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.

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): $X -> 0$	Pos. selection for $d' > d$	Pos. selection for $d' < d$
Replication (a): $0 + nb(X) - > X$	Pos. selection on $c'_{xy} > c_{xy}$ on X and Y	Pos. selection on $c'_{xy} > c_{xy}$ only on X
Catalysis (c_{xy}): $0 + nb(X) + nb(Y) > X$	Stable to parasite invasion	Vulnerable to parasites
ODE (mean field)	New hypercycle can invade	Once only selection
$dX/dt = X(a + c_{xy}Y)$ $(T - \Sigma X_i)/T)$. 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
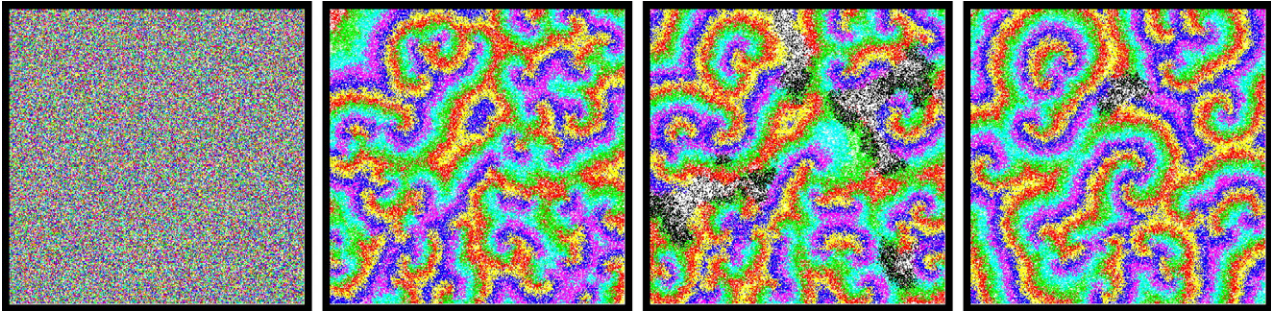
Fig. 1 – Pattern formation and expulsion of parasites in a spatial model of the hypercycle (cf. Boerlijst and Hogeweg, 1991a,b).

We cannot conclude, however, that ecosystem based information accumulation is indeed an adequate scenario of crossing the information threshold because these results are obtained from invasion experiments in 'ecological' models, rather than eco-evolutionary models in which timescales are not apriori separated. Indeed, as shown in Hogeweg and Takeuchi (2003), spiral wave patterns are not robust against high mutation rates. Other interaction topologies, especially of RNA based complementary replication systems are, however, good candidates for ecosystem based information accumulation (Hogeweg and Takeuchi, 2003).

3. Eco-evolutionary models: interlocking timescales

3.1. Eco-evolutionary models

Here we extend the previous results to eco-evolutionary models in which ecological dynamics and mutational dynamics, are both taken into account simultaneously, although replication rates and mutation rates will in general differ by orders of magnitude. Thus we do not consider monomorphic populations, but 'quasispecies' (Eigen et al., 1989) in which variants are present not because of balanced competition, but because of mutational processes. Also in well mixed systems taking mutational dynamics into account may change the ecological dynamics profoundly, and even more so the smaller the mutation rate (van der Laan and Hogeweg, 1995). Here we examine the impact in combination with spatial pattern formation and multiple levels of selection and sticking close to a classical population dynamic model, fixing the basic interaction patterns. To do so we assume 'phenotypic mutations', i.e. mutations only make small changes in the parameters of the model.

3.2. Evolution of directed migration in host parasitoid models

Nicholson and Bailey Host-Parasitoid models (1935) were first studied in a spatial context by Rohani and Miramontes (1995) in a lattice map model. They studied the directed migration of parasitoids, seeking to what extent directed mutation of parasitoids was benefiting the parasitoids. Spatial patterns formed in the model is a mixture of spiral and chaotic waves similar to those found in Complex Ginsburg Landau equation close to the Hopf bifurcation. Savill et al. (1997) extended their ecological model to an eco-evolutionary model with a mutation rate 3 orders of magnitude smaller than replication rates, and studied how spatial pattern formation influenced the direction of selection, as well as how spatial pattern formation itself was affected by the evolved directional migration. Three levels of selection play a role: local interaction between host/parasitoids, spiral and turbulent waves, and competition between regions of spiral waves and turbulent waves. Their main conclusion, and title of the publication, was "self-reinforcing spatial patterns enslave evolution in a host parasitoid system". Parasitoids in a particular type of the spatial pattern evolve migration parameters such that this type of spatial pattern can out-compete the other types of spatial pattern. For details see Savill et al. (1997).

3.3. Diversity through time-dependent fitness

The insight from the study of Savill et al. we want to highlight here, is that in such a multilevel selection system, fitness is not a static property of the dynamics, but a complex time-dependent function. This fundamental property of spatial eco-evolutionary models which is often ignored in discussions on evolutionary systems has also been stressed by Rauch et al. (2002). In the system described above, measuring inclusive fitness as number of offspring in subsequent generation, we see that over a period of 50 generations the higher the chance of migrating toward the host, the more offspring. Despite the different selection pressures in different spatial patterns, this is true everywhere. However, over a longer time period, it is the lower chances of migration toward the host who win out. This is not a transient phenomenon, but true over every window in time. It is this complex time-dependent fitness which maintains high diversity in the system.

4. Individual based diversity and population based diversity as alternative attractors

4.1. Variable genome size

The previous models all properly belong to the class dynamical systems in which the variables and interactions are predefined. For example, despite the fact that the initial question was posed in terms of information accumulation and length of RNA strings, the models were formulated in terms of fixed

length strings and fixed interactions. Also in the type of eco-evolutionary models discussed in which only the parameters of the model are subject to mutations, and only a fixed set of potential values are considered, the structure of the state space of the model is well defined. In the following sections the structure of the model is progressively less well defined apriori.

Although evolutionary processes have been mostly studied in terms of point mutations in a fixed genome structure, the current whole genome sequencing projects have revealed that genome rearrangement involving duplications and deletions at various scales play a very important role. Indeed complexification of genomes is mainly through gene duplication and diversification. To model such a processes a variable genome structure is needed. As a first step we do this by defining individuals with a variable number of genes, which each has a predefined function. Such a model can still be reduced to a fixed genome size model by simply defining 'empty genes', but is nevertheless a useful intermediate to introduce more flexible model structure of the next sections.

4.2. RM systems as model systems for gene multiplication

As the simplest case of a variable genome structure we review the study of the accumulation and loss of plasmids carrying restriction modification (RM) systems in bacteria (Pagie and Hogeweg, 2000a). Restriction enzymes cut a DNA sequence at a specific sequence motif. Bacteria can carry plasmids on which restriction enzymes and protection against them occur together. The 'modification' enzymes methylate the DNA at the motif such that the restriction enzyme will not cut the DNA. Thus the bacterial DNA will be protected against the cutting, whereas foreign DNA (e.g. viruses) may be cut, i.e. the RM systems can provide a defense mechanism against virus infections. Pagie and Hogeweg defined a CA model in which bacteria can carry a variable number of plasmids, each carrying either both enzymes or only the modification enzyme (a bacterium with only the restriction enzyme dies), and viruses which may or may not be modified (methylated)

at various DNA motifs. Plasmids are transmitted most often vertically and occasionally horizontally, and loss of function mutations occur in both their genes. Viruses can infect hosts which do not contain restriction enzymes targeting motifs which are not methylated in their genomes, or with a very small chance those who do in which case they become methylated at those sites. They lose methylation when reproducing in a host without the proper modification enzyme.

Starting from bacteria without plasmids, characteristic "predator–prey" waves form of bacteria, virus infected bacteria and empty space (Fig. 2a). Slowly the bacteria accumulate plasmids containing RM systems with different specificities. However, this does not alter the spatio-temporal dynamics of the system as the virus population also accumulates resistance (methylation) at all these motifs. At some point, however, when loss of two different restriction enzymes in two subpopulations occurs, a progressive breakdown of individual based diversity sets in and it is replaced by population based diversity (Fig. 2c). Simultaneously the predator/prey waves disappear and a relatively stationary patch like structure of the different subpopulations forms (Fig. 2b). Moreover the bacterial density increases dramatically, and the virus population subsides or dies out altogether. In the latter case all plasmids are eventually lost and the cycle can start anew.

4.3. Alternative attractors and scenario's of speciation

Individual based diversity and population based diversity are alternative attractors in this RM system. Over a large range of number of RM types in the population they may occur in either mode (Fig. 2d). Interestingly, it has indeed been shown that very similar orthologous genes may function as basis for population based diversity, where different alleles stably coexist in a population, and as basis for phenotypic plasticity by up/down regulation of its expression. A case in point involving taxonomically very different species, is the population based rover and sitter types of *Drosophila*, and the
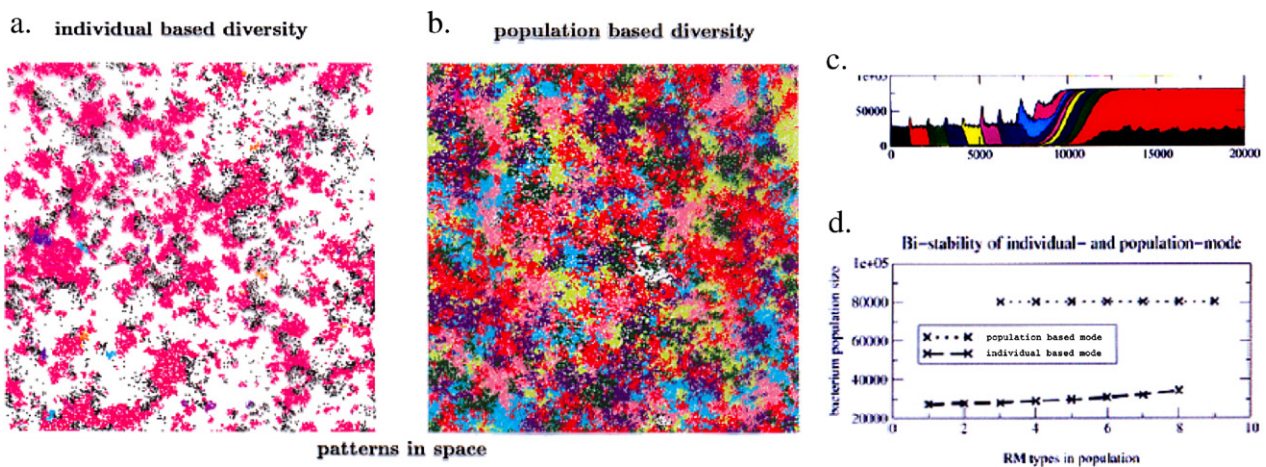

Fig. 2 – Spatial patterns for individual based (a) and population based (b) diversity. (c) Buildup of individual based diversity and sudden transition to population based diversity (colors give number of plasmids per individual). (d) Bistability for intermediate number of plasmids in terms of population size of bacteria: (low individual based diversity, high: population based diversity) cf. Pagie and Hogeweg (2000a).

phenotypic switch to foragers in bees which are both regulated by a very similar (orthologous) PKG (Ben-Shahar et al., 2002).

In the RM system model, a switch from individual based to population based diversity occurs by complementary loss of plasmids in the population. It is interesting to speculate about how frequently a similar scenario may underly speciation. After gene duplication and specialization or sub-functionalization of the genes differential loss of the genes is both a mechanism for speciation (because of mating incompatibility) and an adaptive scenario (niche differentiation). Bioinformatic sequence analysis of gene loss after whole genome duplication in yeasts appears to suggest that such a 'paralog first' mode of speciation (leading to pseudo (or false) orthologs) might indeed have occurred (Scannell et al., 2006). From a dynamical systems point of view it has been demonstrated in simulation studies by Kaneko and Yomo (2000) (see also Hogeweg, 2002). Also, at the phenotypic level, developmental plasticity has been documented to mirror taxonomic diversity (e.g. Gomez-Mestre and Buchholz, 2006).

However, the opposite route, in which allelic diversity precedes retention of duplicated genes has also been proposed (Proulx and Phillips, 2006) and will be discussed in the last section of this paper. In the case of RM systems this route does, however, not occur unless first all plasmids are lost.

5. Evolution of information processing in individuals and ecosystems

5.1. Modeling 'constructive' evolution: evolutionary signatures

In the previous discussed models, the potential phenotypic repertoire of the individuals is predefined. The genotype–phenotype mapping, if considered at all, is very simple. This is certainly not the case in organisms. Nonlinear genotype–phenotype mapping has profound influence on the evolutionary dynamics. Moreover, the previous models, and all population genetic models, do not view evolution as a constructive/creative process, i.e. as a way to create complex information processing systems (as it clearly has). In contrast evolutionary computation does use Darwinian mutation/selection processes as an effective design tool. To this end an external fitness criterion is (artificially) imposed, as an effective way to explore the capabilities of the evolutionary process.

We follow the approach pioneered by Hillis (1990) in using a co-evolutionary protocol in which 'problem solvers' and 'problem cases' co-evolve, and the fitness of the solvers depends on the number of (neighboring) problems solved, and the fitness of the problem cases is in terms of not being solved. Here we use this approach to investigate how the system achieves the higher fitness. We use the term 'evolutionary signatures' to denote the properties of the evolved system which are due to the evolutionary process rather than due to the structure of the problem to be solved. We use two different flexible genotype–phenotype mappings: Genetic programming (GP), i.e. a mapping from LISP programs to what they compute; and CA's, i.e. the mapping from rules to the transformation from initial condition (IC) to an attractor.

Both these mappings are multiple to one so that the evolution can indeed 'choose' how to solve a problem.

We focus on three phenomena:

1. information integration due to spatial pattern formation;
2. red queen dynamics and the evolution of evolvability; and
3. ecosystem vs. individual based information processing.

5.2. information integration in evolutionary time

An often cited requirement for 'sound' evolutionary explanations is that only immediate fitness benefits should be considered (e.g. Maynard Smith and Szathmáry, 1995). Although this requirement is a safeguard against unwarranted inferences, we have seen above that processes at multiple space- and timescales determine the evolutionary trajectory of eco-evolutionary processes. In constructive co-evolutionary models this interplay of multiple timescales is essential for the evolution of complex behavior ("solving the problem"). At every generation only a very small subset of problem cases determine the fitness, yet in the end a problem solver 'integrates' the information seen over many generations, and can evolve a problem solver for all possible cases. Indeed Pagie and Hogeweg (1997) (see also Mitchell et al., 2006) in a function optimization problem, using genetic programming (GP) have shown that under such 'sparse fitness evaluation' better problem solvers evolve than when the 'complete' set of problems is presented at every generation.

Spatial pattern formation appears to be essential in this respect. This was shown by comparing directly a spatial co-evolutionary system with the same system in which pattern formation is disrupted by shuffling all individuals at every generation. (Pagie and Hogeweg, 2000b; see also Pagie and Mitchell, 2002). They used as paradigm system density classification in CA (first introduced by Crutchfield and Mitchell (1995) as paradigm system for 'emergent computation'). Thus CA rules are to be evolved which transform an initial condition with a majority of 0/1 in a homogeneous state of all 0/1.

In the case of spatial pattern formation they achieve an average of ca 70–80% accuracy on a random test set, whereas the shuffled ones are 'correct' in just 50% of the cases, which they achieve by transforming to uniform either 0 or 1 irrespective of the initial condition (Fig. 3b). Note that, no perfect CA density classifier exists, making this an interesting paradigm system for ecological 'problem solving'!

The spatial pattern formation (Fig. 3c), unlike that of the cases discussed above, is not due to interactions of predefined species, but involves 'speciation' (Fig. 3a): separate lineages (species) of problem cases emerge: those with majority 0 and with majority 1 which form chaotic waves so that the problem solvers are confronted with these qualitative different cases at intervals of all different length. Over time 'smart' individuals evolve which sense and process their changing environment appropriately, i.e. solve the density classification problem. Apart from this 'regulatory adaptation' they also continue to change evolutionary to adapt to the changing set of specific problems they encounter: although their average performance on a random set of initial conditions is only 70–80% they solve on average more than 90% of the cases they encounter.
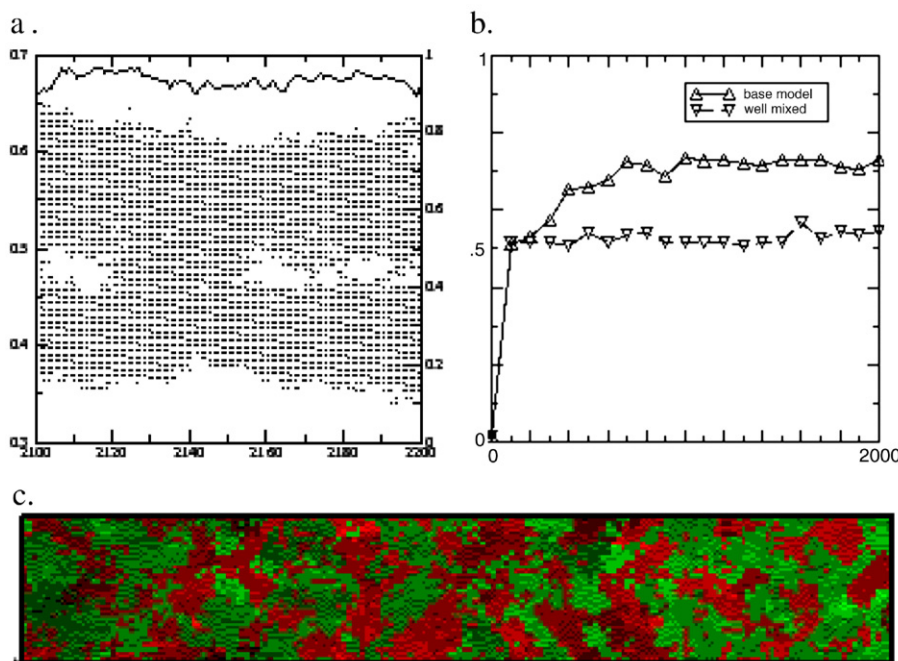
Fig. 3 – Evolution of density classifiers; (a) Speciation of initial conditions: majority 1 (density 1 between .5 and .6) and majority 0 (density 1 between .35 and .45); upper line: average fitness (ca. 90%). (b) Evolved performance on random set of initial conditions: upper line with spatial pattern formation; lower line shuffled. (c) Space time plot of density in initial conditions: green < .5, red > .5 (cf. Pagie and Hogeweg, 2000b).

In the well mixed case, speciation does not occur, the evolved individuals do not 'sense' their environment, and simply 'guess' that all encountered cases will be majority 0 or 1. However, averaged over time they also are 'correct' in over 90% of the cases they encounter! This is explained in the next section.

5.3.   Evolution of evolvability: mutational priming

The high fitness on encountered cases of the non-classifiers evolved in the shuffled case, as described above, is due to the fact that the population of classifiers is most of the time converged to either all majority 0 or all majority 1, although they switch fairly frequently between these states. The non-classifiers have evolved so as to co-evolve very efficiently in a red-queen like manner: in the evolved CAs only 1 mutation suffices to change from processing all ICs to all 1 or all ICs to all 0. We call such optimization of the genotype such that 'appropriate' phenotypic change occurs more easily 'mutational priming'. It is the result of random mutations and selection, but it makes mutations at the phenotypic level less random and evolution more powerful (Pagie and Hogeweg, 2000b; Hogeweg, 2005).

5.4.   Ecosystem based information processing

Attempts to evolve complex information processing (problem solving) so far have been conceived, formulated and studied in terms of information processing at the level of the individuals. In Section 4 it was shown that evolution can lead to either individual based diversity (complexity) or population based

diversity (complexity). As discussed above in Section 5.2 evolution of individual based complexity appears to require complex pattern formation at the level of the ecosystem, which involves a certain degree diversification (speciation) at the population level.

de Boer and Hogeweg (in preparation) are currently broadening the perspective of evolution of problem solvers, such that the problem solvers can be ecosystems as well as individuals and study which mode of problem solving is 'chosen'.

Viewing ecosystems as information processing systems we add to the previously discussed models an aspect of ecosystems which is largely ignored in population dynamic models, i.e. the 'environmental engineering' which occurs as a side-effect of the presence of one species which can be used by other species. This often involves 'preprocessing' of food, but can also involve e.g. retention of water (see e.g. Gilad et al., 2006) or more general niche construction (Laland and Sterelny, 2006).

Here we extend the spatial predator–prey co-evolutionary problem solving systems with 'leftovers' and 'scavengers'. Otherwise we use the Genetic Programming (GP) based function optimization model of Pagie and Hogeweg (1997) mentioned in Section 5.2 in the context of sparse fitness evaluation. The two CA planes of predator–prey system, i.e. the plane of Lisp functions and the plane of XY coordinates on which the function is evaluated, are unaffected by the addition of the two additional CA planes of leftovers and scavengers Leftovers are represented as an XY coordinate (i.e. the original 'prey') and a constant representing what is left after consumption (attempt to solve) of that XY coordinate by
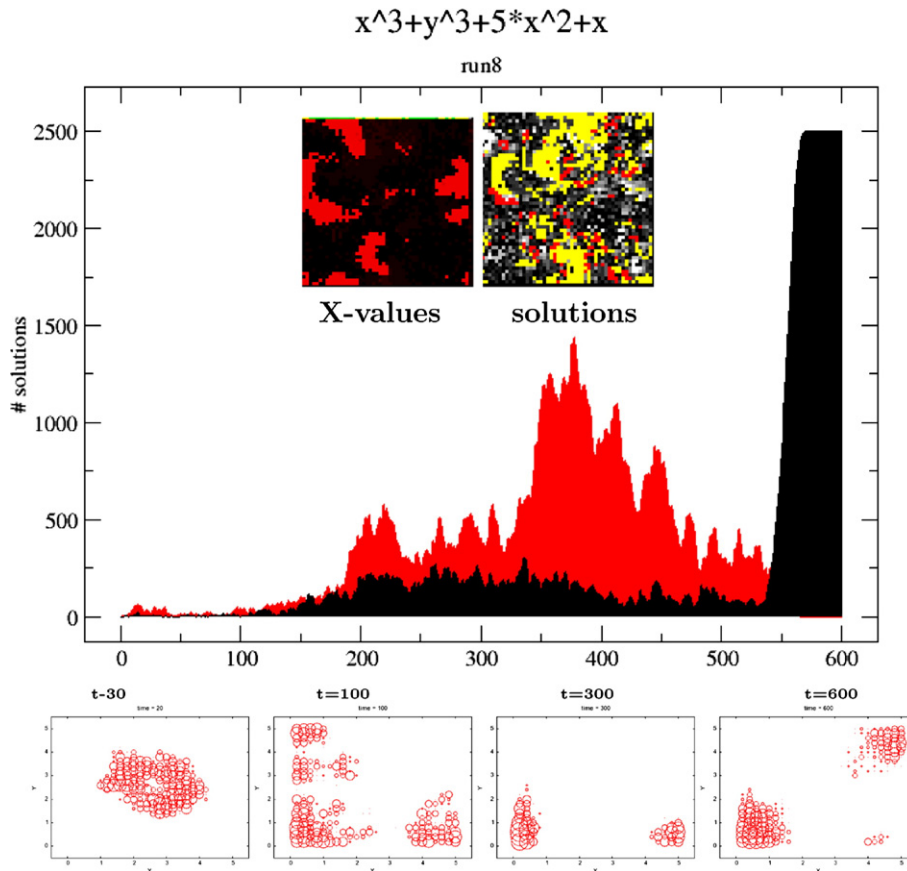
Fig. 4 – Ecosystem based problem solving precedes individual based problem solving in scavenger systems. Upper panel: number of solved cases (=*XY* coordinates) through time: black by predator; red by predator and scavenger together. From *t*~ 200–550 correct solution of cases is done by the collaborative full solution of the function. From *t*=550 onward the solutions are done by the full solution of only the predator. Inserts in upper panel: left: spatial pattern of *X* coordinates (*t*=300). Right: spatial pattern of collaborative solutions (*t*=300). Lower panel: Speciation of the *XY* coordinates, depicted in *X–Y* space (cf. de Boer and Hogeweg, in preparation).

the 'predator'. Scavengers are again Lisp functions which evolve to consume the leftovers. Preliminary results, using a very simple function, are shown in Fig. 4.

It turns out that the system first finds an ecosystem based solution of the function, where part of the polynomial is solved by the predators and part by the scavengers. Interestingly, in the prey (and therewith in the leftovers), a complex speciation process occurs (Fig. 4 lower panel), leading during the period of ecosystem based solutions to a low-X low-Y subpopulations and a high-X low-Y subpopulation which form chaotic wave patterns. Likewise speciation occurs in the evolved Lisp functions of both the predators and the scavengers. The subspecies of scavengers solve, in the example shown, respectively the X^3 and the Y^3 term, whereas the predators solve the rest. The spatial patterns coordinate such that the prey-leftover pairs are often solved completely (yellow in the insert of Fig. 4) by a predator and a scavenger together.

In the end the predator evolves the complete solution, as indeed was found in the earlier work of Pagie and Hogeweg (1997) and Mitchell et al. (2006). As yet it is an open question when the ecosystem based solution prevails over the individual based solution. This might be the case when the function becomes more complex. For now this example shows, in contrast to the case of RM systems discussed above, a scenario of ecosystem based complexity preceding individual based complexity.

The 'ecosystem first' scenario is also interesting relative to the problem of information accumulation in prebiotic evolution with which we started our discussion on eco-informatic processes (Section 2). It suggests that irrespective of information threshold problems, distributed, ecosystem based, 'problem solving' may more easily evolve initially than individual based problem solving. In future work we will address this issue explicitly.

6.   Discussion and conclusions

In analogy with bioinformatics (Hogeweg, 1978, see definition of bioinformatics in Oxford English Dictionary) we use the term ecoinformatics for the study of informatic processes in ecosystems. For this we need static, pattern analysis approaches, as well as dynamic simulation based approaches. Also similar to bioinformatics the first large scale developments in ecoinformatics appear to be in pattern analysis studies and large databases. In this paper we focussed on

developments for studying the dynamics of information processing in ecosystems through simulation studies.

We have first reviewed studies which show conclusively that adding space explicitly to classical population dynamic models alters their behavior profoundly, due to large scale pattern formation and multilevel information processing. The so-called implicit spatial models, including most metapopulation models, as well as low order mean field studies of spatial models, fail to uncover these phenomena. We emphasized that in such multilevel systems ecological and evolutionary timescales cannot be separated, and that processes at multiple timescales determine what evolves.

Next we went beyond spatial eco-evolutionary models based on population dynamic models, in which the interactions between populations are largely predefined, to models in which the interactions evolve more freely. In doing so we imported back the methods which are mostly known as "Biological Inspired Computing" (BIC). We do not use these models for biological data analysis as is commonly done. Instead we can call our approach BIBIC (biological inspired biological inspired computing), as we use them as paradigm systems for studying ecosystems.

In this context we view ecosystems as problem solving systems. We used fully artificial problems, but view them as analogy for ecosystem problems such as: "how to cope with e.g. high temperatures, low levels of some nutrients and drought", or other problems set by the environment (or environmental change). We have demonstrated that alternative modes of problem solving can evolve, focusing on the level of diversification: at the level of individuals, which then may adapt physiologically to different circumstances, or on the level of populations, leading to speciation or to optimized red queen evolution. Although we have emphasized the different signatures, we should note that they are interlinked: we have shown that speciation and pattern formation are essential for the development of general problem solving individuals as well as problem solving ecosystems.

Interestingly, from a geological point of view, it has often been emphasized that species composition of ecosystems may remain virtually invariant despite large changes in e.g. climate (see e.g. Cannariato et al., 1999). Obviously, micro-evolutionary changes are not observable in those studies. Such ecosystem resilience may be due to physiological versatility (individual based diversity) or due to evolutionary 'wiggles' of the species (compare van der Laan and Hogeweg, 1995) as seen in the examples above. It is, however, tantalizing to speculate whether information integration processes may operate on the ecosystem level, when, not only 'problem cases' confronting individuals change over time, but indeed the problem definition changes over time. We will extend our studies in the near future to include changing environments in the form of changing problems (as opposed to problem cases) at multiple timescales.

Acknowledgements

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