An approach to modelling the dynamics of evolutionary self-organization

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ABSTRACT

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We have simulated the dynamics of species evolution in a systems context on a parallel
supercomputer. Population dynamics are represented as generalized Lotka–Volterra sys-
tems defined as points in a generalized phenotype or character space T. Populations which
are closest in T compete most strongly for resources. A variety of systems with varying
assumptions, resource distributions, and number of trophic levels were simulated. Starting
with a random initial seed proceeding through a complex temporal sequence, most cases
converged to essentially the same configuration. The final equilibrium state consisted of a
gridwork of localized population clusters in T, representing individual species. The inter-
cluster spacing was roughly equal to the standard deviation of the resource utilization
function. Thus the systems self-organize to an array of niches which maximally fills the
available volume of resource space while minimizing the overlap of resource utilization
functions.
  The simulations were performed on a Connection Machine (a massively parallel super-
computer) which allowed up to 32000 distinct points in character space to be modelled in
parallel. Simulation allows a more realistic treatment of evolutionary dynamics and greater
flexibility in experimental manipulation than previous analytical approaches.
  We experimented with temporal variations in the resource base. In most cases the niche
structure was not affected; species prospered or declined as a function of local resource
availability but the niche pattern remained invariant. However, in the case in which each
species depends on only one or two resources, increasing randomness in the resource base
resulted in a decrease in the number of species.

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INTRODUCTION

Our purpose in this experiment was to increase our understanding of evolutionary self-organization in communities of species by studying of the dynamics of relatively simple systems. We have attempted to choose a system which is complex enough to capture some of the principal features of systems level evolution, while remaining simple enough to foster insight into its dynamics. We proceed in the spirit of recent findings in nonlinear dynamics (Grebogi et al., 1987), which have demonstrated that very simple systems can produce very complex behavior and exhibit universal properties in common with much more complicated systems. Whereas previous approaches (MacArthur and Levins, 1967; MacArthur, 1969, 1972; May and MacArthur, 1972; May, 1974; Roughgarden, 1976) have emphasized analytical analysis of simple systems, this complementary approach emphasizes experimental exploration of system dynamics as simulated on (super)computers. The experimental approach allows greater depth in the treatment of evolutionary dynamics and greater flexibility in experimental manipulation than previous analytical approaches. We seek to shed some light on the questions: Why are there discrete species? What factors determine the number of species that can coexist in a community? What are the processes which drive speciation and determine the "width" of species in trait space?

To address these questions we define a resource space R whose axes represent continuously varying characteristics of the available resource base such as food size, location, composition, etc. We also assume a space of species T (defined more rigorously in the next section) indexed by the variable i. The ability of a species i to utilize resources with a given set of properties $x \in R$ is characterized by a resource utilization function $f_i(x)$ defined on R. These functions are peaked at the species' preferred resource type $x_0 \in R$ and decrease rapidly with distance from x_0 in R. The "width" of the utilization function $f_i(x)$ is represented by the function's standard deviation Γ_i. In this paper we will consider an organism's realized "niche" to be coextensive with its resource utilization function.

Within this framework we can discuss the species packing problem in terms of the "competitive exclusion principle". Many mathematical models have been developed (MacArthur and Levins, 1967; MacArthur, 1969, 1972; May and MacArthur, 1973; May, 1974; Roughgarden, 1976) to derive a "limiting similarity" among competing species which disallows the coexistence (within an equilibrium community) of different species which utilize the same resources. One class of models (May and MacArthur, 1972) starts with the ecological models of Volterra (1926) and Lotka (1925) and introduces evolutionary factors by treating the ecological constants as

evolutionary variables. These models assume that communities are composed of a set of species which differ by the minimum possible amount, and then proceed to derive the amount of niche overlap which is consistent with stability at equilibrium. Another approach (Roughgarden, 1972) starts with the equations of theoretical population genetics, and introduces evolutionary factors by treating relative fitnesses as varying in space or with population density. These models differ in assumptions and stability criteria, but all lead to essentially the same conclusion: species packing reaches a limiting value roughly equal to the width of the resource utilization function.

These models raise the questions: Do species in communities actually differ by the minimum possible amount? What mechanism would generate such a configuration? The mechanism suggested by May and McArthur (1972) is invasion coupled with extinction; however, according to Roughgarden (1976), evidence for this theory seems lacking. Roughgarden (1976) proposes the alternate theory that resource partitioning among competing species is an evolutionary compromise between the competing pressures of character displacement and the inherent cost of any shift in resource utilization. His coevolution models postulate an initial configuration composed of nonzero populations for every possible phenotype (i.e., point in phenotype space) and then utilize the Lotka–Volterra competition equations to derive the final equilibrium state. The model version which is closest to the models presented here predicts a stable equilibrium in which the convolution of the population distribution (defined below) is equal to the resource distribution, allowing unlimited species packing. (This result is also obtained in our models in the special case of zero death rate and/or geometric resource utilization functions.)

These earlier models focussed on systems that were simple enough to be explored analytically. The final attractors of the proposed systems were solved for mathematically, but the dynamics of the systems were ignored. These models therefore fail to illuminate the evolutionary/population dynamic mechanisms which lead to a community composed of a certain number of discrete species. They are also inapplicable to systems which are too complicated to explore analytically, and to non-equilibrium systems which never settle into a stable attractor. We have attempted to address these limitations by developing computational evolutionary models of population dynamics which include the dynamics of mutation in phenotype space.

Initial work in this direction has been done by Allen and McGlade (1987), but has been limited by insufficient computational resources. In this paper we present a general approach to modelling the coevolutionary dynamics of communities which utilizes massively parallel computation.

This simulation-based approach is applicable to a wide range of systems, including those whose attractors cannot be found analytically. It allows us to follow the dynamics of the system in trait space as it self-organizes into a community of species. Deeper understanding of these dynamics will allow us to better predict the response of the system to parameter changes and dynamic perturbations.

A FORMAL FRAMEWORK FOR DESCRIBING EVOLVING SYSTEMS

We begin by developing a generalization of the resource space framework appropriate for describing evolving systems. This formalism is general enough to describe a wide range of evolutionary processes involving mutation, competition, and selection, but here we will focus on community evolution. Consider an N_T-dimensional phenotype space T, also known as "trait space" or "character space" (Allen and McGlade, 1987). Each point of T will represent a set of morphologies, strategies, or characteristics. For example, the components of T might represent speed, size, reproduction rate, prey-finding and predator-avoiding strategies, geographic location, or habitat height in a rain forest. Alternately, they might represent the spatial and temporal scales which characterize the organism.

The population density at a point $i = \{i_1, i_2, \ldots, i_{NT}\}$ in T will be denoted as $N(i)$. Thus $N(i)$ is proportional to the number of organisms which share the set of characteristics associated with i. A species will be represented as a localized "clump" of individuals in T. If reproduction is perfect (the mutation rate $r_m = 0$), the population dynamics proceeds independently at each point in T; mutation introduces dynamic mixing and coupling among the various points of T. As a first approximation, we make the following simplifying assumptions:

(1) Reproduction in T, whether sexual or asexual, produces a fraction r_s of offspring in the same cell in T as the parents and a fraction r_m of mutated offspring which populate neighboring cells in T.

(2) Mutations produce offspring which are no farther than one cell from one of the parents in T.

With these assumptions, evolutionary processes can be modelled as a diffusive population flow in T. To this end we define r_s to be the self-reproduction rate and r_m to be the mutation rate. Then the population $N(i)$ will reproduce itself at the rate $r_s N(i)$ and contribute to the populations at neighboring points $i + j$ in T at the rate $r_m N(i + j)$. Thus the dynamics of reproduction in character space can be described by the equation

$$B(N) = r_s N(i) + r_m \sum_{|j|=1} N(i+j) \tag{1}$$

where $i + j$ ranges over the neighbors of i in the sum over j, $|j|$ denotes the magnitude of j, and $B(N)$ represents the initial population distribution at the next timestep (generation). The parameter values used in the simulation described below are $r_s = 1.0$ and $r_m = 0.2$. Thus if the selection pressures are homogeneous (independent of i), a population initially concentrated at point i_0 in T will spread out over time and evolve toward a uniform distribution.

A MODEL OF EVOLUTION IN A COMMUNITY OF SPECIES

To describe the evolution of a community of species, we must add selection pressures to the reproduction dynamics described above. We define a resource space R such that point i in R represents the characteristics of the resources which support the population at point i in T. For example, if point i in T represents the time and space scales characteristic of a population of organisms, then point i in R represents the time and space scales characteristic of the resources that support the population. We denote the resource density at point i in R as $K(i)$. We postulate that the ability of a population at point i to utilize resources at j decreases as $|i - j|$ (the distance between points i and j in T or R) increases, and that populations which are nearest in T compete most strongly for resources, such that the magnitude of the competition diminishes as the separation in T increases. In order to incorporate these properties into our model, we postulate that the intensity of competition between populations at point $i + j$ in T and point i in T is proportional to $g_\Gamma(|j|)$, a decreasing function of $|j|$. We have experimented with four $g_\Gamma(|i|)$ functions: the constant function $g_\Gamma(|i|) = g_0$, a power function $g_\Gamma(i) = \exp(-g_0 |i|/\Gamma)$, a quadratic function with a sharp cutoff, and a gaussian distribution. The quadratic function is given by

$$g_\Gamma(|i|) = \begin{cases} 1 - g_0 |i|^2 \Gamma^2 & \text{if } |i| \leqslant \Gamma, \\ 0 & \text{if } |i| > \Gamma, \end{cases}$$

where Γ is the maximum range of competition and typically $g_0 = 0.75$. The gaussian function is given by

$$g_\Gamma(|i|) = \exp\left(-g_0 |i|^2/\Gamma^2\right)$$

where typically $g_0 = 1.3$ and $\Gamma = 5$. The results obtained for the different g_Γ functions are discussed below.

The total population pressure at a point i in T can now be represented as a sum over all neighboring populations within competitive range Γ of i,

modulated by the competition decay factor g, yielding a convolution term

$$C(\Gamma, N) = \sum_{|j| < \Gamma} g_\Gamma(|j|) N(i + j) \tag{2}$$

This convolution is a local weighted average over N, i.e. it can be imagined visually as a "blurred" version of the population distribution N.

We next postulate that the utilization rate of resources at point $i + j$ in R by a population at point i in T is proportional to the same $g_\Gamma(|j|)$ with possibly a different range Γ'. This postulate is based on the assumption that the population at point i in T is maximally adapted to utilize resources at point i in R, and its ability to utilize resources at point j in R decreases as the distance between i and j increases. The available resources at point i can then be expressed as a similar convolution term:

$$C(\Gamma', N) = \sum_{|j| < \Gamma'} g_{\Gamma'}(|j|) K(i + j) \tag{3}$$

This convolution is a local weighted average over K, i.e. it can be imagined visually as a "blurred" version of the resource distribution K. The precise form of this equation is somewhat arbitrary; many variations will lead to essentially the same final result. In a constant resource environment, the model is also fairly insensitive to the value of Γ', i.e. $\Gamma' = 1$ and $\Gamma' = \Gamma$ generate the same dynamics provided K does not vary drastically over range Γ. In a highly fluctuating environment, however, the generalists (relatively high Γ') have an advantage over the specialists (relatively low Γ'), and the model then becomes more sensitive to the value chosen for Γ'. Simulation results are discussed below.

We now model the evolutionary dynamics of $N(i)$ via a generalized Lotka–Volterra system with a saturation term proportional to the ratio of population pressure to available resources:

$$\dot{N}(i) = -\alpha N(i) + B(N, i)\left[1 - \frac{C(\Gamma, N)}{C(\Gamma', K)}\right] \tag{4}$$

where α is a death rate, $B(N)$ is a generalized birth rate given by Eq. 1, and the dot represents time differentiation. The choice of $C(\Gamma, K)$ rather than $K(i)$ in this equation is somewhat arbitrary, both forms lead to essentially the same results in most cases.

SIMULATING COMMUNITY EVOLUTION

We simulated the system described above on a CM with one processor assigned to each point in a two-dimensional phenotype space T. The initial state consisted of a single population concentrated at a single point in T. This population produces mutants which spread like a wave across T (Fig.
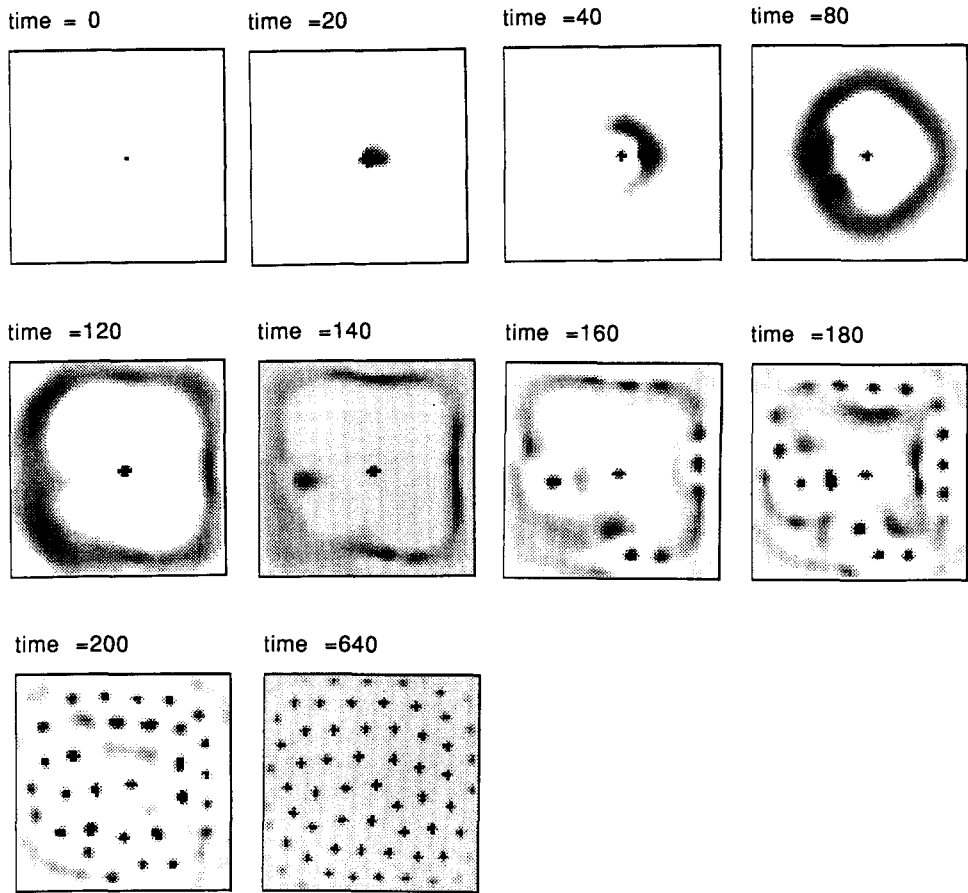
Fig. 1. Evolutionary dynamics starting from an initial seed population and self-organizing to form an array of niches in trait space.

1). The population at each point in T increases until the carrying capacity $K(i)$ is approached, limiting further growth. At this point the effect of competition is seen. The system begins a self-organization process which culminates in one of two possible equilibrium distributions (or "attractors").

The most common attractor is the latticework of "niches" as shown in Fig. 1 at time = 140. This final population distribution is largely independent of the initial starting configuration, and was observed with the constant, quadratic, and gaussian resource distribution functions. Populations are concentrated at points which form a two dimensional array, with the spacing between points equal to Γ, the competition range. Thus each population dominates a cube in T of size (edge-length) Γ, such that no mutant population can grow within the cube. The resources drawn from this cube support the population at its center, and invaders are competi-

tively excluded. The populations arrange themselves in clusters which maximally fill the available resource space, subject to the constraint that each cluster lie outside of the competition range of all the others. When clusters form that are separated from all other populations by a region of zero populations, we consider each cluster to be a different species. Thus we witness the dynamics of the evolution and self-organization of a community of species from a single seed species.

For certain special cases, the system converges to a smoothly varying attractor, such that the final population distribution $N(i)$ approximates the resource distribution $R(i)$. This result is obtained for rapidly decaying resource utilization functions (i.e. $g(i) = \exp(-g_0 \, |i|/T)$ or very small death rate ($\alpha = 0$). Very close packing is allowed in this configuration; quantization into discrete species does not occur; the entire resource space becomes one continuous niche. The models of May and MacArthur (1972) and Roughgarden (1976) converge to similar attractors for the case of geometric resource utilization functions.

EFFECTS OF RESOURCE VARIATION

We have experimented with many forms for the resource distribution $K(i)$, including both stochastic and deterministic spatio-temporally varying distributions, and a resource depletion model described by the equation

$$\dot{K}(I) = R_0 \big(K_{eq}(i) - K(i) \big) - R_1 C(\Gamma, N) \tag{5}$$

where $K_{eq}(i)$ is the equilibrium resource distribution, R_0 and R_1 are parameters, and $C(\Gamma, N)$ is the convolution term described above. The general lattice structure described above seems to be insensitive to the form and dynamics of $K(i)$, however the size of the populations at each of the lattice points does depend on the availability of local resources. Thus the form of the lattice remains invariant under resource fluctuations, but the size of the populations at the lattice points will fluctuate in response to the variations in available resources. In some cases the resource fluctuations will cause an extinction, leaving a gap in the lattice structure. Species with small values of Γ' (i.e. specialists) are particularly vulnerable to extinction due to stochasticity in the resource distribution; this case is described in detail below.

EFFECT OF PREDATORS

We added another trophic level to the model community by introducing predators. The predator dynamics will have the same general form as the prey dynamics, except that N is now considered a resource for P, so that

the population pressure term is proportional to the ratio of the nearby predator population density to the nearby prey population density. The parameters Γ_N and Γ_P will represent the prey and predator competition ranges respectively. The set of equations describing the system is now

$$\dot{N}(i) = -\alpha_N N(i) + B(N, i)\left[1 - c_N \frac{C(\Gamma_N, N)}{C(\Gamma_N', K)}\right] - \text{Pred}(P, N) \tag{6a}$$

$$\dot{P}(i) = -\alpha_P P(i) + B(P, i)\left[1 - c_P \frac{C(\Gamma_P, P)}{C(\Gamma_P, N)}\right] \tag{6b}$$

$$\text{Pred}(P, N) = p_1 N + \frac{C(\Gamma_P, P)}{(p_2 + N)} \tag{6c}$$

$$B(N) = r_s N(i) + r_m \sum_{|j|=1} N(i+j) \tag{6d}$$

$$B(N) = r_s P(i) + r_m \sum_{|j|=1} P(i+j) \tag{6e}$$

$$C(\Gamma_N, N) = \sum_{|j|<\Gamma_N} g_{\Gamma_N}(|j|) N(i+j) \tag{6f}$$

with similar equations for the other convolution terms. Typical parameter values are $p_1 = 0.02$, $p_2 = 5$, $c_P = 0.2$, $c_N = 0.2$, $\alpha_N = 0.1$, $\alpha_P = 0.1$, $r_s = 1.0$, $r_m = 0.2$.

We simulated this system on a CM, using Euler's method. In this case both N and P form population lattices. The herbivore (N) populations converge to a grid of niches (as described above) with spacing Γ_N. Thus the herbivore lattice is essentially unchanged by the addition of predators, except for a reduction in population sizes. The predator populations converge to a lattice which represents a compromise between the opposing pressures to (1) maximize P-N overlap, and (2) form a lattice with spacing Γ_P. We experimented with a number of variations of the model in Eqs. 6; and found that this dynamic attractor seems to be very robust to changes in the parameters and in the structure of the model.

STABILITY–COMPLEXITY INVESTIGATIONS

The relationship between stability and diversity has been long debated by ecologists (May, 1973). We have utilized the evolutionary models discussed above to investigate the hypothesis that high (low) environmental predictability leads to high (low) community diversity. Although precise definitions of predictability exist (Colwell, 1974), for the purposes of these investigations we simply equate decreasing predictability with increasing

fractional resource variation Rf (defined below). We used a stochastic resource distribution function given by

$$K(i) = K_0(i) + r(i) \tag{7}$$

where $K(i)$ is the deterministic component of the resource distribution, and $r(i)$ is a set of independent random variables with amplitude R. The fractional resource variation is given by $Rf = R/K_{max}$, where K_{max} is the maximum value of $K(i)$ at $t = 0$. The behavior of the model is strongly dependent on the value of Γ', the range of resources that can be utilized by the species. For $\Gamma' = 0$ (i.e. $CVN(\Gamma', K) = K(i)$) the number of species drops from 50 to 38 as Rf varies from 0 to 0.5 (with no mutations). Including mutations in the model tends to buffer the impact of the environmental stochasticity, since areas of trait space that have been vacated by extinction can be repopulated by mutants. For $\Gamma' = 7$, however, the number of species remains invariant as Rf varies. A species that averages over a number of resources that vary independently is more stable than a species that depends on a single resource that varies with the same degree of stochasticity. Thus we conclude that in this model increasing (decreasing) resource predictability leads to increasing (decreasing) diversity if: (1) the scale of the resource variation is comparable to (or larger than) the range of resources that can be utilized by the species in the community, (2) the rate of speciation/colonization is smaller than the extinction rate due to environmental stochasticity.

COMPARISON WITH FOOD WEB DATA

These simulation experiments have generated a simulated food web. We now compare the results of these simulations with data gathered from natural food webs. An immense collection of these data has been summarized by Cohen (1990) into a set of invariants. These invariants have been expressed in terms of five laws:
(1) Cycles are rare.
(2) Chains are short.
(3) The proportions of top, intermediate, and basal species remains invariant.
(4) The proportion of basal to intermediate links is invariant.
(5) The ratio of links to species is invariant.
The first two laws are built into our simulations. Our results are consistent with the third law, with the ratio of the number of predator species to the number of prey species equal to 1.00. The data on natural systems yield a value of 0.9 for this ratio.

The fourth law holds exactly, since the number of basal–intermediate links is proportional to the number of intermediate–top links with a proportionality constant of 1.0.

In accordance with the fifth law we find that the ratio of the number of links to the number of species is scale invariant. Data on natural systems yield a constant of proportionality of 1.8. Calculating this constant for our simulated web is problematic, because the number of links is not well defined, due to the presence of many weak, long-distance interactions. If only direct and nearest neighbor links are counted, with nearest neighbor links weighted 0.5 as compared to the much stronger links between species that are directly aligned in trait space, we derive a proportionality constant of 1.75, in close agreement with data from natural systems.

In conclusion, the simulated food webs seem to be consistent with the existing data from natural food webs. It is of interest for further investigations to compare the pattern of strengths of links to natural system data. In our simulated system, each intermediate and top level species had one strong link and several much weaker links to the level below. Data from natural systems (Baird and Ulanowicz, 1989) indicate that the pattern of link strengths is highly variable both seasonally and between different species, reflecting complexities that have not yet been incorporated into our models.

DISCUSSION AND CONCLUSIONS

This simulation illustrates the process of community formation. We have observed a single species bifurcate into many species which pack the available resource space, self-organizing to form an array of niches. The processes of mutation and selection are adequate to generate a community composed of discrete species separated by the minimum possible distance in phenotype space. The quantization of species and self-organization of the ecosystem are driven by a dynamic balance between inter-specific and intra-specific competition. The mutation process combined with intra-specific competition produces a drive to expand in T, generating adaptive radiation. Inter-specific competition produces a repulsive force between species in T, generating quantization of species.

We see that populations are not adapting to a set of preformed niches; rather the niche structure emerges through a process of self-organization which involves the entire system. Although the dynamics are driven by local processes (reproduction and competition among neighbors), the final configuration is a reflection of the global structure of the resource space. Varying the initial conditions may affect the exact placement of the niches, but has little effect on the global structure that emerges.

Ecosystem theorists have often debated whether ecosystem stability and structure can be understood in terms of a simple Darwinian struggle for existence (Okasen, 1988) or whether cybernetic or other global ordering principles (Patten and Odum, 1981) are also needed. In the simulations presented here, global order and stability are seen to emerge from the local dynamics of mutation and competition in the context of global rules and constraints governing the system. Admittedly, these simulations are only a dim reflection of the awesome complexity of natural ecosystems. While they do not provide definitive answers to these long-standing questions, we feel that the general approach has promise and will lead to a better understanding of the subtle interplay between local behavior and global constraints. We now have the computational resources to allow much more realistic simulations. Future work should allow us to carry out more detailed experiments on the dynamics of evolutionary self-organization.

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