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# A Comparison of Evolutionary Activity in Artificial Evolving Systems and in the Biosphere

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#### Abstract

Bedau and Packard [7] devised an approach to quantifying the adaptive phenomena in artificial We use this approach to define two systems. statistics: cumulative evolutionary activity and mean cumulative evolutionary activity. Then we measure the dynamics of cumulative evolutionary activity, mean cumulative evolutionary activity and diversity, on an evolutionary time scale, in two artificial systems and in the biosphere as reflected in the fossil record. We also measure these statistics in selectively-neutral analogues of the artificial models. Comparing these data prompts us to draw three conclusions: (i) evolutionary activity statistics do measure continual adaptive success, (ii) evolutionary activity statistics can be compared in artificial systems and in the biosphere, and (iii) there is an arrow of increasing cumulative evolutionary activity in the biosphere but not in the artificial models of evolution. The third conclusion is quantitative evidence that the artificial evolving systems are qualitatively different from the biosphere.

### **1** Evolutionary Activity Trends

We propose a way to quantify certain long-term trends involving adaptation in evolving systems, and we compare such trends in the fossil record and in data from two artificial evolving systems. Long-term patterns in the history of life on Earth have been actively discussed ever since evolution theory originated with Lamark and Darwin. This is no surprise for those, like ourselves, who agree with McKinney ([22], p. 28) that "[t]he concept of 'trend' is arguably the single most important in the study of evolution."

This discussion of evolutionary trends has become connected with myriad issues, including the role of adaptation in evolution, the directionality of evolution especially with respect to various kinds of complexity or organization—and the allied general notion of progress. Recent work on long-term trends in the history of life on Earth spans the gamut from (i) studies of transitions in the evolution that suggest directionality related to taxonomic diversity [33], taxonomic survivorship [27], or structural and functional complexity of organisms [21]; to (ii) decrial of any suggestion of "progressive" trends [12, 10, 13, 31], including those involving complexity and adaptation; to (iii) an intermediate insistence on "emphatic agnosticism" based on the difficulties of quantifying and measuring complexity [25]. Controversy about the adaptive significance of long-term evolutionary trends partly reflects a broader controversy about the role of adaptation in biotic evolution in general; work on this topic spans another broad gamut, ranging from a rejection of the notion that adaptation is quantifiable or measurable [14] to experimental tests of adaptation in evolving populations of bacteria [36]. And similar themes are now surfacing in studies of artificial evolving systems, in which one finds claims to have observed long-term trends of "open-ended evolution" or "perpetual novelty" [19, 29, 17].

Our concern in this paper is with trends involving adaptation rather than complexity, and our primary aim is to make a quantitative comparison of such trends in model systems and in the biosphere. We think that adaptation is indeed quantifiable and measurable, using *evolutionary activity*, an approach first introduced in the context of model evolving systems [7] and here slightly modified so that it applies to both model evolving systems and to data from the fossil record. Our procedure will be to compare the dynamics of evolutionary activity displayed in the fossil record with that displayed in two artificial evolving systems—the Evita model and the Bugs model. We hope our comparison of evolutionary activity in artificial and natural systems will lead to a better understanding of whether and, if so, why evolving systems exhibit long-term trends involving adaptation.

Evolutionary activity (or "activity", as we will sometimes say for simplicity) is computed from data obtained by observing an evolving system. In our view an evolving system consists of a population of components, all of which participate in a cycle of birth, life and death, with each component largely determined by inherited traits. (We use this "component" terminology to maintain generality.) Birth, however, allows for the possibility of innovations being introduced into the population. If the innovation is adaptive, it persists in the population with a beneficial effect on the survival potential of the components that have it. It persists not only in the component which first receives the innovation, but in all subsequent components that inherit the innovation, i.e., in an entire lineage. If the innovation is not adaptive, it either disappears or persists passively.

The idea of evolutionary activity is to identify innovations that make a difference. Generally we consider an innovation to "make a difference" if it persists and continues to be used. Counters are attached to components for bookkeeping purposes, to update each components' current activity as the component persists and is used. If the components are passed along during reproduction, the corresponding counters are inherited with the components, maintaining an increasing count for an entire lineage. Two large issues immediately arise:

- 1. What should be counted as an innovation? In fact, innovations may be identified on many levels in most evolving systems. We define an innovation as the introduction of a new component into the system. In the case of Evita, the components are entire genotypes. In the case of Bugs, they are also genotypes, though in previous studies, innovations on the level of individual alleles have been measured [7, 4]. For the fossil record, components will be taxonomic families; an innovation is the appearance of a family in the fossil record.
- 2. How should a given innovation contribute to the evolutionary activity of the system? We measure activity contributions by attaching a counter to each component of the system. In all the work we present

here a component's activity counter is incremented each time step if the component simply exists at that time step. Though there are ways to refine this simple counting method, and we discuss some of them below, we use this version because it is directly applicable to the fossil data.

More formally, let  $f_i(t)$  indicate whether the  $i^{\text{th}}$  component is present in the record at time t:

$$f_i(t) = \begin{cases} 1 & \text{if component } i \text{ exists at } t \\ 0 & \text{otherwise} \end{cases}$$
(1)

Then we define the evolutionary activity  $a_i(t)$  of the  $i^{\text{th}}$  component at time t as its presence integrated over the time period from its origin up to t, provided it exists:

$$a_i(t) = \begin{cases} \int_0^t f_i(t)dt & \text{if component } i \text{ exists at } t \\ 0 & \text{otherwise} \end{cases}$$
(2)

Thus,  $a_i$  is the  $i^{\text{th}}$  component's activity counter. Note that a different resolution of the second issue above would result in a different formula for incrementing the activity counters (as in reference [7]). The *cumulative evolutionary activity*, A(t), at time t (which we will often call just "cumulative activity") is simply the sum of the evolutionary activity of all components:

$$A(t) = \sum_{i} a_i(t). \tag{3}$$

The diversity, D(t), is simply the number of components present at t,

$$D(t) = \#\{i : a_i(t) > 0\},\tag{4}$$

where  $\#\{\cdot\}$  denotes set cardinality. Then, the *mean cu*mulative evolutionary activity,  $\bar{A}(t)$ , (which we will often call simply "mean activity") is the cumulative evolutionary activity A(t) divided by the diversity D(t):

$$\bar{A}(t) = \frac{A(t)}{D(t)}.$$
(5)

Note that the cumulative activity is the product of a measure of diversity (the number of components D(t)) with a measure of duration or persistence (the mean evolutionary activity  $\bar{A}(t)$ ). These two aspects have already been noted as characteristic of evolution [15]; we have simply formed a measurable statistic with them.

A system could show significant diversity increase over time but *not* show significant activity increase over time. An example is an evolutionary system with a high mutation rate. Diversity will be high compared to similar systems with lower mutation rates, but activity will be low compared to the same reference group.

The cumulative activity defined by equation 3 is only one of a host of statistics that may be computed from the activity counters  $\{a_i\}$  defined in equation 2. In reference [7], for example, we argue for a different statistic to capture what we might intuitively identify with "adaptive evolutionary innovation". The cumulative activity does not support such an interpretation; we use it here for its computational ease and because we feel it broadly reflects continual adaptive success in the evolutionary processes we consider here.

As we have mentioned, evolutionary activity was first developed and applied in the context of a model evolutionary system [7]. The motivation for viewing evolutionarv activity as a measure of adaptation during evolution is particularly strong for such model systems, in large part because of intuition obtained by the experimental control they offer. In particular, as we illustrate for the Evita and Bugs models below, it is possible to "turn off" adaptation in a simulation, while leaving reproduction and death, resulting in a random sampling of components in the population, with no connection between the components and the survivability of the components. This sort of neutral analogue can then be compared with the normal situation, in which specific properties of components can have a very strong effect on their survivability. The introduction of a new component that has a positive effect on survivability is strongly reflected in the evolutionary activity.

The neutral analogue essentially produces a random walk in the space of possible components, analogous to other models of random evolution [28, 15]. Such models are relevant to biological evolution not necessarily because they are plausible models in themselves but because they highlight those aspects of an evolving system, if any, which are due to adaptation as against those which are due merely to random processes and historical accident.

#### 2 The Evita Model

The Evita model is a limited-interaction system consisting of self-replicating strings of code, akin to Tierra [29] and Avida [1]. As in Tierra and Avida, programs in a customized assembly language replicate while subject to "cosmic-ray" mutation. Unlike Tierra but like Avida, these programs are limited in interaction to their nearest neighbors on a two dimensional grid. And unlike both Tierra and Avida, no code parasitism is allowed in Evita.

The differences between Tierra, Avida and Evita, while not profound in outlook, are significant. The 2-D interaction ensures that the spread of information throughout the population is dependent on the size of the system; whereas Tierra allows instantaneous interaction between widely disparate areas, this cannot happen in Avida or Evita. Blocking parasitism and more complicated interactions (e.g. hyperparasitism and code pirating) allows us to study the root dynamics of these systems. The system is initialized with a single human-written program placed randomly on an N by M grid. This program then executes and reproduces; each offspring is placed within a small radius of the parent program on the grid, and they then also start executing. When a parent program can find no unoccupied grid locations nearby, the system chooses randomly from the oldest of its neighbors, "kills" that neighbor, and places the offspring there. No other interaction between programs is permitted.

During each "timestep" in this system the program at each occupied grid spot receives a fixed amount of the processor time. This time is allocated in a way that is unbiased by position; hence, no organism can gain an advantage in its placement. In fact, the only real advantage position can give is the relative fitness of the surrounding population: it may be that the nearby creatures are less fit, e.g. reproduce more slowly, than the creature placed onto their edge.

Mutation rate is specified in terms of the probability per timestep that each given "codon" or assembly language instruction in a genotype is mutated. Thus, the probability that a given program suffers a mutation somewhere is proportional to its length; longer programs are more likely to suffer a mutation. While the probability that a given program is mutated is independent of the size of the population of programs, the probability that a mutation occurs somewhere in the population is clearly proportional to the population size. Typically, mutation rates are specified in terms of  $10^{-5}$  mutations per timestep: that is, a mutation rate of m would mean that a given codon would mutate on average once every  $\frac{10^5}{m}$  timesteps. This means, for example, that in a run with 1600 creatures with an average length of 30 instructions, a mutation rate of 1 would cause one mutation somewhere in the population approximately every other timestep.

The model has a clear biological analogy. The system represents a biological "soup", full of self-replicating strands of code (similar to RNA). Survival is governed primarily by reproductive speed, and evolution towards faster programs is the behavior usually exhibited. This kind of system, while extremely simple, shows interesting evolutionary behavior. Many people have used Tierra, Avida, and similar simple systems to examine a variety of issues in evolutionary dynamics [29, 30, 1, 20, 35, 2].

Evita is explicitly designed so that the only way the programs interact is through reproduction. On average, programs that reproduce faster will supplant their more slowly reproducing neighbors. A program's rate of reproduction or "gestation time" depends only on its genotype, and a genotype's gestation time is the sole determinant of the expected rate at which programs with that genotype will produce offspring. Thus, all significant adaptive events in Evita are changes in gestation time.

We also define a neutral analogue of Evita, which differs from Evita only in that there is no chance that a genotype's presence or concentration in the population is due to its adaptive significance. Nominal "programs" exist at grid locations, reproduce and die. The neutral model has two parameters: the number of mutations in the population per timestep (possibly a vector), and the number of "programs" that reproduce per timestep (possibly a vector). When the neutral model is due to have a reproduction event, the self-reproducing "program" is chosen at random from the population (with equal probability). When a "program" reproduces, its oldest neighboring "program" dies and the new child occupies the newly emptied grid location. Each "program" has a nominal "genotype" which it's children inherit. Whenever a mutation strikes a "program" it is assigned a new "genotype". The evolutionary dynamics in this neutral analogue is reduced to a simple random walk in genotype space [2]. Genotypes arise and go extinct, and their concentrations change over time, but the genotype dynamics is only weakly linked to adaptation through the reproduction rate parameter determined by the normal model. None of the dynamic of a genotype in the neutral analogue is due to that genotype's adaptive significance for the genotypes have no adaptive significance whatsoever.

By recording mutation rates and reproduction rates from an actual Evita run, the neutral analogue can then be run with these vectors as parameters. The behavior of this neutral analogue allows us to determine which aspects of the behavior of our original Evita run were due to adaptation and which can be attributed to the underlying non-adaptive architecture of the system.

## 3 The Bugs Model

The Bugs model consist of many agents that exist in a spatial grid, sensing the resources in their local environment, moving as a function of what they sense, ingesting the resources they find, and reproducing or dying as a function of their internal resource levels. The Bugs model is in a line of models that originated with Packard [26] and has subsequently been evolving in various hands [7, 8, 3, 5, 4, 6, 11]

The Bugs model's spatial structure is a grid of sites with periodic boundary conditions, i.e., a toroidal lattice. Besides the agents, all that exists in the world are 50 tiny  $(3 \times 3 \text{ sites})$  square blocks of resources, which are spread over the lattice of sites and replenished as needed from an external source. The resource distribution is static in space and time because resources are immediately replenished at a site whenever they are consumed. Nevertheless, since the agents constantly extract resources and expend them by living and reproducing, the agents function as the system's resource sinks and the whole system is dissipative. Adaptation is resource driven since the agents need a steady supply of resources in order to survive and reproduce. Agents interact with the resource field at each time step by ingesting all of the resources (if any) found at their current location and storing it in their internal resource reservoir. Agents must continually replenish this reservoir to survive for they must expend resources at each time step to cover their (constant) "existence taxes" and "movement taxes" (variable, proportional to distance moved). If an agent's internal resource supply drops to zero, it dies and disappears from the world.

Each agent moves each time step as dictated by its genetically encoded sensorimotor map: a table of behavior rules of the form IF (environment j sensed) THEN (do behavior k). Only one agent can reside at a given site at a given time, so an agent randomly walks to the first free site if its sensorimotor map sends it to a site which is already occupied. An agent receives sensory information about the resources (but not the other agents) in the von Neumann neighborhood of five sites centered on its present location in the lattice. An agent can discriminate whether or not resources are present at each site in its von Neumann neighborhood. Thus, each sensory state j corresponds to one of the different detectable local environments (there are about 15 of these in the model studied here). Each behavior k is either a jump vector between one and fifteen sites in any one of the eight compass directions (north, northeast, east, etc.), or it is a random walk to the first unoccupied site. This yields a finite behavioral repertoire consisting of  $(8 \times 15) + 1 = 121$ different possible behaviors. Thus, an agent's genotype, i.e., its sensorimotor map, consist of a movement genetically hardwired for each detectable environmental condition. These genotypes are extremely simple, amounting to nothing more than a lookup table of sensorimotor rules. On the other hand, the space in which adaptation occurs is vast, consisting of up to  $121^{15} \approx 10^{32}$  distinct possible genotypes.

An agent reproduces (asexually—without recombination) if its resource reservoir exceeds a certain threshold. The parent produces one child, which starts life with half of its parent's resource supply. The child also inherits its parent's sensorimotor map, except that mutations may replace the behaviors linked to some sensory states with randomly chosen behaviors. The mutation rate parameter determines the probability of a mutation at a single locus, i.e., the probability that the behavior associated with a given sensory state changes. At the extreme case in which the mutation rate is set to one, a child's entire sensorimotor map is chosen at random. The results presented here were all produced with the mutation rate set to 0.05.

A time step in the simulation cycles through the entire population and has each agent, in turn, complete the following sequence of events: sense its present von Neumann neighborhood, move to the new location dictated by its sensorimotor map unless that site is already occupied, in which case randomly walk to the first unoccupied site, consume any resources found at its new location, expend enough resources to cover existence and movement taxes, and then, if its resource reservoir is high enough or empty, either reproduce or die.

Sensorimotor strategies evolve over generations. A given simulation starts with randomly distributed agents containing randomly chosen sensorimotor strategies. The model contains no *a priori* fitness function, as Packard (1989) has emphasized, so the population's size and genetic constitution fluctuates with the contingencies of extracting resources. Agents with maladaptive strategies tend to find few resources and thus to die, taking their sensorimotor genes with them; by contrast, agents with adaptive strategies tend to find sufficient resources to reproduce, spreading their sensorimotor strategies (with some mutations) through the population.

In resource-driven and space-limited models like the Bugs model observed population size is a good measure of the fitness of the genotypes in the population. Significant adaptive events typically create notable population rises. Populations with behaviorally heterogeneous strategies have a hard time surviving on the tiny  $3 \times 3$ blocks. Agents following different behavioral strategies will tend to collide, which will tend to bump one of them off the block into the resource desert. Thus, typically all agents on a given  $3 \times 3$  block follow exactly the same behavioral strategy. All the agents are in a holding pattern continually cycling over a subset of the resource sites on the tiny block. The strategies are typically simple behavioral cycles which jump through a short sequence of sites on the block. The simplest cycles (period 2) consist of jumping back and forth between two sites. The next simplest strategy (period 3) cycles through a triple of sites.

Behavioral strategies with higher periods have a selective advantage (every thing else being equal). Since a  $3 \times 3$  block contains 9 distinct sites, it can support at most a period 9 strategy. A period *n* strategy has room for at most *n* agents. Thus, longer period strategies can support larger populations because they can exploit more of the available energetic resources. All agents on blocks reproduce at the same rate, so a block with a larger population will produce offspring at a higher rate. Thus, blocks with populations with larger period strategies will exert greater migration pressure and, thus, will enjoy a selective advantage throughout the hundreds of tiny resource islands.

Thus, the main kind of adaptation that occurs in the present Bugs model involves extending the period of an existing strategy, which allows the population to exploit more of the available resource sites. Thus, evolution in a random field of  $3 \times 3$  blocks tends to create populations with higher period strategies.

As we did with Evita, we also create a neutral analogue of the Bugs model, which differs from the Bugs only in that a genotype's persistence is no reflection of its adaptive significance. Nominal "agents" are born, live, reproduce, and die at rates determined exactly by the values of those variables measured in a particular run of the normal Bugs model. (For this reason, the population time series in fig. 3 for the normal Bug model and the neutral analogue are exactly the same.) The distinctive feature of the neutral analogue is that birth, reproduction and death events happen to "agents" chosen at random from among those present in the population. Each "agent" has a nominal "genotype" which it inherited from its parent unless it suffered a mutation at birth (mutation rate is another model parameter). The evolutionary dynamics of the neutral analogue of the Bugs model is a random walk in genotype space. As with Evita's neutral analogue, none of the dynamic of a given genotypes in this neutral analogue of the Bugs model is due to that genotype's adaptive significance for it has no adaptive significance.

## 4 The Fossil Data

The fossil data sets indicate the geological stages or epochs with the first and last appearance of taxonomic families. The Benton data [9] covers all families in all kingdoms found in the fossil record, for a total of 7111 families. The Sepkoski data [32] indicates the fossil record for 3358 marine animal families. The duration of different stages and epochs varies widely, ranging over three orders of magnitude. In order to assign a uniform time scale to the fossil data, we converted stages and epochs into time indications expressed in units of millions of years ago using Harland's time scale [16].

We are most interested in analyzing long-term trends among fossil species, but we study fossil families because much more complete data is available at this level of analysis [37, 34]. Although fossil family data is certainly no precise predictor of fossil species data, there is evidence that species-level trends in the fossil record are reflected at the family level (see [37] and the references cited therein). Sepkoski and Hulver ([34], p. 14) summarize the situation thus: "Although families do not display all of the detail of the fossil record, they should be sufficiently sensitive to show major evolutionary trends and patterns with characteristic timescales of fives to tens of millions of years". The trends we discuss in this paper occur on time scales at least that long.

## 5 Results

We computed the cumulative activity A(t), mean activity  $\overline{A}(t)$ , and diversity D(t) in both the Benton and Sepkoski fossil data sets (fig. 1). We also computed these statistics from data produced by numerous simulations of the Evita and Bugs models and chose representative examples of the behavior of the statistics in Evita (fig. 2, above) and Bugs (fig. 3, above). Finally, we computed the same statistics from data produced by the neutral analogue of Evita (fig. 2, below) and the neutral analogue of the Bugs (fig. 3, below). In each case, the neutral analogues were given parameters that exactly corresponded to those that governed the normal Evita and Bugs runs.

We start the fossil data at the Cambrian explosion, due to the relative crudeness of the preceding data. Visible in the data are the major extinction events, such as the largest one of all which ends the Permian period, and the famous "K/T" extinction which involved the final demise of the dinosaurs and is thought to have been caused by a meteorite impact.

The Evita simulation shows the single ancestral program quickly replicating enough to fill up the  $40 \times 40$ grid. Most of the significant improvements in reproduction rate occur at the very beginning of the simulation. The local peaks in cumulative and mean activity during the course of the simulation correspond to the introduction of new genotypes that are neutral variants, that is, they have the same adaptive significance as the other major genotypes in the population. In other words, the bulk of this simulation consists of a random drift among genotypes that are selectively neutral, along the lines of the neutral theory of evolution [18]. Note that these selectively-neutral variants are highly adaptive they are remarkably effective at the task of survival and reproduction—but they just do this job equally well.

The first fifth of the Bugs simulation shows the population adapting to the tiny blocks by increasing the cycle size of their behavioral strategy. At least three major innovations are recognizable in the population size dynamics. After the third major innovation, the evolutionary dynamics settles down into a random drift among selectively-neutral variant genotypes, as in the Evita simulation.

Notice that there is a striking difference in the behavior of the artificial models and their neutral analogues. The neutral analogues do not produce anything like the same statistics as the normal models (except for the population size in the Bug neutral analogue, of course, and its shadow in the diversity and cumulative activity time series). In particular, the cumulative and mean activity values in the neutral analogues are negligible, by comparison, while their diversity values are significantly higher. Evidently, adaptation has a dramatic effect when it is allowed to affect the persistence of genotypes.

When we compare the evolutionary activity in these three figures, we see another striking difference. The fossil data shows a long-term trend of cumulative activity and diversity increasing more than linearly; fossil mean activity increases roughly linearly into the Permian period but then shows no further trend. But there is no long-term trend in any statistic in the Evita and Bugs data.

#### 6 Discussion

We draw three main conclusions from our comparison of evolutionary activity in artificial systems and in the biosphere:

Conclusion 1: Cumulative evolutionary activity measures continual adaptive success for the evolutionary processes we consider. This is clear for the two model systems primarily from the comparison provided by the neutral analogues.

Conclusion 2: Cumulative evolutionary activity, along with mean activity and diversity, are statistics that enable artificial evolutionary models to be compared quantitatively with evolution in the biosphere. It is clearly possible to measure these statistics in artificial and natural systems. The proof of this pudding (conclusion 2) comes in the eating.

Conclusion 3: If we accept conclusions 1 and 2, then comparison of evolutionary activity in the data from the fossil record and from the artificial evolving systems reveals that long-term trends involving adaptation are present in the biosphere but missing in the artificial models.

Our statistics show that the Evita and Bugs models do not show comparable evolutionary activity to the evolutionary activity of the biosphere indicated in the fossil record. The primary difference is that cumulative evolutionary activity and diversity of the biosphere shows a strong increase on an evolutionary time scale, but the Evita and Bugs models do not. Furthermore, the trends shown in the biosphere are unlikely to be "accidental" products of anything like the artificial models, for to our knowledge the artificial models *never* exhibit such trends. These strong increasing trends imply a directionality in biological evolution that is missing in the artificial evolutionary systems. Specifically, the biosphere shows an arrow of increasing cumulative activity as well as an arrow of increasing diversity. These are directly related since the post-Permian increase in cumulative activity is driven mainly by the increase in diversity. (Recall that cumulative activity is the product of diversity and mean activity.) But the arrow of cumulative activity is especially interesting because of its implications about the directionality of *adaptation* in biological evolution.

We view conclusion 3 as quantitative evidence that the artificial models are qualitatively different from the biosphere. We suspect that *no* existing artificial system is qualitatively like the biosphere. If this is right, then an objective of the first importance is to devise an artificial model that captures the qualitative behavior of the



Figure 1: Cumulative activity (top), mean activity (middle), and diversity (bottom) in the fossil data of Benton and Sepkoski. The labels at the top of each graph show the boundaries between the standard geological periods, thus: Cambrian, Ordovician, Silurian, Devonian, Carboniferous, Permian, Triassic, Jurassic, Cretaceous, Tertiary.





that the population size time series in the neutral analogue is taken directly from the population data generated in the normal Bug simulation above. 9 (bottom) in a Bugs simulation. Below: the same statistics for a neutral analogue of the Bugs simulation above. Note Figure 3: Above: cumulative activity (top), mean activity (upper middle), diversity (lower middle) and population



biosphere.

We should note that the Evita and Bugs models disallow any interesting interactions between organisms; no predator-prey connections, no cooperation, no communication, nothing. But other artificial evolving models do permit such interactions; e.g., Echo [17] and Tierra [29]. We purposely focused this first study on especially simple and well understood artificial models, to make it easier to understand our results. An obvious next step is to extend this study to more complex artificial models, and this is part of current work. However, we conjecture that the conclusions of this pilot study will hold for Echo and Tierra as well.

The spatial and temporal scales of the Evita and Bugs models are vastly smaller than the spatial and temporal scale of the biosphere; and the same applies to the general complexity of the systems. So perhaps these models should not be expected to show evolutionary activity comparable to the biosphere. But we are confident that scaling up space and time in the Evita and Bugs models will not change the qualitative character of their activity curves. This confidence comes in part from observations besides those reported here, but the conjecture is subject to further direct empirical test. We similarly doubt that simply making the models more "complex" will make the quality of their behavior like that of the biosphere. We think that the primary reason behind the biosphere's arrow of cumulative activity is that the dynamics of the biosphere constantly create new niches and new evolutionary possibilities through interactions between diverse organisms. This aspect of biological evolution dramatically amplifies both diversity and evolutionary activity, and it is an aspect not evident in these models.

The cumulative activity curve from the fossils is qualitatively similar to the initial transient of the Bugs cumulative activity curve. So, the explanation of the qualitative difference in the long-term cumulative activity shown in the fossils and in the artificial models might be that the biosphere has been on some kind of "transient" during the period reflected in the fossil record. The eventual statistical stabilization of the artificial evolving systems might be caused by the systems hitting their resource "ceilings"; in this case, growth in activity would be limited by the finite spatial and energetic resources available to support adaptive innovations.

Evolution in the biosphere seems to have been free from any inexorable resource ceilings, but we suspect that this is largely because the biosphere's evolution continues to make new resources available when it creates new niches. In fact, organisms occupying new niches seem to create the possibility for yet newer niches; i.e., the space of innovations available to evolution is constantly growing. We believe that this aspect of biological evolution is the most important aspect missing from artificial models; simply increasing resources to the artificial models studied here does not seem to significantly affect observed patterns of evolution. This suggests it would be interesting to make a more careful comparison of the fossil record data with initial transients of artificial systems, before the systems have exhausted the possibilities for significant adaptation. This will be a topic of future work.

There are problems and pitfalls inherent in using the fossil record to study long-term trends [27]. In particular, the "pull of the present" is a well-known sampling bias due to the fact that there are simply more recent fossils to study than older fossils. Future work will investigate the extent to which our analysis of fossil record trends can be supported more rigorously.

We have tried to illustrate the value of studying evolutionary trends by devising statistics that apply both to data from the fossil record and to data generated by artificial systems. Such statistics provide a normal form for expressing conclusions about the behavior of artificial models and about how those models are relevant to understanding biological evolution. Our work here has focussed on the cumulative evolutionary activity statistic, but this is not the only interesting statistic. As we mentioned in section 1 above, other statistics defined in terms of evolutionary activity highlight other kinds of comparisons among systems, which might provide additional kinds of insights into evolutionary trends. Perhaps yet further statistics unconnected with evolutionary activity might find a similar use.

Comparing cumulative evolutionary activity in artificial systems and in the biosphere has lead to a negative result (Conclusion 3): present artificial models of evolution apparently lack some important characteristic of the biosphere—whatever it is that is responsible for its arrow of increasing cumulative activity. However, this conclusion crystalizes an important constructive and creative challenge: to devise an artificial model of evolution that succeeds where the present models fail. Here, again, statistics like evolutionary activity show their value, for they provide a quantitative test for whether an artificial evolutionary model and a natural evolving system like the biosphere exhibit the same kind of long-term trends in adaptation.

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