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Developmental versus morphological approaches to modelling ecological complexity

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Although modellers intend their models to refer to some (conceivably) observable things, the impact of ecological models has come less from achieving tight correspondence with observations than from models' exploratory role, that is, from their helping ecologists derive new questions to ask, new terms to employ, or different models to construct (Caswell 1988). It is with the aim of stimulating further conceptual exploration by theorists and mathematical modellers that I have framed this rejoinder to DeAngelis and Waterhouse (1987; from here on, D&W).

In their excellent review, D&W present a schema of ecological modelling related to the issue of persistence over time of communities of species. Their starting point is an "eqilibrium" view, in which systems move toward or away from a steady state. Increasing disruption from internal feedbacks or environmental stochasticity leads to emphasis on "biotic instability" or "stochastic domination," respectively. Accounting for the persistence of communities despite these disruptions leads D&W to a "landscape" view, in which a community may persist in a landscape of interconnected patches even though the community is transient in each of the patches.

While endorsing most of D&W's interpretations, this note draws an additional contrast, between a "morphological" approach to ecological modelling, in which complexity is analysed in terms of its current, configuration, i.e., as a "snapshot," and a "developmental" approach, which recognises that complexity can develop over time through the addition and elimination of populations (or other components). The developmental approach is not new, but it suggests pathways for exploration that have generally been overlooked or less travelled by theoretical ecologists and it raises the challenge of modelling complexity that has structure together with a history of structuring and restructuring. Let me expand on this contrast be returning to D&W's idea of "disruption from internal feedbacks."

May (1973) and others found that complexity worked against stability in Monte Carlo samples of models having minimal biological-like detail (e.g. linear models and generalisations of Lotka-Volterra models). To D&W (and many other authors) this result indicates a "potential biotic feedback instability inherent in complex natural systems" (D&W, p.5). Noting the limited success of different attempts to counteract the instability, they conclude that we should not "base any theory of ecological communities solely on the notion of inherent ecological stabilizing mechanisms" (D&W, p.9).

Complex ecological systems, however, are generally not the outcome of a sampling process but of a process of development over time through the addition, growth, decline, and elimination of populations. Several modelling studies have shown that, whereas stable systems may be extremely rare as a fraction of the systems being sampled, they can be readily constructed over time by the addition of populations from a pool of populations and/or by elimination of populations from systems not at a steady state (see Tregonning and Roberts 1979, Taylor 1988a and references therein, Ginzburg et al. 1988). The pool of potential entrants can be visualised as neighbouring systems or patches, refuges in which species persist undetected at low abundances, the seed bank, and so on. (The effectiveness of this means of system construction is explained in Taylor 1988b;

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whether this carries over to systems with more biological-like detail remains an open question.)

Some of the implications of the developmental approach are as follows:

On-going system construction and turnover: A stable system that has been constructed over time by addition and elimination is also one that has been constructed from and supplanted a previous stable constructed system. It may, in turn, be supplanted by another system. Given this turnover, ecological complexity may persist at the expense of any ecological system being transient. This conclusion sounds similar to D&W's but it was derived by different reasoning. Admittedly, when we note that one source of potential entrants would be neighbouring patches, the developmental view does intersect with a landscape view. Remember, however, that the transience of communities in a patch is caused by invasions and not by *intrinsic* biotic instability. Of course, when we turn to observing the real world these distinct causes would probably form a continuous spectrum of degrees of resistance to transience; moreover, transience and persistence become matters of time span of observation.

Expanded range of mathematical possibilities: Under the developmental view, investigations of complexity in models should include the historical development of that complexity not just analysis of its current configuration. The latter, morphological approach focusses on analysis of systems with only a few variables (or many identical variables yielding a statistical simplicity). It considers a model to be an unlikely candidate for representing natural systems if the model is stable only in a small region of parameter space. In contrast, under a developmental approach, this small region may be more easily accessed and, because most results of time development are derived by simulation rather than analysis, more complex systems can be considered.

Few mathematical ecologists have appreciated or explored the developmental approach (though see Maynard-Smith 1974:107 and references in Taylor 1988a). For example, much of the mathematical theory of complex systems in general relies on the condition of diagonal dominance (Siljak 1978), or the equivalent concept in hierarchy theory, namely, decomposability. I community ecology diagonal dominance translates into intraspecific interactions overshadowing interspecific, that is, autecology dominating over community ecology. (Strictly speaking, the condition may be loosened to quasi-diagonal dominance or near-deomposability, corresponding to weakly interlinked blocks of populations.) Yet richly interacting systems can be readily produced by development over time (Taylor 1988a, b). Although this result does not rule out natural complexity being decomposable, mathematicians should take note that nature does not have to restrict itself to hierarchies of weakly interlinked components (contra Simon 1969).

Ecological development versus evolution: D&W refer in passing to time development: "structures and parameter values [conferring stability] could have evolved through a long process of natural selection operating at the system level" (D&W, p. 9). This evolutionary interpretation is unfortunate, on two counts: 1) Natural selection at the system level is an unfamiliar or controversial notion for most population biologists. (In any case, since it is not clear what is being selected for, the description reduces to a statement that populations persist for different periods, i.e. are differentially represented over time.) 2) More importantly, development occurs in ecological time, i.e. without requiring genetic fine-tuning of population interactions (contra Lawlor and Maynard-Smith 1976, Roughgarden 1977, Lawlor 1980). The microecosystem experiments of Robinson and Dickerson (1984) and Drake (1985), in which changing the order of colonisation produces different resulting communities, show how historical ecology need not be evolutionary (in the sense of requiring genetic change). Under the developmental approach these experiments, and presumably other situations, can be modelled without conflating ecological with coevolutionary time and processes (Drake 1985).

Systems or temporary accommodations?: The developmental view, like the landscape view, suggests that persistence at one scale (in time, space and degree of aggregation) may be the outcome of processes at other scales; here, addition of populations from surrounding patches and local elimination. If we move down to the scale of such constituent processes we may find that the very same processes yield a range of outcomes other than persistence, for example, a mosaic of communities continually shifting over time and space. The idea of shifting or indeterminate boundaries, in turn, invites us to question not only the equilibrium view but even the concept of system. Of course, "system" may be used simply to denote that there are many elements interacting, but it usually has stronger connotations, of an entity with natural boundaries and coherent internal dynamics governing its development. If systems in this latter sense exist, this should, under the developmental view, be a contingent outcome to be explained – not a starting point for theory and modelling.

Certain anthropologists arrived at this position some time ago. Wolf (1982: 387), for example, rejects the concept of any "fixed, unitary, and bounded culture." If we observe " transgenerational continuity, institutional stability and normative consensus," we should seek to understand the conditions for their "emergence, maintenance, and abrogation." Wolf remarks suggestively that "'a culture' is... better seen as a series of processes that construct, reconstruct, and dismantle cultural materials, in response to identifiable determinants." It may

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be fruitful to examine debates in other fields between theorists who assume the existence of systems (in some guise) and those who stress intersecting processes and historical contingency. We should not, however, expect to find any shortcuts; if complexity is a series of temporary accommodations to forces operating at a diversity of scales, then the appropriate conceptual road for modelling ecological complexity is a matter quite open, as DeAngelis and Waterhouse imply, for further exploration.

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Erratum

Keddy, P. A. and Shipley, B. 1989. Competitive hierarchies in herbaceous plant communities. – Oikos 54: 234–241.

1) Equation 4, page 240: The correct version of this equation is

$$\sum_{x=m(L)}^{T(L)} \binom{T(L)}{x} p^x q^{(T(L)-x)}$$

The published probabilities, listed in Tab. 1 (page 236), were calculated with the correct equation and should not be changed.

2) Last paragraph, page 240: replace:
"… and that (L=1) elements equals zero …" by:
"… and that (L+1) elements equals zero …".

Ed.

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