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From population dynamics to ecoinformatics: Ecosystems as multilevel information processing systems

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ABSTRACT

In classical ecological theory the concept population plays a central role. Most models are formulated in terms of changes in the number/biomass/fraction of interacting populations. In the passed 30 years slowly alternative viewpoints have been developed. In this paper we trace some of these alternative developments which lead to viewing ecosystems in terms of local multilevel information processing and evolution. We will sketch the methodological developments, indicate some fundamental insight gained through the methodological innovations and focus our discussion on the central problem of the development and maintenance of diversity in ecosystems. We will explore the circumstances in which individual based diversity (plasticity, regulatory adaptation, intelligence) or population based diversity (speciation) develops.

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1. Introduction

In this paper we discuss three major stages in the transition of population dynamic models to models which describe ecosystems as multilevel information processing systems. The first step is the transition from populations as the basic unit of description to individuals, localized in space, as the basic information processing unit. The next step considers these individuals not as fully predefined entities, but subject to a Darwinian evolution, and the realization that evolutionary and ecological timescales cannot be apriori separated. While in the second step Darwinian evolution takes place at the phenotypic level, in the third step the genotype phenotype mapping is taken into account and is itself evolvable. This allows us to study the evolution of different modes of information processing, and under which circumstances these modes may be favored.

Ecosystem diversity is a fundamental question in ecology which is also central in ecosystem management. In this paper we focus our discussion of the methodological developments around this question. In particular we will focus on the

generation and maintenance of diversity at different levels of organization. We will contrast “population based diversity” in which lineages diversify, leading to species with different roles in the ecosystem, and “individual based diversity” in which each individual can play different roles through plasticity, physiological regulation and behavioral versatility. At the molecular level these two modes of diversification both involve duplication and divergence of genes. In the case of population based diversity in the form of the divergence of orthologous genes, whereas in the case of individual based diversity, within genome gene duplications (paralogs) and their (regulatory) divergence lead to an increased behavioral repertoire.

The organization of this paper is as follows. In each of the sections we first describe a major step in modeling methodology, we then review a specific example from our own work in which the power of that methodological step has been illustrated and finally highlight a fundamental insight obtained from that study. Thus reading the first subsections tells the methodological story, reading the last subsections tells the biological theory developed through the methodology.

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2. Spatial pattern formation and multiple levels of selection

2.1. Adding space to population dynamic models

Every ecosystem is embedded in space. Interactions between individuals are local. Even in relatively well mixed systems, like oceans, spatial pattern formation (e.g. plankton clouds) is prevalent. Classical population models ignore this defining property of ecosystems. The most straightforward way to incorporate this basic fact about ecosystems is to consider individuals localized in space.

Stochastic cellular automata (CA) are the simplest convenient formalism in this respect (Hogeweg, 1988) when the state of the automata represents the type of individual present at that location. In CA the transition rules depend on the state of the cell under consideration and its neighbors (however defined) and thus local interactions between individuals are established in the model. Local movement of individuals can be implemented, e.g. as a diffusion process (for an introduction of Cellular Automata as modeling tool see Toffoli and Margolus, 1987).

Cellular automata models differ from classical reaction diffusion systems in considering discrete individuals which are present in some locations and absent in other locations. In contrast, in reaction diffusion systems, everything is everywhere but possibly in arbitrary low concentrations. As Durrett and Levin (1994) pointed out in their paper “the importance of being discrete...” this is an important, and obviously realistic difference. Fully individual based models, in which individuals are embedded in a continuous space, and events take place in continuous time, are a more versatile alternative (Hogeweg and Hesper, 1990). For our purpose here (individual based) CA models do, however, suffice.

The biological assumptions of classical population based models can be straightforwardly translated into a CA model, such that the only difference is the spatial embedding and the local interactions. The classical population based model is than the first order mean field ‘approximation’ of the CA. I put ‘approximation’ between quotes, because the bottom line will be that the spatial embedding profoundly alters the properties of the system and therefore the mean field version does not describe the system even approximately. Also higher order mean field approximation fails to capture the properties of the spatial system because large scale pattern formation plays an essential role. By implementing well studied population models in space we can analyze the influence of space precisely.

2.2. Information accumulation in prebiotic evolution

The issue of individual based vs. ecosystem based information accumulation was first posed by Eigen and Schuster (1979) in the context of prebiotic evolution. Information accumulation in replicators through Darwinian evolution is limited by mutation rate (the so called information threshold, cf. Eigen et al., 1989). Because mutation rate can supposedly only be reduced by a more sophisticated replication process they proposed that interacting populations of replicators might be a potential scenario to overcome the ‘catch 22’ in

early evolution. To this end they proposed the Hypercycle model, formulated in ordinary differential equations (ODE) in which replicators cyclically catalyze each others replication (similar to ODE model in Table 1).

Thus although the problem posed was an evolutionary one, where large mutation rates were inherent to the problem, they studied an ‘ecological’ model of monomorphic populations and fixed interactions. Evolution only comes in the form of invasion of mutants, i.e. ecological and evolutionary time-scales are separated.

So defined hypercycles are not a feasible solution for the information threshold problem e.g. because they are unstable to the invasion of ‘parasites’, i.e. molecules who get more catalysis of their predecessor in the cycle, but do not give catalysis to their successor, as was first stressed by Maynard Smith (1979). Indeed it is well known in ecology that cooperative systems are vulnerable to ‘cheaters’.

2.3. Spatial pattern formation and multiple levels of selection

All dynamic properties of hypercycles change qualitatively, when the molecules are embedded in space (Boerlijst and Hogeweg, 1991a,b) (see Table 1). For $N > 5$ the dynamics of the CA model give rise to spiral wave patterns (Fig. 1). It is the dynamics of the spiral wave patterns which alter the fate of the replicators drastically, and for example expels invading strong parasites from the system (Fig. 1). Other differences are listed in Table 1. The 3 crucial aspects of spiral wave dynamics responsible for these differences are (1) spiral waves form separate domains; (2) all offspring in the long run originate from the core of the spirals, and (3) faster rotating spirals expand their domain into that of slower rotating spirals. For further details see Boerlijst and Hogeweg (1991a,b).

We conclude that spatial pattern formation leads to the generation of new levels of selection (here competing spirals) which may overrule the selection at the level of competing replicators. Such multilevel dynamics is still overlooked in most ecological and evolutionary models, but appears to be a defining property of ecosystems and their evolution.

Table 1 – Comparison of Hypercycle models in space (CA model) and well mixed (ODE model): the differences are due to spiral wave dynamics (cf. Boerlijst and Hogeweg, 1991a,b)

CA transition rules	Properties CA	Properties ODE
Decay (d): $X \rightarrow 0$	Pos. selection for $d' > d$	Pos. selection for $d' < d$
Replication (a): $0 + nb(X) \rightarrow X$	Pos. selection on $c_{xy}' > c_{xy}$ on X and Y	Pos. selection on $c_{xy}' > c_{xy}$ only on X
Catalysis (c_{xy}): $0 + nb(X) + nb(Y) \rightarrow X$	Stable to parasite invasion	Vulnerable to parasites
ODE (mean field)	New hypercycle can invade	Once only selection
$dX/dt = X(a + c_{xy}Y)$ ($T - \sum X_i$)/ T . N number of species, Y gives cat. to X	N decreases if $N > 6$ for similar catalysis	Increase and decrease of N only dependent on catalysis

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