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Optimum complexity in ecohydrodynamic modelling: an ecosystem dynamics standpoint

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1. Introduction

Although it is becoming increasingly evident that ecosystem models must be sufficiently sophisticated to incorporate the effects of hydrodynamic and physicochemical constraints and, at the same time, include the essential mechanisms of cogent biological interactions, there are limitations, if not on computing power and computing time in the foreseeable future, at least on the volume of computer products, the (technical and human) ways and means of exploiting them for the advancement of basic scientific understanding or the development of rational management schemes, within a reasonable time.

The dilemma is very often expressed as a competition between the necessity of a sufficiently detailed physics and the need of a *refined*, *adequate* description of the ecosystem's dynamics. This, however, hides an important question, viz.: how *refined* must the ecosystem's description be to be *adequate*?

The state variables describing an ecosystem must be defined not only by their nature (e.g. phytoplankton, zooplankton...) but also by: (1) their time scales and length scales (the latter tending to match those of the constraining physical processes having similar time scales); (2) their position in the biological hierarchy (if only in the simple form of a size distribution); and (3) their state of (physiological, behavioural...) functionalism, which affecting essential processes, such as feeding, excretion, reproduction..., is a determinant factor of the translocation of material between ecological compartments.

The first step, in the construction of an ecosystem model, is the selection of a limited number of state variables and the formulation in mathematical terms of the interactions between them. The grounding of the selection lies in the inspection of the data base and the identification of those chemical and biological variables (concentrations and biomasses) which must be known to provide a satisfactory *picture* of the system.

The word '*picture*' is used here on purpose to emphasize the fact that the main criterion for the selection (and limitation) of a set of state variables is really the requirement that, at essential stages of the system's evolution, models' results provide a good, recognizable *photograph* of the ecosystem. With this approach, the dynamics is subjacent (leading the system from one photograph to the next), but it is not the major concern of the selection.

In the following, ecosystem models' complexity is re-examined from the standpoint of the system's dynamical behaviour and arguments are presented recommending that more consideration be given to

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the possible dynamical comportment of the system in setting its structure in state space.

2. Ecosystem box models

The evolution equations of an ecosystem box model can be presented, after the introduction of state variables' derivatives and, when necessary, time, as additional variables, if needed, as a system of 'autonomous' first-order differential equations of the form:

$$\begin{aligned}\dot{y}_1 &= f_1(y_1, y_2 \dots y_n)\\ \dot{y}_2 &= f_2(y_1, y_2 \dots y_n)\\ &\vdots\\ \dot{y}_n &= f_n(y_1, y_2 \dots y_n)\end{aligned}$$

i.e. in vectorial form:

$$\dot{\boldsymbol{y}} = \boldsymbol{f}(\boldsymbol{y}) \tag{2}$$

The n-dimensional space of coordinates $y_1, y_2 \dots y_n$ is the *phase space* and the evolution of the system may be viewed as a *trajectory* in phase space. One emphasizes that the dimensions of the phase space result directly from the selection of (and restriction to) a limited set of state variables. A more refined description of the ecosystem would lead to a broader set of state variables and a phase space of more dimensions. In fact, one must regard the n-dimensional phase space of variations of $\boldsymbol{y}$ as a *sub-space* of a *natural* phase space of dimension N (N as large as needed).

The study of the trajectories in phase space begins naturally by the identification of *fixed points* (where $\boldsymbol{f}(\boldsymbol{y}) = 0$) or closed cycles and surfaces which may attract or repel trajectories according to their stability.

The restriction to an n-dimensional sub-space of the *natural* phase space implies that fixed points and limit cycles are only sought in this particular sub-space and that their stability to small perturbations is only examined for perturbations confined to the n-dimensional sub-space. One may argue that the *identification* of fixed points and limit surfaces in the n-dimensional sub-space is meaningful because, in many cases, they are also fixed points and limit surfaces of spaces of more dimensions (i.e., for instance, a fixed point $\tilde{y}_1, \tilde{y}_2 \dots \tilde{y}_n$ in the n-dimensional sub-space is also a fixed point $\tilde{y}_1, \tilde{y}_2 \dots \tilde{y}_n$, $y_{n+1} = 0, \; y_{n+2} = 0 \dots y_{n+p} = 0$ of a $(n+p)$-dimensional space), but the *stability analysis*, restricting attention to perturbations confined in the n-dimensional sub-space, is more questionable.

Muratori and Rinaldi (1989) made a thorough study of a three-species ecosystem assuming that the population of the higher level predator remains constant. In other words, they had a three-dimensional phase space, but were only considering sections of it by planes $y_3 =$ constant. They showed a great diversity of dynamical behaviours with stable or unstable fixed points and limit cycles according to the values of parameters and to levels of y_3. The stability analysis, however, was, in each case, made under the assumption that perturbations were restricted to the phase plane of cross-section (i.e. no perturbation of y_3 was allowed).

Hastings and Powell (1991) made a similar study of a three-species ecosystem, but, while the equations for y_1 and y_2 were the same as (actually a particular case of) the corresponding equations of Muratori and Rinaldi, they allowed the variations of y_3 according to a prey–predator equation of the classical 'Michaelis–Menten' type (e.g. Nihoul and Djenidi, 1998). For values of the parameters for which the model of Muratori and Rinaldi would predict a stable limit cycle in the cross-section phase space, Hastings and Powell found a chaotic behaviour with a strange attractor resembling an upside-down teacup. Adding a fourth species (with a fourth prey–predator evolution equation of the same general type) shows (for seemingly not unreasonable values of the parameters in the fourth equation) a possibility of extinction of the two top-predators and an attraction of the trajectories to the two-dimensional limit cycle predicted by the model of Muratori and Rinaldi.

In ecosystem modelling, one is used to the scaring prospect of the oversensitivity of the models to the values of parameters which can only be determined within a rather broad range of variations. One must be as attentive to the system's sensitivity to the dimensions of the phase sub-space where the model system is defined, i.e. to the preliminary selection of state variables which expresses one's preconceived, intuitive vision of the ecosystem's structure.

3. Three-dimensional ecosystem models

Conceptually, one can reduce a system of three-dimensional partial differential evolution equations to a system of first-order differential equations by expanding the state variables in series of spatial eigen-modes with time-dependent amplitudes. Standard procedures yield differential equations for the amplitudes and by the introduction as before of derivatives or time as additional variables, if necessary, one may write these equations as a first order 'autonomous' system.

The dimensions of the associated phase space are now functions of the number of state variables and of the number of spatial modes retained in the expansions.

In the same way as the phase space dimensions, and possibly the whole ecosystem's dynamics, can be changed by selecting a different number of state variables, they may now be modified by taking more or less modes of spatial variations into account, i.e. by modifying the spatial resolution. In addressing the dilemma, detailed physics versus detailed ecology, one must then take into account that refining the determination of physical fields not only allows a better understanding of the effect of physical constraints (advection, diffusion...) on ecosystems, but may also modify notably the ecosystems' intrinsic dynamic behaviour. (For instance, unnatural chaotic comportments could be avoided by involving more species or generating more detailed spatial structures).

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