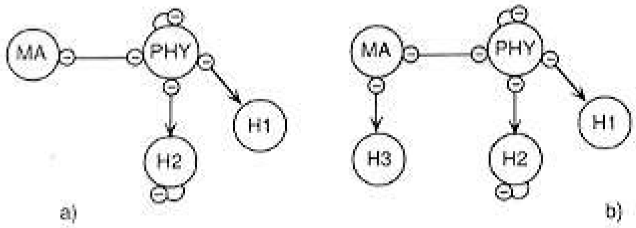
Qualitative modelling of ecological systems

All what is written in this section is based on thoughts and ideas that Richard Levins and Charles Puccia developed in scientific papers and reports, but also during informal discussions I had with them when I was in the Department of Population Sciences, Harvard School of Public Health, Boston, MA. I am indebted to both.



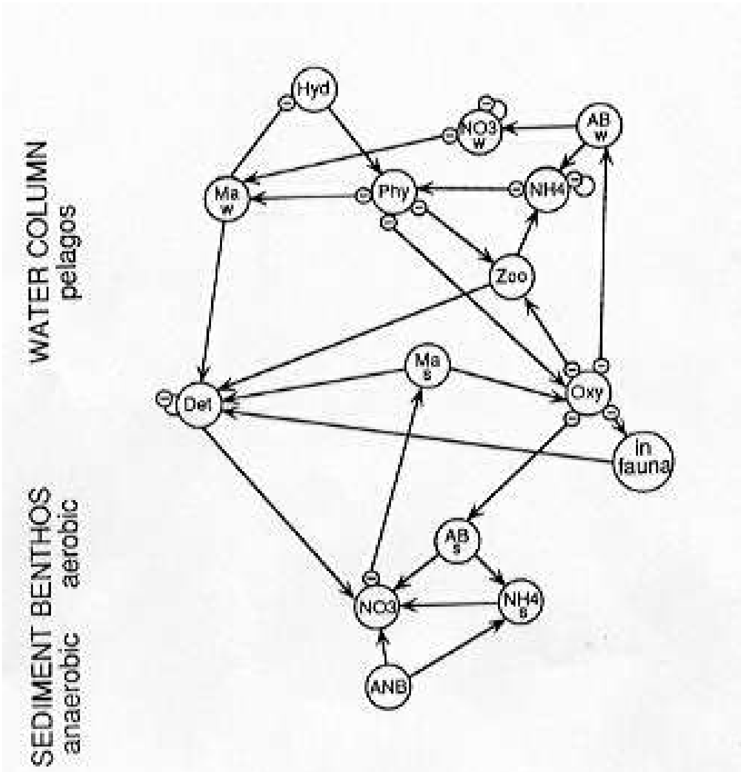
Qualitative modelling respresents ecosystems as signed digraphs. MA=macroalgae; PHY=phytoplankton; H1, H2, H3=herbivores.

Modelling plays two distinct roles in the analysis of ecological systems. On the one hand models are built and analyzed to obtain numerical predictions of natural phenomena. They are used to predict outcomes and guide interventions. On the other hand modelling can help to understand mechanisms and educate intuition to interpret counterintuitive behaviours. The first goal can be achieved by using tactical models: they rely on specific information, detailed knowledge, accurate measurements and aim to give precise results. They also sacrifice generality to realism and precision. Understanding is the main goal of strategic models, instead. They sacrifice precision to realism and generality. Strategic models, in fact are characterized by their wide applicability (often the question of interest is not a particular system but a whole class of systems with some similarity of structure); they emphasize the understanding of mechanisms, are often of a qualitative nature and reach qualitative conclusions.

While there is an ever-growing tendency to consider quantitative models the best tools for predictions and, as such, the most useful instruments for practical applications, it must be emphasized that qualitative models offer several advantages.

- They permit the inclusion of variables that are not readily measurable. Quantitative models require precise equation and quantification of parameters but there are variables that are not quantifiable or cannot be easily translated in appropriate functional forms, although they are very real and affect the dynamics of the system as well as the usual variables. Among these variables one can include social traps and behaviours, coefficients of bureaucratic inertia, illegal activities, ambiguous decision rules. Yet, although quantification and mathematical description may be in principle possible, the urgency of the problems at hand do not leave enough time to develop sophisticated models before at least a preliminary answer is given.
- They allow the use of variables that differ dramatically in physical form, such as rate of profit from fishing and the rate of reproduction of fish, contagion rates of an epidemics and the caution or panic of the ministry of public health.
- They provide criteria for constructing models of the system, indicating which variable should be include and which to treat as external influences; also they provide indications about what to measure before going into the field.

- In environmental related questions, as well as public health, often access to data and information is precluded to those who are more likely to be in opposition to the policy makers and public as well as private enterprises; qualitative models can help to study the problem to obtain qualitative predictions about the trajectories the system is going to follow.



**Qualitative representation of the ecosystem of the Lagoon of Venice (modified from: Transport Processes and the Hydrological Cycle. Environmental Dynamics Series II.
Istituo Veneto di Scienze, Lettere ed Arti)**

The method of signed digraphs

A loop model (a signed digraph) is a pictorial representation of a community matrix. Coefficients a_{ij} of the matrix represent interactions between species and abiotic variables. Positive coefficients are depicted as arrows. Negative values in the matrix appear as circle head links in the loop model. The diagonal terms of the matrix are self-effect on the system variables. The correspondence between a community matrix and a signed digraph for a simple resource-consumer system is given in Figure 1.

$$\frac{d}{dt}\begin{bmatrix} X_1 \\ X_2 \end{bmatrix} = \begin{bmatrix} -a_{11} & -a_{12} \\ a_{21} & 0 \end{bmatrix}\begin{bmatrix} X_1 \\ X_2 \end{bmatrix}$$

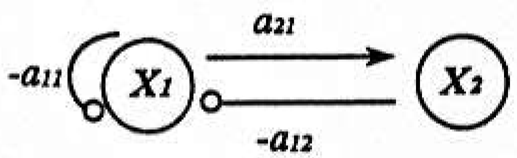


Fig. 1. Community matrix and signed-digraph of a resource-consumer interaction (X_1 = resource; X_2 = consumer).

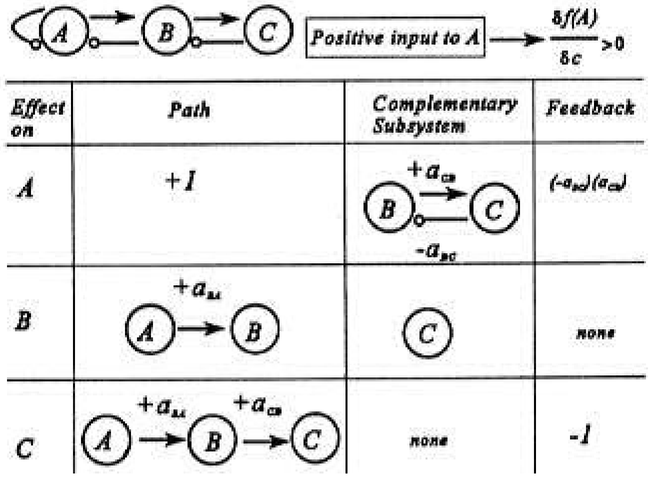
Disturbances may act on ecosystem components by changing one or more parameters that govern their rate of change. In complex systems there can be effects beyond the direct target of the perturbation. Interconnections form pathways through which actions imposed to one or more variables percolate into the system. Loop analysis identifies those pathways as combinations of links and qualitatively predicts effects of parameter changes, also called inputs, on the abundance of the various components. This analysis may tell one whether a variable is expected to increase, decrease or remain the same. The new level of each component can be calculated by the loop formula

$$\frac{\delta x_j}{\delta c} = \frac{\sum_{i,k} \left[\frac{\delta f_i}{\delta c}\right] \times \left[p_{ji}^{(k)}\right] \times \left[F_{n-k}^{(comp)}\right]}{F_n}$$

where *c* is the changing parameter, such as mortality, fecundity, predation rate, and so on; $[df_i /dc]$ designates whether the growth rate of the *i-th* variable is increasing, decreasing or not changing; p_{ji} is the pathway connecting x_i, the variable that undergoes parameter change, and x_j, that whose equilibrium value is being calculated. The pathway includes *k* variables none of which are visited more than once. The last term of the numerator is the complementary feedback. It is associated with the complement, a subsystem that comprises all the remaining *(n-k)* variables not on the path and their associated links. Finally, *Fn* is the overall feedback of the system.

The loop formula allows one to calculate expected changes in the equilibrium level of variables in response to parameter inputs. Besides the sign of the input, indicated by the term , the loop formula makes use of the concepts of path, complementary feedback and overall feedback. They refer to structural elements that can be identified in any graph. Their meaning can be fully understood by referring to the correspondence between matrix algebra and the formalism of loop analysis, that can be found in Levins (Levins, R., 1975. Evolution in communities near equilibrium. In: Cody, M.L. and Diamonds, J.M., eds, Ecology and Evolution of Communities. Harvard

University Press, Cambridge, MA, USA, pp 16-50.). Instead, in what follows criteria to identify such elements in a graph are provided by referring to the graph depicted in the following scheme



Circuits and Feedbacks. In loop analysis a pathway that starts at one node and, by following the direction of links, returns to it without crossing intermediate nodes more than once is called loop, or circuit. Any circuit produces a feedback. It can be positive or negative depending on the product of the signs of the links that form the loop. As there may be circuits of different length (1, 2, 3...n variables involved) in a system there are as many levels of feedback as variables. Each level of feedback considers all the circuits(feedbacks) involving that particular number of variables. In the system of Figure there are 3 levels of feedback.

Overall Feedback (Fn). It is computed only once and corresponds to the highest possible level of feedback in a system. In model A1 it is the third level of feedback. It includes all the feedbacks of the circuits involving the three components. No disjunct loop of length three exists in the graph, and in this case the level of feedback includes all the products of disjunct loops that have a combined number of variables equal to 3. As disjunct loops are those that share no variables, the overall feedback in the graph of Figure A1 is composed by the self-damping on A (a self-effect link is a loop of length 1) plus the two-node loop [B-C]. Its sign is obtained by multiplying the sings of the links involved, further multiplied by the factor $(-1)^{m+1}$, where m is the number of disjunct loops entering the feedback. As the links involved are two negative and one positive, and the number of disjunct loops is 2, the overall feedback is negative.

Path. A path is a series of links starting at one variable and ending on another without crossing any variable twice. Suppose a positive input occurs on A (its rate of change increases>0). To predict the new equilibrium value of, say, B, the path along which the effect travels must be identified. It is the positive link from A to B. It involves two *(k)* variables and its sign is positive.

Complementary Feedback (F_{n-k}) If the *k* variables in the path and their links are ideally excluded from the graph, what remains is called complementary subsystem. The complementary feedback is the highest possible level of feedback that can be found in the complementary subsystem. In this case, for positive input on A and effect on B, what remains is C, and the highest possible level of feedback is level 1. As C has no self-effect link, there will be a null (0) complementary feedback. For completeness, it has to be noted that a path from a variable to itself is equal to +1, while if all the variables are included in the path (for example in the case of input to A and effect on C), there is a null complementary subsystem, but the complementary feedback is equal to -1, an algebraic

convenience. The summation sign in the loop formula considers the fact that two variables can be connected by more than one path.
Responses of abundance or biomass to parameter changes are arranged within tables of predictions for the system. The entries in a table denote variations expected in all the variables column when a parameter change affect raw variables. Conventionally the calculation is done by considering positive inputs ,, those increasing the rate of change of variables. Consequences of negative inputs can be obtained by simply reversing the signs in the table. In Figure 2 a table of predictions for a simple predator-prey system is given as an example.

Increase in the rate of change of	*Effect of parameter change on the abundance of* X_1	X_2
X_1	0	+
X_2	-	+

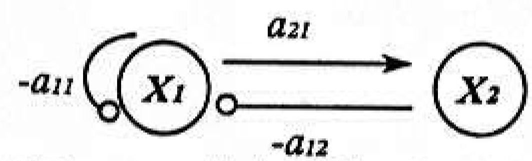


Fig. 2. A predator-prey model: signed digraph and table of predictions.

Qualitative modelling is a tentative answer to the dramatic failing of applied science to treat environmental problems in the small, without taking into account interconnections and consequences in the large. We are taught to isolate problems, to change things one at a time, to assemble all the information without thinking about it, and then put it in a computer. However all of the important mess-ups that have occurred in environmental management, in public health, in agriculture, in land use planning and in managing natural resources have come about because we haven't looked at interconnections. An example of this is the use of pesticides to fighting hunger. The syllogism which is used to justify the argument is that since the pesticide kills insects and insects destroy crops, killing the insects should increase the crops. As the crops produce food , increasing the crop should reduce hunger. This is a linear sequence of steps, each of which is more or less plausible. Now what really happens is something very different. First of all the physiological fact that a poison kills an insect is not the ecological fact that poison controls the insect population. A lot of things can happen. One is that the insects adapt to the pesticide, a second one is that the pesticide is killing the predators of that insect as much as the target insect, so from the point of view of the noxious insect more of them are getting poisoned but fewer are getting eaten and the population may actually increase. Third, if one insect is reduced by spraying new opportunities are opened up for other insects, and a secondary pest problem arises. The pesticide is also getting into the soil affecting the invertebrates that speed up the decay of crop residues, or running off into the ponds where people are producing shrimps and fish. Suppose however that in fact the crop has been successfully increased because of spraying. Economic response may be to displace the labor force, to stop growing other kinds of crops, to displace traditional agriculture. The net result of this pattern is an increase in hunger but that is nobody's department. The plant breeder worries about increasing yield, the entomologist worries about bugs and nobody seems to have responsibility for the evolution of the system as a whole. The shortsightedness of much of applied science is not simply an intellectual failing. Rather it reflects the social organization of research with its narrow compartimentalization, fear of touching political questions, technocratic ideology and timidity. Qualitative models educate intuition to consider the trajectories of the system as a whole when decision are taken about one single variable or a limited set of variables that enter the system of interest. So the use of an herbicide may cut costs but create unemployment among women for whom weeding is the only job possible; dwarf, high yielding grain may not produce enough straw to cook the harvest; improved protein balance in maize may make it a suitable host for a new pest; increased yield which depends on higher input may lead to land concentration.

A detailed description of qualitative techniques and their applications can be found in:

Puccia, C.J. and Levins, R. 1985. ***Qualitative Modelling of Complex Systems. An Introduction to Loop Analysis and Time Averaging***. Harvard University Press, Cambridge, MA.