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Can we model Darwin?: Reducing Darwin to a set of equations may never be possible. But a promising computer model shows that mass extinctions could have happened naturally as a consequence of the simple principles of evolution

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Physics has been immensely successful in finding mathematical laws that help it describe the Universe. All matter obeys Einstein's equations of general relativity. The way elementary particles interact are described mathematically by the Standard Model. And Schrodinger's equation describes atoms, their nuclei, chemical compounds, crystals and many other states of matter. Even the life and death of stars have well-established formulas.

But when it comes to the most complex system, mathematics has so far failed. Life on Earth involves a myriad species interacting with each other in ways that constantly change as they evolve, differentiate and become extinct. There are no 'Darwin's equations' to describe the evolution of life on Earth into complex, interacting ecologies.

Scientists accept that Darwin and his followers have convincingly described the principles governing the evolution of life. Darwin's theory of natural selection identifies in a qualitative way the cause of evolutionary change: natural selection operating through a struggle among individual organisms for reproductive success. But the absence of a more quantitative framework means that Darwin's principles have not been tested against observation in the same rigorous manner as physical laws. This also means that there is no way of predicting the outcome of Darwin's theory.

BURSTS OF CHANGE

Nevertheless, most scientists believe that life - or evolution - can, in principle, be described by the laws of physics. So far, the problem has simply seemed too big and scientists have concentrated on parts of the system, creating such disciplines as population biology and biogeography. This approach has been extremely successful in explaining many of the details of evolution. But we argue that evolution must be viewed as a whole, and that an understanding of it may not lie in those details. Over the past decade, for the first time, new mathematical ideas used to describe the behaviour of large, interacting, dynamical systems have begun to make this holistic approach possible.

The big new idea in this approach was conceived in the late 1980s by Per Bak, a physicist at Brookhaven National

Laboratory in New York state, and Stuart Kauffman, a theoretical biologist at the Santa Fe Institute in New Mexico. They argued that life is a dynamical system which, far from existing in a state of balance or equilibrium, organises spontaneously into a characteristic and much more precarious 'critical' state.

Surprisingly, this model of evolution predicts that life does not evolve gradually but intermittently, with long periods of inactivity or stasis, interrupted by bursts of change which are characterised by mass extinctions and the emergence of many new species. It is just this pattern that many palaeontologists say exists in nature. In 1972, Niles Eldredge of the American Museum of Natural History and Stephen J. Gould of Harvard University proposed from their study of fossil records that the evolution of single species takes place in steps separated by long periods of stability. They named this phenomenon 'punctuated equilibrium'. During the 1980s, David Raup and John Sepkoski at the University of Chicago found from their studies of records of thousands of fossil genera that extinctions occur in waves.

Evolutionary biologists have always assumed that rapid changes in the rate of evolution are caused by external events - which is why, for example, they have sought an explanation for the demise of the dinosaurs in a meteorite impact. On the other hand, if life organises into a critical state, catastrophes, no matter how large, are a natural part of evolution. External causes, such as a meteorite impact, are not necessary to explain, for example, those cataclysmic mass extinctions in the late Permian, 245 million years ago, or the extinction of the dinosaurs 65 million years ago.

This new insight has come from recent advances in understanding how large, interacting systems work. In 1987, Bak, working with Kurt Wiesenfeld and Chao Tang, also physicists from Brookhaven, simulated on a computer some simple examples of complex systems, which are 'driven' by feeding energy into them at a constant rate. These are 'open' systems - they are kept far from equilibrium. Such systems are ubiquitous in nature. For example, the continuous motion of tectonic plates builds tensions in the Earth's crust, and these tensions are intermittently relieved in earthquakes. The Sun shines continuously on the rotating Earth, thereby creating complex patterns of currents and winds, climates and weather.

The computer simulation is best imagined in terms of a sand pile, formed by constantly adding sand to an existing pile (see 'The self-organising sand pile', New Scientist, 15 June 1991). The grains of sand in the computer simulation behaved in a 'cooperative' manner that differed radically from the state of equilibrium of flat sand. The behaviour of a single grain affected that of all the others. As sand was continuously added, the system evolved into a critical state characterised by large periods of static behaviour, or stasis, interrupted by intermittent bursts of activity. The heap gradually became steeper, and there were bigger and bigger avalanches, until the heap built up a critical slope that produced avalanches of all sizes.

If the computer model is adapted to use wet instead of dry sand, the pile will grow steeper for a short time - until it reaches a new critical state with avalanches of all sizes. If one tries to prevent avalanches by putting up snow screens, the pile will reorganise itself for some time - until it reaches the critical state again. It is this resilience of the self-organised critical state which made us think it might be applicable to a wide range of natural phenomena.

We monitored the avalanches and counted how many were of a particular size. Despite the complexity of the system, this distribution follows a simple law: the number of avalanches in which s grains topple is just a power of s,s-r, where r is approximately equal to 1. This law shows that if in a certain time period there is one event of size 10 000, there will be approximately 10 events of size 1000, approximately 100 events of size 100, approximately 1000 events of size 10, and so on. The 'power' law means that the physics of small avalanches is the same as that of large ones. There is no characteristic timescale to separate large and small-scale behaviour.

Earthquakes follow precisely this type of pattern. It is known as the Gutenberg-Richter law and it suggests that the crust of Earth on which, for instance, Californians are living, is in the critical state. In 1991, an Italian team led by Paulo Diodati of the University of Perugia in Italy measured the acoustic activity around the volcano Stromboli.

They found that the volcanic activity also followed the laws of self-organised criticality. X-ray bursts emitted from solar flares, sudden variations in the frequencies of pulsars, and light emitted from quasars follow a similar pattern, with bursts of all sizes. In these cases, the variable s can be attached to the amount of energy released.

Less surprisingly, real sand piles also follow the sand pile model. In 1992, at the University of Michigan, Michael Bretz, Franco Nori and colleagues used a video camera to study sliding sand where sand on a tray was 'driven' to produce avalanches by being slowly tilted. Information from the camera was transformed into a digital signal and fed into a computer, which measured the size of the avalanches. These were of all sizes, as the sand pile model predicts.

CRITICAL LEAP

The main purpose of studying self-organised criticality, however, is not to understand the physics of sand but to apply the idea to other systems: to an ecology of interacting species, for example, or perhaps to an economy of interacting elements (see Complexity, New Scientist supplements, 6/13 February 1993). As long ago as 1966, Benoit Mandelbrot of IBM's Thomas J. Watson Research Center in New York suggested that fluctuations in economics follow the same type of law as earthquakes. Do economies operate in a critical state, far from the traditional view that they are in equilibrium? The observations of Eldredge, Gould and Raup in the 1970s and 1980s of punctuated equilibrium behaviour in biology are perhaps more interesting still. Is it possible to leap from sand piles to biology? In fact, constructing a model to describe punctuated equilibrium in biology turned out to be much more complicated than merely changing the language of the sand pile model.

A good place to start seemed to be the Game of Life, a computer model invented in the 1970s by John Conway that consists of a chessboard-like arrangement in which squares can be either 'alive' or 'dead'. Starting from a random setup, the pattern of squares evolves according to simple rules. Live squares die if they have too few, or too many, live neighbours. New live squares are born when the number of live neighbours is just right, allowing for a balance between creation and extinction.

In 1989, Michael Creutz and Kan Chen, physicists from Brookhaven National Laboratory, and Bak discovered that they could produce criticality in the model by adding new live squares at random to the Game of Life at some low rate,: punctuated equilibrium occurs in the form of avalanches of activity of death and birth of all sizes. But the Game of Life does not have much to do with real biology. And unfortunately, changing the rules of the game only slightly made the criticality disappear: it was not a robust property of the system.

In 1990, Kauffman and Sonke Johnsen, a research associate from Norway, were also hunting for self-organised criticality, this time in computer models of ecologies of interacting species. The environment of a real species depends on its interaction with other species in the system: for instance, the genes of a zebra determine how it is built, and hence how fast it can run. But its fitness to its environment depends just as much on how fast the local lions can run. In Kauffman and Johnsen's model, each species is characterised by a 'genetic code', and a species' fitness depends on both its own 'genes' and on a number of genes - let's call this number C - in other species.

If C is small, a species will experience its environment as essentially unchanging. It will stop evolving once it has adapted to it. In this way it becomes an unchanging part of the environment of those other species that depend on it. So they are even more prone to stop evolving, and so on. This ecology evolves to a state of arrested evolution, in which species are unable to improve their fitness. It remains low. On the other hand, if C is large, each species depends heavily on the state of many other species and is continually trying to maximise its fitness to an ever-changing environment. The ecology never stops evolving: it is in a state of continued chaotic evolution. The fitness species acquire in this state is low, too.

So, assuming that the goal of evolution is to optimise the mutual adaption of species, does it self-organise to a critical point somewhere between these two extremes? When Bak and Henrik Flyvbjerg working with Benny

Lautrup of the Niels Bohr Institute at the University of Copenhagen, applied mathematics to this model, it appeared that here, too, the criticality relied on a judicious choice of model - in this case the value of C. Increasingly, it seemed impossible to find a model of evolution that mirrored the real world without 'cheating'.

But then we discovered a key insight from another field. Kim Sneppen, and Mogens Hogh Jensen at the Niels Bohr Institute had been working on computer models of the growth of surfaces of crystals. They had developed a model of self-organised criticality for such a system. Their model differed from previous such models in a minor, yet important way. It allowed the least stable site, rather than sites chosen at random, to grow and change. When Sneppen came to visit Brookhaven, we realised that, translated to the language of evolution, this modification says that the least fit species is the most susceptible to change by mutation. We had left this - the most fundamental component of Darwin's theory - out of our early studies.

This additional insight, combined with our previous attempts, enabled us to construct a mathematical model we hope has captured the essence of biological evolution - not in terms of its details, such as the birth and death of individual organisms, but in terms of the evolution of species. Our model is quite simple. We start with a large number, say 1000, random numbers placed on, say, a circle. The model 'evolves' over several time steps. First, the computer replaces the smallest number on the circle with a new random number. It also changes the two nearest neighbours of this random number on the circle to two new random numbers. In the next time step, the number which happens to be lowest is replaced by a new random number. This could be one of the three numbers already changed in the previous step, or it could be another number somewhere else on the circle. Its two neighbours are also assigned random numbers.

The computer repeats the process again and again. After very many, say 1000, such steps, the numbers reach a more or less stationary distribution. They stop increasing - they converge on an average value that is not particularly high. For a time, all the changing numbers cluster together at one part of the circle. Then suddenly, the position of the next number selected is somewhere entirely different - a new cluster begins to form. The clusters may be of any size, large or small: the model has self-organised to the critical state.

RANDOM NUMBERS

The random numbers in our model represent the fitness of the species situated on the circle. The selection of the smallest number represents selection of the species that is least fit for mutation. The change in the value of the random number on the neighbouring sites represent, at a very general level, biological connections such as food chains, predator-prey and parasite-host relationships. In our model, the random changes to the selected number affect its neighbours - just as in the sand pile model, where the toppling of a single grain can affect its neighbours. And since the evolution takes place in terms of avalanches - in mathematical terms, the formation of clusters of random numbers - our model also shows punctuated equilibrium behaviour, just as real biological evolution does.

We have studied many different versions of this model, and in all cases we found self-organised criticality. The behaviour is robust - as it must be to represent real evolution since our models will certainly differ from the real thing when it comes to details. In the models, within the large avalanches of hectic activity, the average fitness is low. The same species are mutating again and again in search of better fitness. The fitness of the various species is also low during mass extinctions, and high during the periods of stasis with low evolutionary activity.

So how far can all this be applied to real biology? According to our model, large avalanches take place without any external force. So large events in the history of evolution - such as the Cambrian explosion 570 to 510 million years ago and the extinction of the dinosaurs 65 million years ago - may have taken place without being triggered by large cataclysmic events; they may be intrinsic consequences of the dynamics of biology, that is, they are self-organised.

Another interesting observation is that species with many connections - that is, those with a high degree of complexity - are more sensitive to the environment. They are more likely to participate in the next co-evolutionary avalanche and become extinct. So complex species should exist for a relatively short time, compared with the time that simpler species can exist before becoming extinct - according to our model, cockroaches will outlast humans.

But the most interesting feature of the model is its extreme simplicity and robustness; it has no subtle structure. We believe that only a few conditions need to be satisfied for the model to work. The picture which seems to emerge from our model is that while evolution does take ecology to the critical point by its self-organising dynamics, the fitness of that point is not particularly high. The critical point is not, as Kauffman once described it, 'a nice place to be'. So 'survival of the fittest' does not imply evolution to a state where everybody is well off. On the contrary, individual species are barely able to hang on - like the grains of sand in the critical sand pile.

We also noticed that in the critical state all species interact, as illustrated by the existence of large avalanches. Since all species affected by any given avalanche share their fate, they might be regarded as a single 'organism'. As the ecology evolves from its original state towards its critical state, this kind of organism grows in size until the entire system is effectively one organism.

We have not found the equivalent of Darwin's missing equations - we are not even close to doing that. But we do have a simple model for a vastly simplified Darwinian evolution. This model is a mathematical model, formulated as a set of equations that can be solved on a computer. Despite its simplicity, the model has already taught us that punctuated equilibrium, stasis, and intermittency can be direct consequences of simple principles of evolution, as expressed by Darwin. No extra explanations beyond those principles are required.

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