The Qualitative Analysis of Community Food Webs: Implications for Wildlife Management and Conservation

Antonio Bodini, Giovanni Giavelli and Orazio Rossi

Institute of Ecology, University of Parma, Viale delle Scienze, 43100 Parma, Italy

Biodiversity, the array of organisms living on earth, is experiencing now, more than ever, the uncontrolled assault of human activities. The consequence of this aggressive behaviour is that populations of plants and animals are being decimated across a broad geographic scale. Reducing the current rate of biodiversity loss has become an urgent task, and contributions are expected from many disciplines: ecology, economy, social sciences, political sciences and others. The ecological side of this challenge is filled with many unresolved issues still open to research, among which the understanding of how populations react to environmental stress occupies a central place.

In this article the role of community structure as a factor conditioning the response of populations to environmental disturbances is discussed. Four community food webs are examined through the use of a qualitative technique called loop analysis. Results obtained suggest that the structure of the interactions can be an appropriate locus of explanation for patterns of population response to environmental stress. Yet, complex functional networks may show counterintuitive behaviours that challenge our comprehension of effects of disturbances upon ecological communities, and yield results of interventions aimed to protect wildlife uncertain.

Keywords: conservation, environmental restoration, biodiversity, food webs, network, loop analysis.

1. Introduction

Biological diversity is commonly perceived as a value, and there is no doubt that mass extinction of plant and animal species represents one of the most pressing problems of the present environmental crisis. Preservation of biodiversity is among the prime objectives to be pursued in the close future for preserving the very sustainability of Earth. To prevent major losses of biodiversity, prompt interventions are required, but, to be effective, they must be supported by a solid ecological understanding of natural populations' history. In particular, scientists should strengthen the ability to understand and, whenever possible, to predict the effects of human impacts on ecosystems. Only by gathering a detailed knowledge on how populations respond to perturbations, and to what extent they are able to withstand disturbances, ecologists will be able concretely to

support decision makers, planners and government agencies in their attempts to launch adequate policy measures to curb and, eventually, constrict, human activities so as to reduce their interference with the habitat.

Clues to answers to questions about the way organisms and populations respond to environmental stress certainly lie in their physiology and genetics; however, these may not be the only areas to be explored for the comprehension of mechanisms governing the dynamics of coenoses facing disturbed habitats. Specifically, the condition of being functionally connected with many other species in natural communities conditions the response of populations to disturbance. This statement has received impetus from the increasing amount of evidence concerning the role of community structure in population dynamics (Brown *et al.*, 1985; Carpenter, 1988; McQueen *et al.*, 1989; Carney, 1990).

A natural community may be seen as an ecological network (Patten, 1991), of which predation, competition, mutualism and parasitism are the main functional determinants. Because of the multiplicity of interrelations, any variation experienced by one of the components may spread out, with consequences on other species. This view roots in a pioneer investigation of the Italian zoologist Lorenzo Camerano (1880; cf. Cohen, 1992), but only in the last two decades it has become more than a fascinating intuition, and acknowledged as plausible hypothesis of the functioning of ecosystems (Kerfoot and Sih, 1987). Accordingly, when an environmental cause of stress modifies the life history of a population, and changes some of its ecological attributes, there may be effects in the community beyond the target of the perturbation. Essential features of this network effect cannot be grasped by looking at populations as isolated entities, and studies on natural communities as functional wholes are required.

This paper attempts to frame the problem of understanding the consequences of anthropogenic disturbance on coenoses through the analysis of interconnections. It emphasizes the role of ecological networks as cause of diffusion of environmental stress, and elucidates in what sense the "position" that a population occupies within a community is crucial for its response to exogenous impacts.

Studies on community structure have mainly focused on the effects of species' introduction and deletion (Paine, 1980; Pimm, 1980; Elser and Carpenter, 1988). This approach may provide valuable contributions to conservation science: very often human impacts are so severe as to cause extinction of plants and animals. It occurs, for example, when indiscriminate harvesting (Claro, 1991), rapid and uncontrolled deforestation (Parsons, 1989), dispersal of hazardous chemicals (Evans and Nettleship, 1986) or introduction of exotic species (Dobson, 1988, Coblentz, 1990) take place. Human interventions impose sudden structural changes to communities that may be followed by dramatic readjustments, leading to a cascade of further extinction (Greenwood, 1987; Ligtvoet and Witte, 1991).

This paper does not focus on those environmental disturbances that cause structural transformations in natural communities; rather, it considers the many forms of stress that exert continuous pressure on communities with changes in populations' growth rate. The interference of pesticides, acid deposition, increased carbon dioxide level or heavy-metal concentrations produces changes in parameters governing the growth of plants and animals, such as mortality, fecundity or efficiency to exploit resources. Growth alterations, in turn, do reflect on abundance and turnover rate of populations, with consequences on their chance of survival. In this article, the qualitative analysis of community structures, performed through a technique called loop analysis, is proposed as a research option to understand the role of ecological networks, and to predict long-term effects on species embedded in complex ecological coenoses of parameter changes
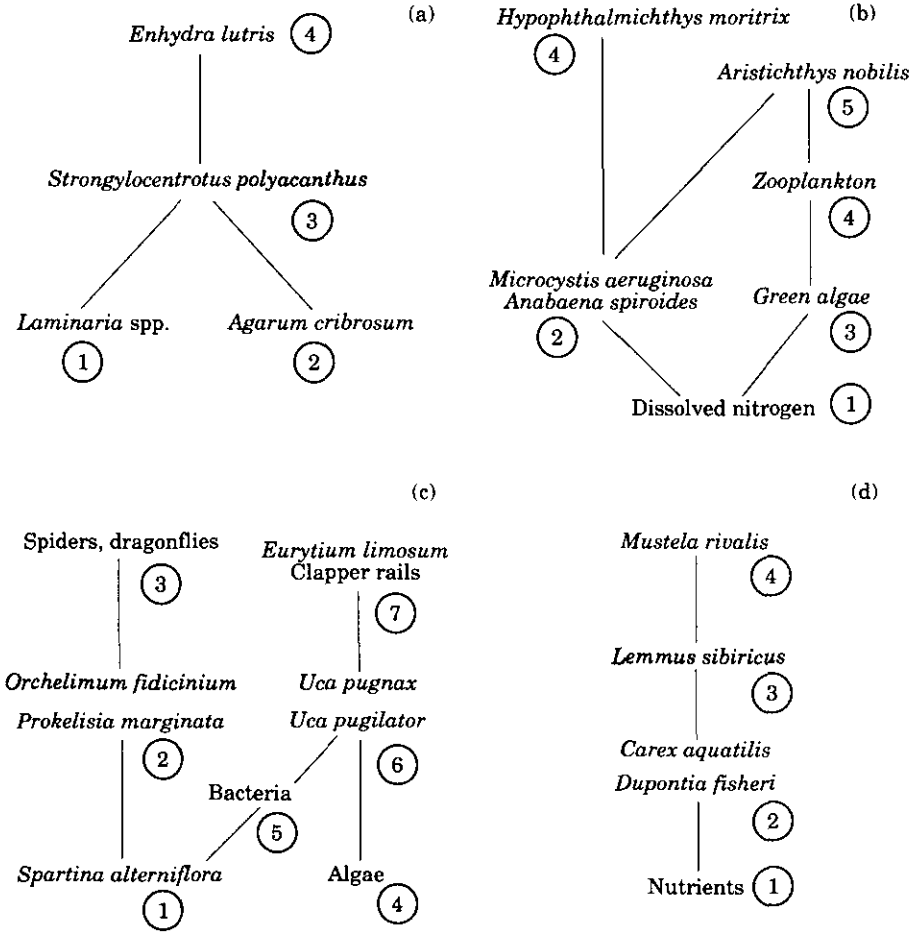
Figure 1. Community food webs: (a) Western Aleutian Islands (Alaska); (b) East Lake (China); (c) salt marsh (Georgia, U.S.A.); (d) Arctic zone.

due to environmental disturbances. Four community food webs are taken as examples of applications, and implications for management and conservation are discussed.

2. Materials and methods

Four communities described in the literature have been chosen and represented as schematic food webs (Figure 1). These will serve as starting points for the construction of signed digraphs for the analysis.

2.1. FOOD WEBS

In the Western Aleutian Islands, between the North Pacific Ocean and the Bering Sea, the nearshore community is essentially a three trophic-level structure (Estes *et al.*, 1978). The primary producers are dominated by two algae groups, namely the association *Laminaria* spp. and the species *Agarum cribrosum*. Next up the food chain is the sea urchin *Strongylocentrotus polyacanthus*, that serves as source of food for a predator, the sea otter *Enhydra lutris* [Figure 1(a)].

Miura (1990) described the pelagic community of East Lake, an eutrophic body of water in the middle basin of the Yangtzi River, China. Blue–green algae, chiefly *Microcystis aeruginosa* and *Anabaena spiroides*, compete with green algae for dissolved nitrogen. Green algae, in turn, are fed upon by zooplankton, i.e. rotifers, copepods and cladocerans. The web is completed by a phytoplankton feeder, the silver carp *Hypophthalmichthys moritrix*, and by an omnivorous plankton feeder, the bighead carp *Aristichthys nobilis* [Figure 1(b)].

A more complex web is found in some salt marsh ecosystems of Georgia, U.S.A. Teal (1962) presented a simplified structure of the community, that matches the scheme proposed by Cohen (1978). Primary production is sustained by *Spartina alterniflora* and by the algae living in the marsh. *Spartina* sustains the grasshopper *Orchelimum fidicinium* and suffers from the pressure of a sucking insect, the plant hopper *Prokelisia marginata*. Herbivorous insects are preyed upon by secondary consumers, such as spiders and dragonflies. A relevant part of the available energy flows through the detritus chain, essentially based on decomposition of *Spartina*. Bacteria play a central role in this process, and they represent a source of energy for detritus–algae feeders like the crabs *Uca pugilator* and *Uca pugnax*. The mud crab *Eurytium limosum* and clapper rails are conspicuous consumers of detritus–algae feeders [Figure 1(c)].

Arctic communities are simpler than those living in other less-physically constrained environments. Batzli (1983) indeed considered simple trophic structures involving the brown lemming *Lemmus sibiricus*, feeding mainly on monocotyledons and mosses (*Carex aquatilis, Dupontia fisheri, Euriophorum* spp.). Other important components of the food chain are nutrients in the soil, and the weasel (*Mustela rivalis*), a predator of lemmings [Figure 1(d)].

2.2. SIGNED DIGRAPHS

The food webs of Figure 1 are not collections of hierarchically inter-linked populations; in several cases populations are lumped into compartments, defined trophic species (Cohen *et al.*, 1990) sharing diet and predators. Since this work investigates the role of interconnections on the response of communities to environmental stresses, the use of trophic species instead of populations does not affect the conclusions. In addition, it has to be noted that the clumping of populations into compartments is a well-accepted practice in ecological investigations (Levitan, 1987).

The specified food webs provide the necessary information to draw the corresponding signed digraphs. Loop analysis utilizes circles for variables (populations or trophic species), and has two kinds of links: when a component enhances the growth rate of another component, as a prey species does its predator, an arrow leaves the prey toward the predator, while a link ending with a circle head symbolizes the negative effect exerted by a predator on the rate of change of its prey. Loop analysis is a qualitative technique, so the magnitude of interactions needs not to be specified, only their signs: positive for arrows and negative for circle heads. A simple resource–consumer system is diagrammed in Figure 2.

Figure 3 shows the models obtained from the structures of Figure 1. These schemes are not mere translations of food webs into a signed digraph: a food web indicates only direct trophic connections between components, but it does not specify the dynamics of the interactions, better represented by a set of differential equations for the rate of change of the variables. Signed digraphs come directly from these equations.
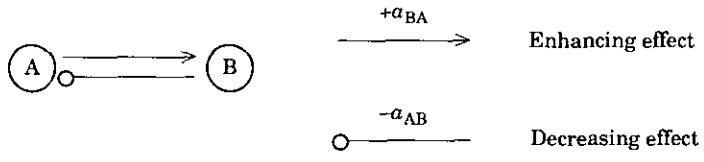
Figure 2. Signed digraph of a predator–prey interaction (A = prey species, B = predator).
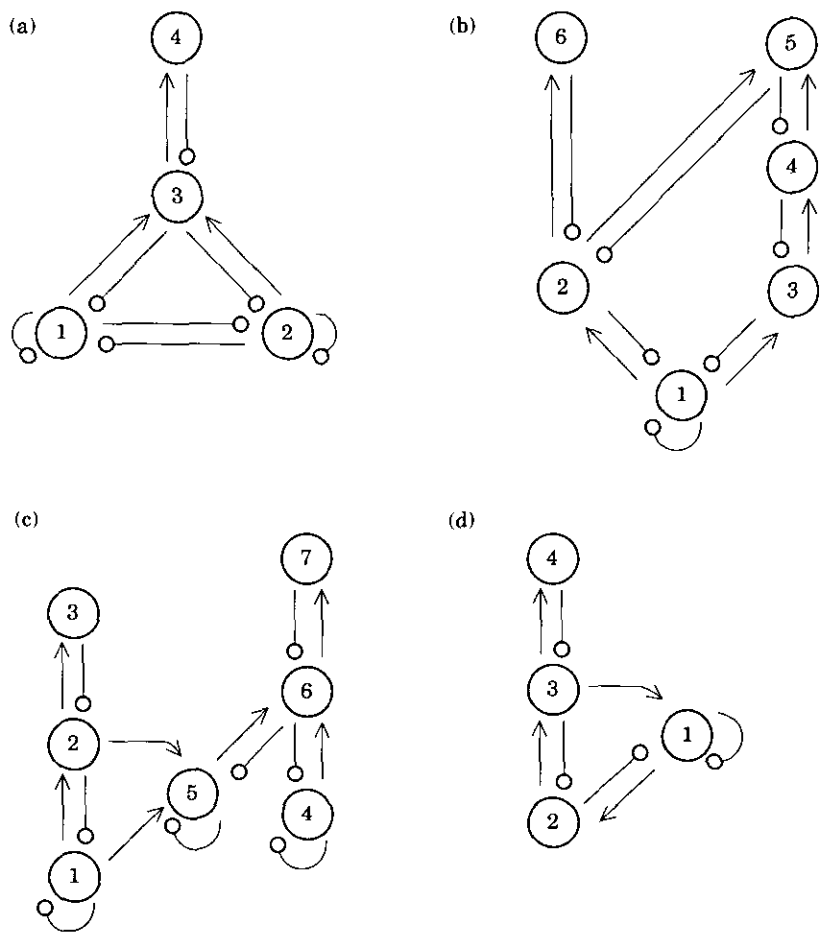

Figure 3. Loop models describing interactions between the components of food webs of Figure 1.

A self-limiting rate of change is assumed for basal variables (Yodzis, 1988). In signed digraphs, a self-limiting growth rate takes the form of a negative link connecting a variable with itself. In the case of abiotic compartments, like nutrients in Figure 1(b) and (d), the self-damping reflects a continuous supply coming from outside the system. When non-self-reproducing variables are omitted, as in the case of nutrients in Figure 1(a) and (c), their self-damping is transferred to the next compartments (primary producers, bacteria).
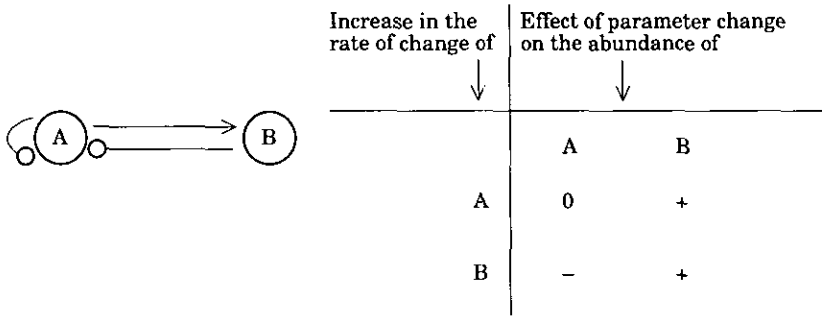
Figure 4. Table of predictions for a simple predator–prey system with self-damped prey.

In Figure 1(a), strong competition for space or light may occur at the first trophic level, hence the two components belonging to it are depicted as inhibiting each other's growth rate. Figure 3(c) shows a positive direct link from herbivorous insects to bacteria, because the decomposition of *Spartina* is enhanced by herbivores. Actually, the process occurs at expense of dead material, whose accumulation is accelerated by the feeding activity of herbivores. In Figure 3(d) a positive direct link connects lemmings to nutrients: rodents provide a considerable input of material to the soil (Batzli, 1983).

When the rate of change of a component is altered by some environmental cause, there may be consequences upon its abundance, as well as others. By qualitatively analysing the structure of the interactions in a signed digraph, it is possible to predict whether the new abundance of each component is expected to increase, decrease or remain unchanged.

The mathematical details of the technique used to make predictions are omitted here because they have been exhaustively reported by Puccia and Levins (1985); the foundations of the algorithm are presented briefly in the Appendix. Loop analysis differentiates between parameter changes that increase the growth rate of variables (positive inputs) and parameter changes that decrease it (negative inputs): conventionally, the calculation is performed by considering positive inputs only, and the results summarized in tables of predictions (Figure 4). Predictions for negative inputs are easily obtained by simply reversing the signs of the table.

The entries in a table denote changes expected in the abundance of all the species column of the community when a species row is affected by a parameter input: [+] predicts an increase, [−] predicts a decrease, [0] means no change expected in the level of that component. Question marks [?] express uncertainties due to either multiple pathways or subsystems with both positive and negative feedbacks. The tables of predictions for the selected structures are grouped in Figure 5.

3. Community response to parameter changes and implications for management and conservation

3.1. WESTERN ALEUTIAN ISLANDS COMMUNITY

Figure 5(a) shows changes in populations' abundance brought about by alterations in parameters governing the growth rates of species in this coenoses. The row and the column corresponding to the top variable are filled with question marks, due to the presence of multiple pathways of interaction with opposite effects. It is possible to solve most of the ambiguities by making assumptions concerning the dynamics of the model.

(a)

	1	2	3	4
1	+	−	0	?
2	−	+	0	?
3	0	0	0	?
4	?	?	?	?

(b)

	1	2	3	4	5	6
1	0	0	+	0	+	−
2	0	0	0	0	0	+
3	−	0	+	0	+	−
4	0	0	0	0	+	−
5	−	0	+	−	+	−
6	+	−	?	+	?	?

(c)

	1	2	3	4	5	6	7
1	+	0	+	0	+	0	+
2	0	0	+	0	0	0	0
3	+	−	+	0	?	0	?
4	0	0	0	+	0	0	+
5	0	0	0	0	+	0	+
6	0	0	0	0	0	0	+
7	0	0	0	+	+	−	+

(d)

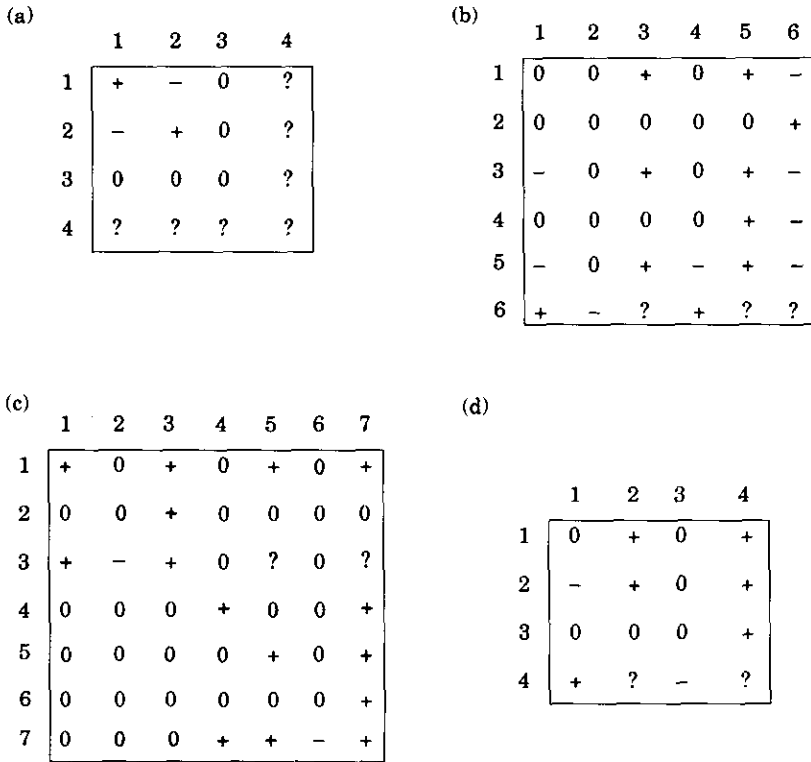|	1	2	3	4
1	0	+	0	+
2	−	+	0	+
3	0	0	0	+
4	+	?	−	?

Figure 5. Tables of predictions for the signed digraphs of Figure 3.

Bodini (1991) showed that in a community model like that of the graph in Figure 3(a), local stability primarily depends upon the balancing of intra- and interspecific processes at the bottom of the trophic hierarchy. In particular, the product of self-damping terms must be greater than that of interspecific processes. This condition is necessary but not sufficient to assess stability; for a locally-stable community, therefore, it is necessary that $[a_{11}a_{22}] > [a_{12}a_{21}]$. Since these two terms act as complementary feedbacks (cf. Appendix) for the path "sea urchin–sea otter", if the above inequality holds, any positive parameter change entering the system through the primary consumer would increase the sea otter's abundance, while a positive input from top would reduce the sea urchin's.

Algae populations are influenced by parameter changes of the secondary consumer, because indirect interactions between the top and bottom of the web are established by the presence of sea urchins. Predictions of expected changes in the abundance of algae groups are, however, uncertain, since inputs on the sea otter reverberate on basal variables by following two paths with opposite effects. For instance, the fate of variable No. 1 (*Laminaria*), can be summarized as follows: a positive input to the predator percolates along (No. 4)—o(No. 3)—o(No. 1) and (No. 4)—o(No. 3)—o(No. 2)—o(No. 1). The former pathway increases the abundance of *Laminaria*: it utilizes the self-damping on *Agarum cribrosum* as complementary feedback. The alternative path reduces the level of No. 1: its complementary feedback is − 1 (cf. Appendix). Since the negative pressure of the sea otter on the growth of the primary consumer ($−a_{34}$) belongs to both paths, one needs to know whether $[a_{13}a_{22}]$ is greater or less than $[a_{12}a_{23}]$.

	1	2	3	4
1	+	−	0	+
2	−	+	0	+
3	0	0	0	+
4	+	+	−	+

Figure 6. Table of predictions for the Western Aleutian Islands model, obtained by assuming a locally stable community and no food preference by the herbivore No. 3 (cf. text for details).

If the sea urchin exploits the two resources with the same efficiency (no food preference), under the hypothesis of a system locally stable, the self-damping $-a_{22}$ would likely render the left term of the inequality greater than the right term, which includes the competitive inhibition coefficient $-a_{12}$. Consequently, the net effect of a positive parameter change to the sea otter on the abundance of No. 1 (and No. 2, being the system symmetrically structured) would be an increase. The same assumptions of a locally-stable community and a primary consumer with no food preference bring to an increase of sea otter level for positive input to it and to algae groups. According to these conclusions, a new table of predictions is produced (Figure 6).

There are two most striking results from the table of predictions: (1) the sea urchin abundance does not change, except for inputs to its predator; (2) external impacts always emerge as changes in the level of the top species, no matter what population is perturbed. The sea urchin is protected against effects of external perturbations, since inputs on three (the primary producers and the herbivore) out of four components do not affect its abundance. On the contrary, the sea otter seems vulnerable to outside pressure on the community.

If a toxic substance killing *Laminaria* is released into the environment, this negative input reverberates on the other components, with consequences predicted by the first row of the table (the signs must be reversed). *Laminaria* and the sea otter are expected to decrease, the sea urchin remains unchanged, while the other algae population is predicted to increase.

The biological explanation that justifies these predictions is, in terms of cause–effect mechanisms, that the initial decrease of *Laminaria* diminishes the abundance of the sea urchin; such a reduction percolates up to the secondary consumer, whose level decreases, since there is not enough food to maintain the same amount of individuals. Fewer sea urchins are eaten by predators: the lower predation counterbalances the reduction in food supply, and the population returns to the previous level. Consequently, *Laminaria*, whose decrease initially could be compensated for the reduced number of primary consumers, is now exploited at the same rate as that when the community was perturbed, and its abundance remains low.

Analogous considerations apply to the other path through which the negative input to No. 1 spreads out in the community. The initial decrease in No. 1 improves the competitive role of the other primary producers; their higher abundance means more food for sea urchins, whose increment provides conditions for raising the abundance of the sea otter. As a consequence, sea urchins experience heavier predation, and their level drops; *Agarum cribrosum* is exploited less intensely, and its level remains high, with negative consequences on the abundance of *Laminaria*.

Effects along the two paths act simultaneously in the whole community; they have been discussed separately for ease of explanation. As it has been shown, however, the intuitive interpretation of mechanisms at work in the community agrees with the predictions from the mathematical analysis of the loop model: *Laminaria* decreases, *Agarum* is augmented, *Strongylocentrotus polyacanthus* remains unchanged, *Enhydra lutris* level is unpredictable [Figure 5(a)].

Laminaria is connected to *Agarum* even through the sea urchin. But the path's complement is a subsystem with no feedback, since the top variable is not self-damped, therefore the path has no effect. In biological terms, any variation imposed by *Laminaria* to the sea urchin is taken up by the predator, since it is only hampered by its source of food. It reacts promptly to changes experienced by its prey, while No. 2, being self-damped, behaves as if it were more autonomous in interacting with the sea urchin in comparison with the sea otter.

A reduced number of sea otters comes from negative inputs on any variable in the community. So multiple inputs, that easily occur in natural environments, augment the risk of extinction for this population. Examples of harmful inputs for the survival of sea otters are pollutants lethal for all the primary producers, or, conversely, multiple toxicants with specific targets simultaneously released in the environment. The welfare of No. 4 is threatened by negative impacts on its own, but in some instances the reasons for a decline of sea otters remain obscure, if no attention is paid to interconnections to other populations.

The sea otter acts as a sink which absorbs the effects of parameter changes in the growth rate of the other populations, and this makes it so vulnerable. The suggested strategy to preserve sea otters from declining is to keep external disturbances at a minimum, but it is not always possible, because causative agents of disturbance are too often out of control. A tentative tactic to preserve sea otters from local extinction when they reach very low density is to add individuals from outside. Done systematically, the growth rate function of this population changes, because a supply is provided. The loop model, modified by a self-damping on the top variable, leads to two main consequences. First, every path connecting the base trophic level to the primary consumer has a complementary feedback, and all the zeroes that previously filled the row and the column of No. 3 are replaced by signs according to the paths involved. This intervention, aimed to protect the sea otter population, increases the vulnerability of the sea urchin to external impacts, as well as that of the whole community, whose components become more susceptible to changes in the growth rate of the herbivore.

Second, if the subsystem [*Laminaria–Agarum–Strongylocentrotus*] does not violate conditions requested for local stability, the self-damping on No. 4 reinvigorates the overall feedback, and variations in the abundance of species due to parameter inputs are less pronounced. Therefore, the management action increases the sensitivity to stressful episodes, but reduces the intensity of their effects on populations. This suggests that the ultimate decision on the actual effectiveness of this management should not be taken unless further studies supported by quantitative data are carried out.

3.2. EAST LAKE COMMUNITY

Expected responses to parameter changes are summarized in Figure 5(b). The table of predictions reveals that fish populations are very sensitive to external events: any parameter change percolates up the food web, producing alterations in the level of silver carp and bighead carp. The trend is not verified only for inputs to blue–gree algae: they

do not affect the abundance of the omnivorous fish. Lower species are buffered by fish populations with respect to inputs from below: zooplankton and primary producers show high inertia. On the other hand, the entire community suffers from variations occurring in the growth rate of top species.

Besides an input to blue–green algae, with no consequence on No. 5 and an uncertain effect on the bighead carp, the loop model predicts that top species change in opposite directions in response to outside pressure. This might represent a major complication for conservation. In the Western Aleutian Islands, only negative inputs reduced the level of the top predator, while positive impacts were beneficial for it. In the East Lake, conversely, any kind of input, either positive or negative, can be dangerous for fish populations: because they are negatively correlated, a parameter change beneficial for the abundance of one of them is detrimental for the other. In particular, the model predicts that positive changes on No. 1, No. 3, No. 4, No. 5 tend to assess more favourable conditions for the omnivorous fish, whereas negative impacts seem advantageous for the silver carp.

Because of this negative correlation, management actions might have deleterious effects. Improved life conditions for the bighead carp, yielding an increased growth rate, could be harmful for the survival of the herbivorous fish, whose abundance is expected to diminish for positive inputs to No. 5; interventions must be carefully evaluated to safeguard top components.

It is unclear whether the correlation holds when No. 6 changes its growth rate: it depends on the strength of the path "silver carp—blue–green algae—bighead carp" multiplied by the feedback of the complement subsystem "zooplankton—green algae" times the self-damping on nutrients compared with the long path from No. 6 to No. 5, whose complementary feedback is -1. If the effect along the shorter path prevails, the abundance of the bighead carp increases, and the fish populations remain positively correlated. Conversely, if the effect along the longer path is stronger, the negative correlation is maintained. In the former case, the model indicates the silver carp as an appropriate point of intervention for conservation strategies, since its ameliorated life conditions would result in an increased abundance of both. On the other hand, a diminished growth rate of the herbivorous fish (e.g. heat stress, acidification) would be more damaging if top species were positively correlated.

Exotic organisms frequently cause acute stress on biological communities. In freshwater ecosystems, pernicious effects induced by new species colonizing the habitat have been extensively documented (Miller, 1989; Harper et al., 1990; Reinthal and Stiassny, 1991). Some consequences of the introduction of exotic species into the East Lake can be evaluated by the table of predictions. When a predacious fish becomes part of the community, expected consequences vary in relation to its feeding habits. If the species selectively preys upon silver carps, the mortality of this latter population increases and its rate of change diminishes, with two interlinked consequences: the level of both silver carp and bighead carp goes down, assuming they are positively correlated, and the risk of extinction for them increases. Also, blue–green algae attain higher densities, and the lake moves towards acute eutrophication.

Selective predation upon bighead carps would be beneficial for the herbivorous fish, whose abundance is expected to increase, whereas the survival of the omnivorous fish is threatened, inasmuch as its level diminishes. The introduction of a generalized predator would produce a double-negative input, with more severe consequences on the bighead carp. On the contrary, the reduced level of silver carp, due to its augmented mortality rate, is counterbalanced by the increment related to the impact of predator on the

growth rate of the other fish. Whether the omnivorous planktonic fish actually increases or decreases in the presence of a generalized predator depends on the magnitude of paths and feedbacks, and quantitative measures are required. Qualitative predictions suggest the avoidance of the introduction of exotic predators, at least in the context of the cause–effect relationships produced by this network.

Further insight about East Lake dynamics could be gained by considering a more ample network with protozoa and bacteria, and pathways belonging to the detritus chain. As more dimensions are added, however, the more complex the network becomes, which enables new opportunities for counterintuitive events to occur.

3.3. SALT MARSH COMMUNITY

Much effort must be devoted to preserve this very peculiar ecosystem. These wetlands host plants and animals adapted to unique physico–chemical conditions, so they give an important contribution to preserve genetic diversity within these ecosystems. There are also reasons for considering salt marshes as ideal environments for ecological research, especially for energy-flow studies (Howarth and Teal, 1980).

Figure 5(c) reports predictions on how this community is expected to respond to external events. The community may be considered not very sensitive to perturbations: the many zeroes in the table are indicators of good stability against environmental stress. This statement must be taken with scepticism, since in a community there may be even only a few species whose abundance is perturbation sensitive, but it may happen so seriously as to jeopardize their survival and, consequently, the equilibrium of the whole coenosis.

In this food web, "risk populations" are included in No. 7. Parameter changes entering the community through any variable, except for herbivores feeding on *Spartina*, are expected to reverberate upon *Eurytium limosum* and clapper rails. As in the case of the sea otter, only inputs reducing the rate of change of system variables may threaten the survival of secondary consumers No. 7.

Although spiders and dragonflies are located on top of the web they seem sufficiently protected against consequences of external impacts, because of the peculiar structure, that does not allow inputs on Nos 4–7 to percolate to components of the grazing chain. Variable No. 3 changes only when the growth rate of *Spartina* and that of herbivorous insects is modified.

Particularly harmful for the community are contaminants (herbicides or products of acid rain that accumulate into the soil) that interfere with the growth rate of *Spartina*. They act as negative inputs that reduce the abundance of the plant, and spread up to the grazing chain with negative effects on spiders and dragonflies levels, and diminish the abundance of bacteria, with possible consequences on the dynamics of decomposition processes and nutrient cycling. Finally, negative inputs on No. 1 diffuse along the detritus chain, yielding to reduced abundance of secondary consumers.

The action of pesticides is fraught with danger: chemical compounds are widely used in agriculture to fight noxious organisms, but it is nowadays acknowledged (Pimentel and Levitan, 1986) that only a small fraction, as little as 0·1%, of the amount of pesticides reaches the target. Thus, a large quantity of toxicants is free to move a long distance into ecosystems, especially as fallout of aerial applications, and it is plausible that even non human-managed areas suffer from the residuals of pesticides.

In this community, insecticides may alter the growth rate of No. 2 and No. 3. In the first case, the second row of the table of predictions shows that changes (decrease) are

expected only for the spiders' and dragonflies' level (variable No. 3). Plant hoppers and grasshoppers are protected against the effects of increased mortality by predators included in No. 3; such component absorbs the effects of parameter changes in the growth rate of its prey. The strongest impact of chemicals comes through the augmented mortality of No. 3 on top of the grazing chain. Consequences are expected at primary producers' level (decrease), but the effects of augmented mortality for spiders and dragonflies reverberate even onto components of the detritus chain, bacteria and secondary consumers.

Since the connection between the grazing and the detritus chain lies in the interaction plant–herbivore (the precise form of the relationship is not given here), to resolve the ambiguity about the level of bacteria, it should be assumed that the direct links (No. 2)→(No. 5) and (No. 1)→(No. 5) are equally strong. Consequently, the new abundance of No. 5 depends on the relative strength of exploitation of *Spartina* by the herbivores, compared with plant self-damping. If the negative effects of the herbivores prevails, the level of bacteria is predicted to decrease, and the interference of pesticides with spiders and dragonflies may be pernicious for bacteria and may alter decomposition processes, with damage on the nutrient cycling.

3.4. ARCTIC COMMUNITY

In this community, the predator protects its prey, the brown lemming, against effects of parameter changes to nutrients, vegetation and lemmings. Also, the table of predictions of Figure 5(d) indicates the predator as the main controlling factor of lemmings, since their number varies only in response to changes in the growth rate of that component. This has practical consequences for management, when it becomes necessary to reduce lemmings' abundance in order to preserve vegetation from major damages, and to avoid strong competition for resources that could expose herbivores to infectious diseases as well as other stresses.

The table of predictions shows that when lemmings are the target of interventions, actions are not beneficial, since the herbivores' abundance is buffered by the predator, and, after initial decrease, it returns to the original level. Without detailed information on the community structure, planners' efforts risk to have no practical impact.

Useless interventions may not be the worst case; sometimes actions injurious for wildlife are financed. The Arctic community is a good example; when external impacts enter the community from the top, they yield uncertain outcomes on predators and vegetation (two question marks in the last row of the table). The expected predators' and plants' new level depends on the inequality $[a_{23}a_{11}] \lessgtr ? [a_{21}a_{13}]$; if the self-damping on nutrients multiplied by the reduction of the growth rate of plants by the brown lemming is greater than plant efficiency to exploit nutrient multiplied by the release of nutrients into the soil by the herbivore, predators and plant biomass are expected to go up. If this is not the case, positive inputs to the predator would lead to a diminished level of predators and vegetation, with interesting consequences. If the predator is an endangered species, any intervention aimed to preserve it from extinction (e.g. creation of refugees to increment fecundity or to protect from hunting) would actually reduce the individuals and increase the risk of extinction, a counterintuitive effect due to the peculiar structure of this food web.

Possible strategies aimed to decrease the pressure exerted by lemmings on vegetation could imply predators, as common sense would suggest; however, if the goal were pursued through interventions favouring predators' growth (reduced mortality or

genetic manipulation of physiological performances), a diminished abundance of predators and a decreased level of plant biomass would result, with no changes at the herbivore level.

Possibly, genetic alterations enabling individuals to improve capacity to prey upon lemmings occur. Clearly, such a trait would be selected, but since it acts as a positive parameter change on No. 4 and a negative impact to lemmings, its main consequence is a reduced number of predators, and this population might become endangered. These results should warn about the potential danger implied in the use of genetics manipulations for management and conservation practices. Risks and benefits should be evaluated in the light of the community structure, to avoid undesirable, fatal consequences.

4. Conclusions

Preserving biodiversity has become an extremely urgent task. For several reasons, however, effective management strategies aimed to protect wildlife have not been developed yet. One of the reasons is the scarce knowledge of how changing physical and chemical conditions affects the behaviour of ecosystem components.

The degree of comprehension of response mechanisms to anthropogenic disturbance is very uneven, particularly for communities where complex interactions produce dynamics that challenge the human perception of cause–effect processes. It is not sufficient to account for the inherent complexity of an ecosystem; it is necessary to refine appropriate tools well tuned to a formal and rigorous approach to complexity. This is the sole possibility to explain patterns of community response to disturbances and, thus, to provide concrete contributions to the development of feasible conservation strategies.

Loop analysis seems very promising: (1) through the identification of interactive pathways it allows to predict how variations, that take the form of parameter changes in the growth rate of variables, diffuse in natural communities, and what effect they have on populations' abundance; and (2) it anticipates consequences of human interventions and, consequently, it can adequately support planners and managers devoted to conservation biology practices.

In this study, loop analysis has been applied to four network models, and effects of external impacts have been investigated in their implications for conservation and management. The results confirm the key role of top predators: they protect lower trophic levels against effects of perturbations entering the community from the bottom, but, at the same time, they may suffer more than other components the effects of environmental stresses. Nevertheless, variations in the rate of change of top predators have the strongest impact on these communities: on average, the number of components whose level varies is larger than in any other case. Perturbations entering from the top seem to have more severe consequences, because they spread out more easily.

These results, however, should not be taken as definitive for any community. Rather, it is important to define accurately patterns of interactions, case by case, since even a small structural change, like a self-damping on the top predator, may have deep functional consequences. The importance of the structure in affecting the response of populations to environmental stresses can be generalized. Analysis carried out with isolated species often leads to misinterpretation of what actually occurs in nature, and to design ineffective, if not fraught with danger, management interventions. In this context loop analysis helps in reducing or avoiding some of management mistakes.

References

Batzli, G. O. (1983). Responses of Arctic rodent populations to nutritional factors. *Oikos* **40**, 396–406.

Bodini, A. (1991). What is the role of predation on stability of natural communities? A theoretical investigation. *BioSystems* **26**, 21–30.

Brown, J. H., Davidson, D. W., Munger, J. C. and Inouye, R. S. (1985). Experimental community ecology: the desert gravinore system. In *Community Ecology* (T. J. Case and J. M. Diamond, eds), pp. 41–61. New York: Harper and Row.

Camerano, L. (1880). Dell'equilibrio dei viventi mercé la reciproca distruzione. *Atti della Reale Accademia delle Scienze di Torino* **15**, 393–414.

Carney, H. L. (1990). A general hypothesis for the strength of food web interactions in relation to trophic state. *Verh. Internat. Verein. Limnol.* **24**, 487–492.

Carpenter, S. R. (1988). Transmission of variance through lake food webs. In *Complex Interactions in Lake Communities* (S. R. Carpenter, ed.), pp. 119–135. Berlin: Springer-Verlag.

Claro, R. (1991). Changes in fish assemblages structure by the effect of intense fisheries activity. *Tropical Ecology* **32**, 36–46.

Coblentz, B. E. (1990). Exotic species: a dilemma for conservation biology. *Conservation Biology* **4**, 261–265.

Cohen, J. E. (1978). *Food Webs and Niche Space*. Princeton: Princeton University Press.

Cohen, J. E. (1992). Lorenzo Camerano's contribution to early food web theory. Unpublished draft.

Cohen, J. E., Briand, F. and Newman, C. M. (1990). *Community Food Webs*. Berlin: Springer-Verlag.

Dobson, A. P. (1988). Restoring island ecosystems: the potential of parasites to control introduced mammals. *Conservation Biology* **2**, 31–39.

Elser, J. J. and Carpenter, S. R. (1988). Predation-driven dynamics of zooplankton and phytoplankton communities in a whole-lake experiment. *Oecologia* **76**, 148–154.

Estes, J. A., Smith, N. S. and Palmisano, J. F. (1978). Sea otter predation and community organization in the Western Aleutian Islands, Alaska, *Ecology* **59**, 822–833.

Evans, P. G. H. and Nettleship, D. M. (1986). Conservation of the Atlantic Alcidae. In *The Atlantic Alcidae* (D. M. Nettleship and T. R. Birkhead, eds), pp. 427–488. New York: Academic Press.

Greenwood, S. R. (1987). The role of insects in tropical forest food webs. *Ambio* **16**, 267–271.

Harper, D. M., Mavuti, K. M. and Muchiri, S. M. (1990). Ecology and management of Lake Naivasha, Kenia, in relation to climatic changes, alien species' introductions, and agricultural development. *Environmental Conservation* **17**, 328–336.

Howarth, R. W. and Teal, J. M. (1980). Energy flow in a salt marsh ecosystem: the role of reduced sulfur compounds. *Am. Nat.* **116**, 862–872.

Kerfoot, W. C. and Sih, A. (1987). *Predation: Direct and Indirect Impacts on Aquatic Communities*. Hanover: University Press of New England.

Levitan, C. (1987). Formal stability analysis of a planktonic freshwater community. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (W. C. Kerfoot and A. Sih, eds), pp. 71–100. Hanover: University Press of New England.

Ligtvoet, W. and Witte, F. (1991). Perturbation through predator introduction: effects on the food web and fish yields in Lake Victoria (East Africa). In *Terrestrial and Aquatic Ecosystems* (O. Ravera, ed.), pp. 263–268. London: Ellis Horwood.

MacQueen, J. D., Johannes, M. R. S. and Post, J. R. (1989). Bottom-up and top-down impacts on freshwater pelagic community structure. *Ecological Monographs* **59**, 289–309.

Miller, D. J. (1989). Introduction and extinction of fish in the African great lakes. *Trends in Ecology and Evolution* **4**, 56–59.

Miura, T. (1990). The effects of planktivorous fishes on the plankton community in a eutrophic lake. *Hydrobiologia* **200/201**, 567–579.

Parsons, P. A. (1989). Environmental stresses and conservation of natural populations. *Annual Review of Ecology and Systematics* **20**, 29–49.

Paine, R. T. (1980). Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**, 667–685.

Patten, B. (1991). Network ecology: indirect determination of the life-environment relationship in ecosystems. In *Theoretical Studies of Ecosystems* (M. Higashi and T. P. Burns, eds), pp. 288–351. Cambridge: Cambridge University Press.

Pimentel, D. and Levitan, L. (1986). Pesticides: amount applied and amount reaching pests. *BioScience* **36**, 86–91.

Pimm, S. L. (1980). Food web design and the effect of species deletion. *Oikos* **35**, 139–149.

Puccia, C. J. and Levins, R. (1985). *Qualitative Modeling of Complex Systems*. Cambridge: Harvard University Press.

Reinthal, P. N. and Stiassny, M. L. J. (1991). The freshwater fishes of Madagascar: a study of an endangered fauna with recommendations for a conservation strategy. *Conservation Biology* **5**, 231–243.

Teal, J. M. (1962). Energy flow in the salt marsh ecosystem of Georgia. *Ecology* **43**, 614–624.

Westman, W. E. (1990). Managing for biodiversity. *BioScience* **40**, 26–33.

Yozis, P. (1988). The indeterminacy of ecological interactions as perceived through perturbation experiments. *Ecology* **69**, 508–515.

Appendix

LINK

Loop analysis represents ecological systems as graphs with vertices; that is, the species connected by links. Attached to each link there is a coefficient, a_{ij}, positive for arrowheads (j favours the growth of i) and negative for circleheads (j inhibits the growth of i). These coefficients are calculated as:

$$a_{ij} = \frac{\mathrm{d}f_i}{\mathrm{d}x_j},$$

where f_i is the function describing the rate of change of variable i. This function is usually given in the form: $\frac{\mathrm{d}x_i}{\mathrm{d}x_j} = f_i(x_1, x_2 \ldots x_n; b_1, b_2, \ldots b_n)$, to express the dependence of x_i from n variables $(x_1, x_2, \ldots x_n)$ and from a number of parameters $(b_1, b_2, \ldots b_n)$, such as mortality, fecundity, etc. The coefficient a_{ij} indicates how the growth rate of variable i is affected by variable j. All the coefficients form the so-called community matrix, of which the loop model is a pictorial representation.

LOOP

By definition, a loop is a closed circuit formed by links connecting vertices in a signed digraph. A loop starts from a variable and, by following the direction of links, must return to it without crossing other nodes more than once. Only one loop in a predator–prey system, such as that of Figure 2, exists [cf. graph of Figure A1(a)], while in complex ecological communities links may be variously combined so as to compose a higher number of loops, not necessarily of the same length, as shown in graph of Figure A1(b). There are also loops that leave a variable and return to it without crossing any other component [graph of Figure A1(c)]: they occur when a population affects its own growth rate (e.g. density-dependent growth, immigration, emigration); these self-loops are expressed, in the community matrix, by the diagonal terms a_{ii}.

FEEDBACK

Every loop produces a feedback, that can be either positive or negative. The sign of a feedback is given by the product of the coefficients attached to the links forming that loop. The predator–prey loop in Figure 2 involves two links with opposite sign: the feedback is thus negative $[(+a_{BA})(-a_{AB})] = (-)$. In a complex ecological community there are loops of different length, and different feedback levels must be considered. A level of feedback includes the feedbacks produced by all possible loops of a certain length. For example, the third level of feedback is composed by the feedbacks of all possible loops of length three (i.e. loops connecting three variables). There are as many levels of feedback as variables in a stable model.
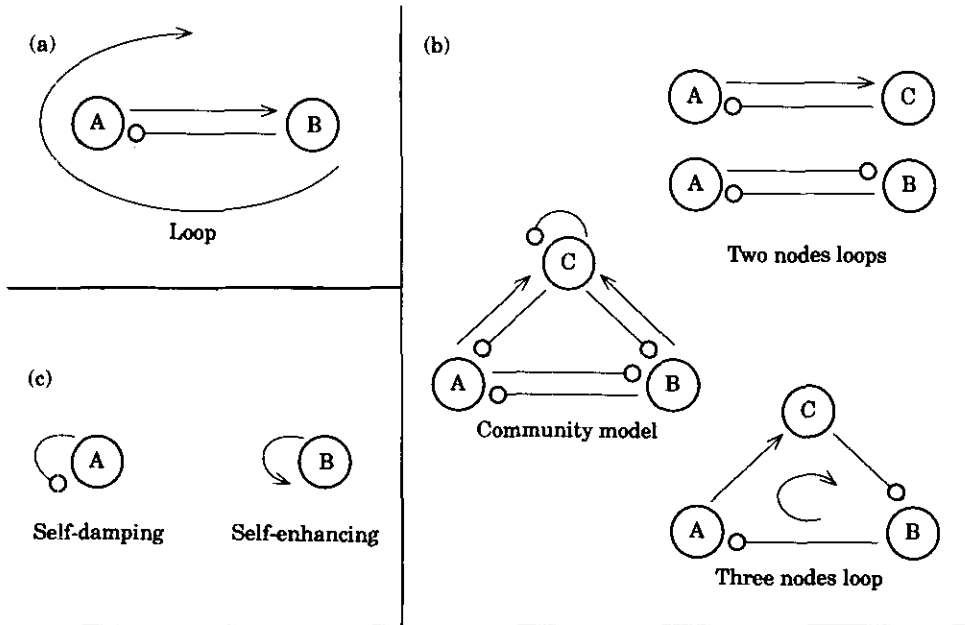
Figure A1. Terms and symbols used in loop analysis.

A feedback is not necessarily associated with a single closed circuit; independent loops (with no shared variables) may be combined to produce feedbacks of higher level. In the community model of Figure A1(b), the loop of length one (self-damping on C) and the competitive loop of length two (A–B) must be combined, as part of the third level of feedback. The sign of this feedback is still given by the product of the coefficients a_{ij}, but the result must be further treated, by multiplying it by $(-1)^{m+1}$, where m is the number of disjunct loops involved. This is the general rule applied to any feedback; in the case of a single loop, is $m = 1$, and the sign of the feedback, as calculated by simply multiplying the terms by a_{ij}, is maintained.

PATH

Loop analysis defines a path as a series of links that starts at one node and ends on another, without crossing intermediate components more than once. To each path a

coefficient ($p_{ji}^{(k)}$) is attached, given by the product of the a_{ij} forming the path, while k indicates the number of components belonging to the path. The loop analysis algorithm allows a path to cross no variable: it ends on the same node it starts. In this case k is equal to zero and $p_{ji}^{(k)} = 1$. Paths in a community model may have different lengths, and some of the paths found in the model of Figure A1(b) are depicted in Figure A1(d), together with their complementary feedbacks.

COMPLEMENTARY FEEDBACK

For each path in a graph, a complementary subsystem may be found; it includes all the variables not on the path and their connections. If the complementary subsystem's links form one or more loops, the feedbacks produced are called complementary feedbacks, identified by the symbol $F_{n\ k}^{(comp)}$, where n is the total number of variables in the model, and k those included in the path. The complementary feedback is only that of the $(n-k)$th level; that is, it must include all the remaining components once the path is excluded from the system, no matter if lower levels of feedbacks in the subsystem can be found. If no loops of length $n-k$ are found, the complementary feedback is null. When all the variables of a community model belong to a certain path ($k = n$), its complementary subsystem does not exist, then the complementary feedback $F_{n\ n}^{(comp)}$ is assumed equal to -1, another algebraic convenience. An open path may have more than one complementary feedback. Examples of paths and related complementary feedbacks are given in Figure A1(d).

QUALITATIVE PREDICTIONS

Once loops, paths and complementary feedbacks of a given structure are identified, one can predict qualitatively the effects of parameter changes on the abundance of system variables. This is made possible by the formula:

$$\frac{\partial x_i}{\partial c} = \frac{\sum_{i,k} \left(\frac{\partial f_i}{\partial c}\right) \times (p_{ji}^{(k)}) \times (F_{n\ k}^{(comp)})}{F_n},$$

where c is the changing parameter; f_i symbolizes the function for the growth rate of the ith variable; $\frac{\partial f_i}{\partial c}$ designates whether the growth rate of the ith variable is increasing ($+$), decreasing ($-$) or not changing (0) for changes in parameter c; $p_{ji}^{(k)}$ is the path connecting x_i, the variable whose rate of change is altered, to x_j the variable whose equilibrium value is being calculated; $F_{n\ k}^{(comp)}$ is the feedback of the complementary subsystem; F_n is the overall feedback, computed only once for the whole system of n components.

The outer i-indexed summation accounts for all the possible functions affected by parameter c, and the inner k-indexed summation considers all the possible paths connecting x_i to x_j and their complementary feedbacks.