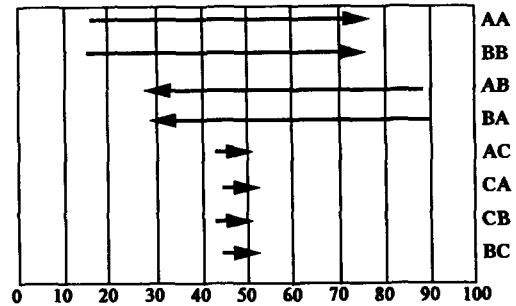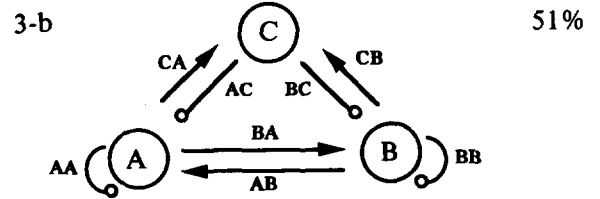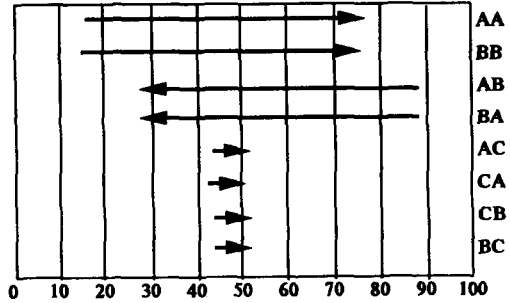
3-a 48%

3-b 51%
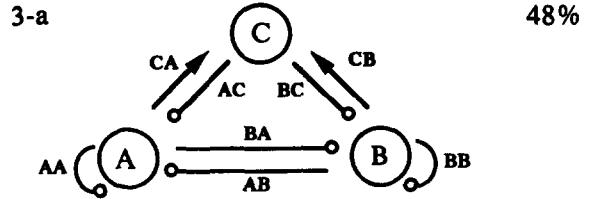
Fig. 3. A predator feeding upon two competitors (3a) and two mutualists (3b).

values assigned to its coefficient a_{ij} by the computer were grouped within 20 intervals of magnitude $(0.0 - 0.05, 0.05 - 0.1, ..., 0.95 - 1.00)$. For each interval a certain number of stable cases resulted from the matrix coefficient analysis, and, consequently, a frequency distribution of stable cases could be observed for every link as related to its intensity. Labelled diagrams used here summarize the frequency distributions obtained for the selected models.

Fig. 4. A three-trophic level community model with a top predator.

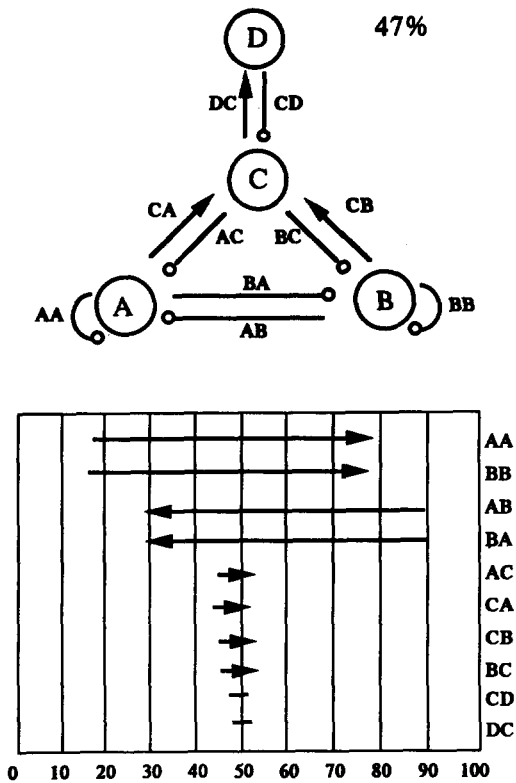Loop models discussed in this work represent simple hypothetical communities, and may be obtained through linearization of generalized Lotka–Volterra equations of the form (Granero-Porati et al., 1982; King and Pimm, 1983; Maertens, 1987)

$$\frac{dN_i}{dt} = N_i \left[r_i + b_{ii}N_i + \sum_{i\,=\,j\,=\,1}^{n} b_{ij} N_j \right]$$

where $b_{ii} = 0$ for predators (only hampered by their source of food) and $b_{ii} < 0$ for the prey species, according to a logistic growth.

However the same loop models presented here may be produced by more complicated equations, which account for many dynamical features of interspecific processes not considered in Lotka–Volterra systems (Giavelli and Bodini, 1990).

Results and discussion

Figures 2–5 show the models analyzed, with their percentage of stable cases in the upper right hand corners. The feedback calculation for selected examples is presented in the Appendix.

The simplest models investigated refer to interactions within a single trophic level involving two competitors (Fig. 2a) and two mutualists (Fig. 2b). In both schemes there are two levels of feedback: F_1 is negative, because of the self-damping terms $[AA]$ and $[BB]$, whereas the sign of F_2 remains ambiguous. Both mutualism and competition generate a two-node loop with positive feedback that contrasts with the self-limiting action in F_2, whose expression is

$$F_2 = -\{ [AA][BB] \} + \{ [AB][BA] \} \tag{1}$$

Matrix stability coefficient analysis gives 50% of stable cases for both these graphs. The labelled diagrams shown in Fig. 2 suggest that in both models the probability of stability increases as self-damping terms approach 1, and coefficients of interaction decrease, according to analytical conditions for a stable equilibrium, which require the product of intraspecific competition terms to be greater than that of interspecific processes (May, 1973; Berrryman, 1981; Post et al., 1985):

$$|-[AA][BB]| > |+[AB][BA]| \tag{2}$$

The two models depicted in Fig. 3 are derived from the previous pair, with the addition of a predator (C) feeding on both populations $(A$ and $B)$. Simulation, with 48% (model 3a) and 51% (model 3b), shows only a small, quite insignificant difference in the percentage of stable cases in comparison with competitive and mutualistic systems of Fig. 2. It suggests that no improvement in the probability of stability comes from the presence of the predator. Feedback analysis (see Appendix) enables us to interpret simulation outcomes. The predator adds two negative feedbacks at F_2. It can be negative even when condition (2) is not met. Yet, species (C) has increased the complexity (number of species) of

the systems, with respect to models of Fig. 2. A new level of feedback, F_3, must be considered. Its sign is unknown for model 3a, since two positive and two negative feedbacks belong to it, whereas it is negative in model 3b.

In the latter graph the three node loops produce negative feedbacks, and the first criterion for stability can be violated only through F_2. Are we allowed to say that the stronger the predation the higher the probability of stability for graph 3b should be? Such a conclusion does not hold if we consider the second criterion for stability. It must be $F_1F_2 + F_3 > 0$, and long loops (those which enter in the expression of F_3) with negative feedback increase the probability that oscillatory instability occurs.

In model 3a, the longest loops have positive feedbacks and the first criterion seems crucial for stability, though the sign of the second criterion is still unknown. If we now hypothesize that predation is strong enough (at least as strong as required for F_2 to be negative) the second criterion will possibly be met, but F_3 still would remain ambiguous and asymptotic instability could occur.

Models depicted in Fig. 3 suggest that a predator feeding upon two competitors or two mutualists introduces two negative feedbacks due to direct predator-prey relationships. They contrast, at level F_2, with positive feedbacks associated with competition and mutualism, and therefore have a stabilizing effect. However, at a higher level of feedback, the presence of a predator generates, through combinations of links, either positive feedbacks or negative feedbacks with time lags. Both types of feedback are destabilizing forces.

Matrix coefficient analysis of single links confirms the ambiguous role of species (C). Only small changes in the percentage of stable cases follow variations in the intensity of predation links ([AC], [CA], [BC], [CB]) from 0 to 1. Also, it seems that stability of models 3a and 3b greatly depends on the magnitude of links belonging to the subsystem at the lowest trophic level, where species are competitors or mutualists. Similar conclusions were drawn previously (Berryman, 1981) for a two competitor – one

predator system, analogous to model 3a, assuming equal predation on both prey. The outcomes of eigenvalue analysis, however, reveal that such a condition seems not strictly necessary and the strength of inter- and intraspecific competition is the most important factor for stability, besides any constraint imposed on the predator.

A more complex community (Fig. 4) is obtained by adding a terminal predator (D) to model 3a. Simulation gives 47% of probability of stability. Here too it seems that predation does not have a stabilizing action on the system. A detailed analysis of stability criteria (shown in Appendix) confirms such a conclusion. First of all it should be noted that the same feedback loops enter the expression of the second criterion for models 3a and 4; it means that the top predator is neutral with respect to the second condition for stability, and oscillatory instability occurs only if the subsystem [C-A-B] violates it. To avoid this, suppose there is a strong primary predator (C). This is not sufficient to guarantee stability to our model, and the first criterion must be carefully evaluated. The secondary predator (D) introduces more negative feedbacks at different levels, but, under the assumption of a very strong primary predator we made, action of species (D) at level F_2 is not important to ensure stability. In contrast, the stronger the predation on (C), the greater the probability that F_3 is negative, especially considering that predator (C) produces positive feedbacks and its prey experiences heavy predation. Although an extremely efficient top predator could be necessary to avoid a positive sign at the third level of feedback, instability is always possible through F_4. Only two feedback loops belong to F_4, and they have opposite signs. Predator (D) enters the composition of both loops, whereas the intermediate predator (C) is not involved at all. Rewriting F_4 as follows

$$F_4 = [DC][CD]\{-([AA][BB]) + ([AB][BA])\} \quad (3)$$

shows that the sign depends only upon the subsystem at the first trophic level. For F_4 the first criterion is met if and only if the inequality (2) is

verified. This condition is necessary for model 4 to be stable: is it also sufficient? If the product $[AA][BB]$ is greater than $[AB][BA]$ the sign of F_2 is negative, whatever the intensity of other feedbacks, and the first criterion for stability will be met. So it will happen for the second criterion. $F_1F_2 + F_3 > 0$ may be violated only through the negative factors: $-[AA][AB][BA]$; $-[BB][AB][BA]$. If we now consider the terms $+[AA]^2[BB]$ and $+[AA][BB]^2$, both belong to the expression of the second criterion. We can easily compare positive and negative feedbacks after rewriting them in the following forms:

(i) negative feedbacks: $-[AB][BA]\{[AA] + [BB]\}$

(ii) positive feedbacks: $[AA][BB]\{[AA] + [BB]\}$

Such a comparison enables us to conclude that condition (2) is sufficient to avoid oscillatory instability.

Unfortunately it is not possible to come up with an answer when we handle F_3 because of the three node loops, unless we consider equal predation (May, 1973; Berryman, 1981) of (C) upon (A) and (B). In such a case, condition (2) becomes necessary and sufficient to guarantee stability to model 4.

Simulation results (see table below the graph in Fig. 4) confirm the importance of the first trophic level, besides the hypothesis of equal predation. It suggests that stability is not sensibly affected by variations in magnitude of predation links. Moreover, the presence of a top predator imposes a further constraint on the community described in model 4 in comparison with that of model 3a: the subsystem of two competitors must be stable for the community to be stable.

Graphs depicted in Figs. 3 and 4 are only examples of the structural complexity which characterizes natural communities. Different structures could be stabilized by predators, as shown in Fig. 5. Model 5a refers to a community in which a predator feeds upon only one competitor. Here the probability of stability was not plotted as a function of the magnitude of the links, but feedback calculation justifies the increased percentage of stable cases in comparison with models 2a and 3a. The predator (C) introduces only stabilizing factors. It reduces the effect of competition in F_2, and yields the third level of feedback completely negative. Since the long loop in which (C) is involved ($[CA][AC][BB]$) is balanced in the expression of the second criterion, instability could be brought into the system only by competition between (A) and (B). A strong predator, contrasting the destabilizing action of interspecific competition in F_2 and in $F_1F_2 + F_3$, would increase the probability that model 5a is stable. One should be aware, however, that a predator would not be sufficient to guarantee stability, whereas stability of the subsystem $[A-B]$ automatically renders model 5a stable. Figure 5 also shows a three competitors community (model 5b, 21% stable) that is stabilized by a predator (model 4c, 41% stable).

The models presented here do not offer a univocal answer to the controversial issue of predation as a stabilizing factor in natural community. Rather, they suggest that the ecological features of predator could help to clarify the problem.

Model 5d shows a predator feeding upon two species of the subcommunity 5b. Simulation tells us that the difference in probability of stability between the two models is only 3%, whereas if the predator (C) preyed upon only one species (graph 5c) the resulting community would be more stable. The same consideration applies to models 3a and 5a; it seems that stability is favoured by the presence of specialized predators.

Since only prey species producing positive feedbacks, as competitors or mutualists, have been considered, the hypothesis of specialized predators as stabilizing forces has to be tested in cases in which the two preys form a predator–prey system. A linear food chain (model 5f) is obtained by adding a top predator (D) which feeds only upon predator (C), while in community 5g the terminal predator preys upon both the intermediate predator and its prey (A).
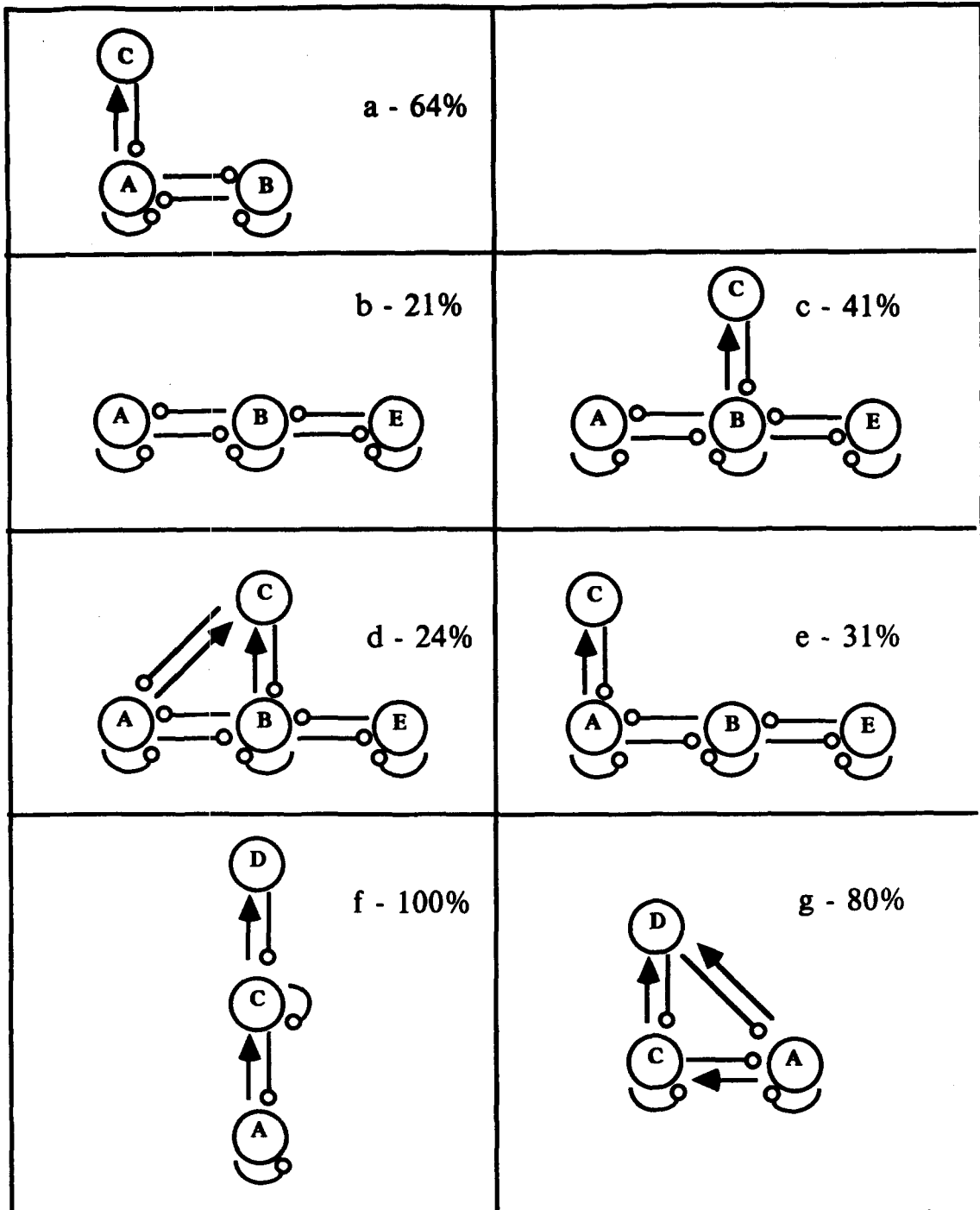
Fig. 5. Five models with different combinations of predation and competition. A predator feeding upon one competitor (5a); three competitors (5b); a predator feeding on one of the three competitors (5c, 5e); community in which two out of three competitors are preyed upon (5d); a linear alimentary chain (5f); a predator-prey system in which both species, in turn, are preyed upon by a top predator (5g).

The percentage of stable cases decreases by 20% when (C) and (A) are both preyed upon. Comparing this to model 5f, 100% stable, in which destabilizing forces are not present at all, shows that double predation produce two three-node loops, whose associated feedbacks can lead to either asymptotic or oscillatory instability (the first criterion can be violated as well as the second).

In a broad sense, generalized predators feeding upon interacting species decrease the probability of stability, because they render networks rich in long loops that introduce instability at different levels. Such a conclusion is in agreement with results obtained by other authors (Hubble, 1973; Granero-Porati et al., 1982).

Another aspect that seems to affect stability is food preference, an issue previously investigated mostly within the framework of predator-mediated coexistence (Lubchenco, 1978; Vance, 1978; Berendse, 1985). Models 5c and 5e both have a specialized predator, and the only difference between the two communities is the prey species involved. This yields a difference of 10% in the probability of stability. Different choice of prey can activate different feedbacks and, consequently, affect stability. This greatly depends on the structure of the sub-community in which the prey is embedded.

Conclusions

To evaluate the effects on stability of natural communities of predation, several models were analyzed using loop analysis combined with computer simulation. Although loop analysis allows only qualitative analysis of models, it enables us to discriminate between stabilizing and destabilizing factors in community models.

For models presented here predation does not have a univocal role. Sometimes it promotes stability, sometimes it does not. This ambiguity suggests that the network effect plays an important role on dynamics of species when they interact within complex communities. However an increased percentage of stable cases was found in those models characterized by specialized predators, whereas generalized predators often introduce destabilizing factors like positive feedbacks and negative feedbacks with time lag. Also, other ecological features, e.g. food preference, seem to complicate the problem, and the role of a predator should be evaluated case by case. Discriminating between predators on the basis of their ecological characteristics may help in clarifying their effect on stability of natural communities. The models discussed here focus mainly on the effects of interconnections on community stability rather than on the importance of the form of interactions. Increasingly complex models, however, need to be investigated before coming up with any generalization. For example a more detailed description of the relationship between the predator and its prey, as in cases of different functional response of predators to prey density, an issue largely investigated (Armstrong, 1976; Hassel, 1978; Armstrong, 1979), should be included in community models. Also a deeper analysis becomes necessary to interpret, from an ecological point of view, the outcomes of even simple models.

Finally, some of the models investigated raise the problem of "stability at one trophic level versus web stability" (May, 1973), which will be discussed elsewhere.

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Appendix: Feedback calculation

Model 3a

$$F_1 = -[AA] - [BB] < 0$$

$$F_2 = +[AB][BA] - [AA][BB] - [AC][CA] - [CB][BC] = ?$$

$$F_3 = - [CA][AC][BB] - [CB][BC][AA] + [AC][BA][CB] + [CA][BC][AB] = ?$$

$$F_1F_2 + F_3 = -[AA][AB][BA] + [AA]^2[BB] + [AA][CA][AC] - [BB][AB][BA]$$
$$+ [AA][BB]2 + [BB][CB][BC] + [AC][BA][CB] + [CA][BC][AB] = ?$$

Model 3b

$$F_1 = -[AA] - [BB] < 0$$

$$F_2 = +[AB][BA] - [AA][BB] - [AC][CA] - [CB][BC] = ?$$

$$F_3 = -[CA][AC][BB] - [CB][BC][AA] - [AC][BA][CB] - [CA][BC][AB] < 0$$

$$F_1F_2 + F_3 = -[AA][AB][BA] + [AA]^2[BB] + [AA][CA][AC] - [BB][AB][BA] + [AA][BB]^2$$
$$+ [BB][CB][BC] - [AC][BA][CB] - [CA][BC][AB] = ?$$

Model 4

$$F_1 = -[AA] - [BB] < 0$$

$$F_2 = +[AB][BA] - [AA][BB] - [AC][CA] - [CB][BC] - [CD][DC] = ?$$

$$F_3 = -[CA][AC][BB] - [CB][BC][AA] + [AC][BA][CB] + [CA][BC][AB] - [DC][CD][AA]$$
$$- [DC][CD][BB] = ?$$

$$F_4 = +[CD][DC][AB][BA] - [CD][DC][AA][BB] = ?$$

$$F_1F_2 + F_3 = -[AA][AB][BA] + [AA]^2 [BB] + [AA][CA][AC] - [BB][AB][BA] + [AA][BB]^2$$
$$+ [BB][CB][BC] - [AC][BA][CB] - [CA][BC][AB] = ?$$

Model 5a

$$F_1 = -[AA] - [BB] < 0$$

$$F_2 = +[AB][BA] - [AA][BB] - [AC][CA] = ?$$

$$F_3 = -[CA][AC][BB] < 0$$

$$F_1F_2 + F_3 = - [AA][AB][BA] + [AA]^2 [BB] + [AA][CA][AC] - [BB][AB][BA] + [AA][BB]^2 = ?$$