

Connectivity and Catastrophe - Towards a General Theory of Evolution

David G. Green, David Newth and Michael G. Kirley

School of Environmental and Information Science
Charles Sturt University, Albury NSW 2640 AUSTRALIA

Abstract

Here we show that connectivity and catastrophe play a key role in driving species evolution within a landscape. They also form a special case of a more general process, which occurs widely in natural and artificial systems. In this process, catastrophes cause a temporary phase change in the connectivity of a system. Different mechanisms (selection and variation) predominate in each phase. The system passes through the critical point without being poised there. The "chaotic edge" associated with the phase change may be an important source of variety in biological and other systems. In species evolution (and landscape ecology) the process is mediated by cataclysmic events, which fragment widely distributed species and trigger population explosions of new species. The proposed mechanism explains a number of biological and physical phenomena, as well as certain algorithms used for optimisation and evolutionary programming.

Introduction

One of the great challenges facing science is to understand the processes by which complex systems adapt and change (Bossomaier and Green 2000). An important lesson of complexity theory is that superficially different systems show deep similarities in their structure and behaviour (Green 1992). The existence of these universal properties raises the possibility that deep similarities exist also in the mechanisms underlying self-organization and other processes of system change. In other words, can we identify universal processes that operate in a wide range of different systems and circumstances?

The concept of evolution has been a central idea in science for over 150 years. From protein structure and function to taxonomic hierarchies, the theory underlies most of modern biology. More recently the idea has crept into other fields, especially computing. For example, genetic algorithms and other evolutionary methods now play an increasingly important role in problem solving. Given the importance of evolution,

it is an obvious question to ask how widespread are evolutionary processes?

The aim of this discussion is to explore the potential for generalizing the concept of species evolution to encompass a much wider range of phenomena. In particular we will show here that certain aspects of species evolution form a special case of a general process of self-organization, which acts in many different kinds of systems.

Models of Evolution and Self-Organization

In the sense that they involve systems changing through time, many processes are akin to species evolution.

An important theme in research into complexity and artificial life has been to understand how systems evolve, adapt and change (Langton 1989; Kauffman 1992; Depew and Weber 1997). For example, Prigogine (1980) introduced the idea of dissipative systems, which are thermodynamic systems that produce energy internally and exchange it with an external environment. Dissipative systems include living organisms as well as many physical systems, such as certain chemical reactions and interstellar gas clouds. In such systems, which are far from equilibrium, global patterns can emerge out of minor, local events.

Holland (1995), who introduced the genetic algorithm, has stressed the role of adaptation in self-organization. He suggested that seven basic elements are involved in the emergence of order in complex adaptive systems. These include four properties - aggregation, nonlinearity, flows, and diversity - and three mechanisms - tagging, internal models, and building blocks.

The role of criticality in system change is well known (eg. Bak and Chen 1991). Several authors, including Kauffman (1992) and Langton (1990, 1992), have suggested that the critical region between ordered and chaotic behaviour plays a central role in evolution. Sys-

Copyrighted Material

tems that are in a state lying close to this “edge of chaos” have the richest, most complex behaviour. Natural systems with these properties would adapt better and therefore have a selective advantage over other systems. Thus these authors suggest that many systems tend to evolve so that they lie close to the edge of chaos. These ideas are consistent with conclusions of others (eg. Freeman 1975), based on experimental observations, that chaos appears to be an important source of novelty and variety in living systems.

Another important model is that of the “fitness landscape” (Kauffman 1992; Depew and Weber 1997). In this model the entire range of potential genotypes that a population may possess is mapped onto an imaginary landscape in which the axes denote particular factors or properties of the organisms (eg. size, drought tolerance). The entire population can then be viewed as a scatter of points in the landscape, with each point being an individual in the population. Processes such as mutation and selection can be seen as forces pushing the cloud in particular directions. *It is important not to confuse these imaginary fitness landscapes with the real landscapes that we discuss below.*

Evolution in a Landscape

The neo-Darwinian theory of evolution is based around three main elements:

- Populations with genetic structure;
- Competition and selection of the fittest individuals;
- Mutation and variation.

The assumption is that populations change by slowly accumulating genetic changes, with natural selection weeding out unfit individuals. “Fitness” refers to how well an individual’s adaptation to environmental conditions helps it to survive and reproduce. Environmental factors that affect survival impose selective pressures on a population.

The slow accumulation of new characters mentioned above is often termed a gradualistic theory. In the Nineteenth Century it replaced earlier theories of catastrophic evolution. However catastrophism underwent a revival in the late Twentieth Century as the mounting fossil evidence revealed a picture of intermittent mass extinctions (Raup 1986; Raup and Jablonski 1986; Kauffman and Walliser 1990), often followed by a burst of speciation. These observations are inconsistent with a purely gradualistic view, which would predict a more or less constant turnover of species.

Punctuated Equilibria

Seeking to explain the evident stop-start nature of the fossil record Eldredge and Gould (1972) proposed the

theory of punctuated equilibria. According to this theory, species tend to remain stable for long periods of time. The equilibrium is punctuated by abrupt changes in which existing species are suddenly replaced. Many biologists have queried the theory, arguing that speciation could not occur so rapidly. They also point to the incompleteness of the fossil record to explain missing transitional forms.

Perhaps the best known explanation for sharp boundaries in the fossil record is the idea that comets and other cataclysmic events in the past caused sudden mass extinctions. This idea had been around for a long time but was not taken seriously until Alvarez et al. (1980) found evidence that a massive cometary impact had coincided with the extinction of the dinosaurs. Their evidence was a thin layer rich in the metal iridium. This layer coincided precisely with the Cretaceous-Tertiary (K-T) boundary. Subsequent research has identified that this iridium layer is worldwide. It seems to have resulted from an impact on the Yucatan Peninsula in central America.

Landscape Connectivity

It has always been acknowledged that the spatial distribution of plants and animals plays a role in evolution. In particular the popular expression “speciation by isolation” sums up the key role that landscapes play in the origins of new species. However, the exact mechanism by which isolation occurs is a much neglected question.

In previous studies (eg. Green 1989, 1994a, 1994b) we have shown that spatial distributions play an important role in the dynamics of natural communities. In particular, landscape connectivity plays a crucial role. “Connectivity” here means processes that affect genetic “communication” within a population. Examples include animal migration, seed dispersal, disturbances, and the distribution of potential habitats. Sites in a landscape are “connected” if there are patterns or processes that link them in some way. These links arise either from static patterns (eg. landforms, soil distributions, and contiguous forest cover) or from dynamic processes (eg. dispersal, fire). Note that a particular landscape may have radically different degrees of connectivity with respect to different processes. For instance following a major fire that clears (say) 90% of forest within a region, the forest remnants are likely to be genetically isolated from one another. However to a population invading the same landscape, the sites that are available for colonization are highly connected.

The key result to emerge from studies of connectivity (Green 1994a) is that landscapes can exist in two differ-

Copyrighted Material

ent phases: connected and disconnected (Fig. 1). Sites in a landscape are “connected” if the local populations interbreed with each other (i.e. share genetic information). Dispersal between sites is essential to maintain genetic homogeneity within populations. Should this dispersal connectivity fall below a critical level, then a regional population effectively breaks up into isolated subpopulations (Fig. 2).

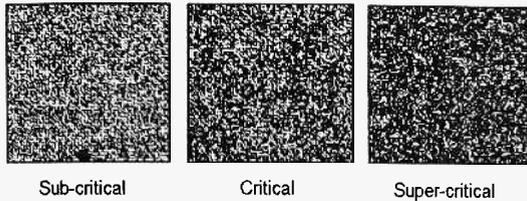


Figure 1: Phase change in the connectivity of a cellular automaton grid as the proportion of “active” cells increases (after Green 1994a). Grey denotes active cells; white denotes inactive cells. The proportion of active cells increases from left to right. The black areas indicate connected patches of active cells. Notice that a small change in the number of active cells produces a phase change in the system: from many small patches, isolated from one another, to essentially complete connectivity of the entire system.

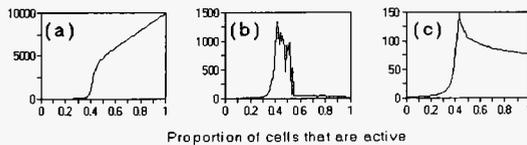


Figure 2: Critical changes in connectivity of a CA grid (cf Fig. 1) as the proportion of “active” cells increases (x-axes). (a) Average size of the largest connected subregion (LCS). (b) Standard deviation in the size of the LCS. (c) Traversal time for the LCS. Each point is the result of 100 iterations of a simulation in which a given proportion of cells (in a square grid of 10,000 cells) are marked as active. Note that the location of the phase change (here ≈ 0.4) varies according to the way we define connectivity within the model grid.

Landscape Phases and Evolutionary Processes

We can briefly summarize the process of evolution as follows. For most of the time the system - that is populations of plants and animals in their environment - sits in an undisturbed state. In this state, individual

species exist in either of two states: connected and fragmented.

For species that consist of a single, connected population, genetic information is constantly being circulated throughout the entire population. The effect of this constant genetic mixing is to inhibit variation. Wild mutations are culled out and the entire population is kept within narrow bounds (Fig. 3). Under these conditions only natural selection can produce change. Poorly adapted members of the population are culled out and well-adapted individuals produce most of the offspring. The net result is that the average adaptation of the population gradually increases through time.

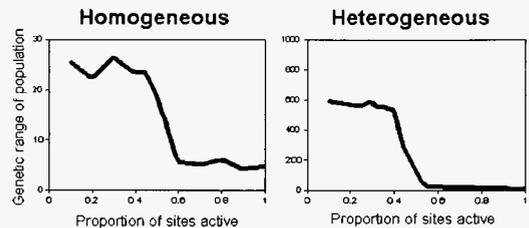


Figure 3: Simulated genetic drift in a landscape. The figure shows the range of gene values (G), after 10,000 “generations” of a population that initially is: (left) homogeneous ($G = 0$ everywhere); and (right) heterogeneous ($-100 < G < 100$), in response to the proportion P of active sites. In each case, the range $0.4 < P < 0.6$ forms a critical region.

By way of contrast, neutral variations are bound to increase in species that consist of fragmented populations (Fig. 3). Isolated subpopulations may be small enough that random mutations can become fixed. Also there is nothing to stop different subpopulations from randomly drifting apart in their genetic makeup. This is true even in the absence of selective pressure. When selective pressure does operate, its strength and direction usually varies from place to place. So under these conditions selection acts to accelerate and magnify the differences between subpopulations.

The Role of Cataclysms

The above account summarizes what happens in the environment most of the time. However the slow, steady accumulation of changes is often interrupted by disturbances. The history of life is peppered with cataclysms, both great and small. Most discussion of cataclysms has focused on the impact of comets and other events with the potential to disrupt the entire planet. However the biosphere is continually subjected to cataclysms of all sizes. Great events, such as the impact

of a comet, are as rare as their effects are vast. Smaller events are more common. So common are small disturbances that every year the Earth's surface is marked by thousands of fires, storms, volcanic eruptions, and innumerable other events. On a smaller scale these small, but common cataclysms, add up to have a similar effect to that of really large events.

The most important effect of a cataclysm is to clear large tracts of land at a single stroke. In doing so the cataclysm plunges an ecosystem into a different phase. Suddenly the normal rules, described above, no longer apply. The absence of restrictions has two main effects. First it carves up widespread species into isolated subpopulations. Sometimes those subpopulations will again spread and recombine. However the opposite happens too. That is, cataclysms often act to break subpopulations for long periods of time. When this happens speciation begins.

The other effect of cataclysms is to free up large tracts of land that were formerly occupied. This sets all the species back to square one. Species that were formerly dominant have to compete against newcomers. In normal times, dominant species exclude competitors for the simple reason that they already occupy territory. After a cataclysm they are set back to the same state as their competitors. If climatic conditions have changed, or if some new, superior competitor appears, then they may lose their dominant position.

The final point to note about these cataclysms is that after they clear territory, the surviving populations expand to fill the void. In doing so they compete and rearrange both their territories and their relationships to each other. When this resorting dies down the system re-enters the "normal" phase that we described first.

Phase Changes and Punctuated Equilibria

The above effects help to explain the phenomenon of punctuated equilibrium. The normal conditions effectively prevent speciation in common, widespread species. On the other hand they promote speciation in fragmented populations. Importantly they also prevent new species from spreading. So new species, which form in small, isolated populations, remain as small isolated populations.

Cataclysms act to release the above restraints. A consequence is that any new species that have formed are no longer suppressed. If conditions favour them, they spread rapidly, perhaps even replacing the species that spawned them. So the proliferation of new species after a cataclysm is not necessarily a speeding up of evolution, but rather an unleashing of new species that had already formed.

Several lines of evidence exist to support the above theory. One is the phenomenon of hybridization (Barber 1970; Levin 1970), which occurs when genetically distinct, but related populations come into contact. Field studies (Briggs 1986) reveal that the extent of hybridization is much greater in disturbed environments, which allow much greater movement of plants. Another line of supporting evidence arises from the dynamics of long-term vegetation change, which we address in the next section. It provides not only an analogy, but also a possible fine scale mechanism.

Phase Changes in Vegetation History - An Analogue for Evolution

The above model for species evolution emphasizes the role of landscapes and disturbances. Similar mechanisms within landscapes also exist on finer scales. An excellent example is provided by vegetation history. Studies, using preserved pollen, of postglacial vegetation history in Europe and northeastern North America (Davis 1976) reveal that the sequences of forest changes during the last 10,000 years were remarkably uniform over vast areas. It was assumed that these "pollen zones" represent periods of more or less constant forest composition. Before the advent of radiocarbon dating, pollen zones were used to establish the relative chronologies between sites. Subsequent research has shown that these zones are associated with post-glacial migrations of tree populations (Davis 1976, Webb 1981). Most significantly, the zone boundaries, which are usually defined by invasions and other sudden changes in plant populations (Fig. 4), often coincide with major fires (Green 1982). Pollen and charcoal records (Green 1987, 1990) show that competition from established species suppresses invaders. By clearing large areas, major fires remove competitors and trigger explosions in the size of invading tree populations.

The parallels between vegetation change and evolution are striking: pollen zones versus geologic eras, sudden changes in community composition versus mass extinctions, and major fires versus cometary impacts. This correspondence is so striking that it implies some fundamental process underlies the similarities (Green 1994b). Simulation studies imply that biotic processes in landscapes are responsible. In the case of forest change seed dispersal acts as a conservative process (Green 1989). Because they possess an overwhelming majority of seed sources, established species are able to out-compete invaders. By clearing large regions, major fires enable invaders to compete with established species on equal terms. Conversely seed dispersal also enables rare species to survive in the face of superior

Copyrighted Material

competitors by forming clumped distributions. This process also provides a mechanism that maintains high diversity in tropical rainforests (Green 1989).

A Model for Catastrophe Induced Phase Changes

One of the strongest indicators of the possibility of a universal theory of evolution is the existence of common properties underlying the structure and behaviour of all complex systems (Green, 1992, 1994b, 1994c, 1999). In any complex system, connectivity is best expressed as a directed graph (X, E) ("digraph"). This is a set X of "nodes", of which some or all are joined by a set E of "edges". We represent elements of the system as nodes and interactions by edges. The universal nature of digraphs is assured by the following theorems (Green 1994c).

Theorem 1 *The patterns of dependencies in matrix models, dynamical systems, cellular automata, semi-groups and partially ordered sets are all isomorphic to directed graphs.*

Theorem 2 *In any array of automata the state space forms a directed graph. If both the array and the number of states are finite, then so is the resulting set of directed states.*

The first theorem shows that digraphs are inherent in all of the ways we represent complex systems. So, assuming the models are valid, digraphs are present in the structure of virtually all complex systems. The

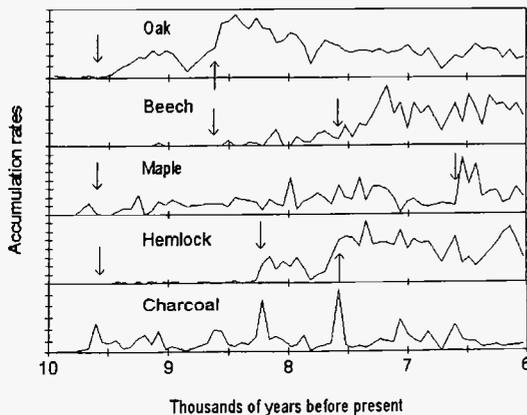


Figure 4: Cataclysmic change in postglacial forests (after Green 1990). Pollen and charcoal records (from Everitt Lake, Nova Scotia) show that competition from established species suppresses invaders. Major fires clear large tracts of land, remove competitors and trigger explosions (arrows) of invading tree populations.

second theorem shows that we can also regard the behaviour of complex systems as directed graphs.

The most important consequence of the above theorems is that properties of directed graphs explain many phenomena, such as criticality, in systems that had previously been treated as distinct (Green 1992; 1994b). Most prominent of these properties is the "connectivity avalanche". Erdos and Renyi (1960) examined what happens if one takes a set of nodes and adds edges progressively to pairs of nodes chosen at random. At first the set of connected nodes are very small. But at a certain point in the procedure, a "connectivity avalanche" occurs. Adding just a few extra edges suddenly joins virtually all of the nodes into a single "giant component". This amounts to a phase change in the system - from essentially disconnected to fully connected.

The above theorems imply that the connectivity avalanche is responsible for many kinds of phase changes in complex systems (Green 1992; 1994b). For example, if we represent a landscape as a grid of cells (using the formalism of cellular automata), and represent the distribution of (say) a plant species by cells in a particular state, then we find that as the occupied proportion of the landscape increases, a phase change occurs in the size of the largest "patch" (Fig. 2).

We can regard this phase change as an elementary form of chaos (a "chaotic edge"). Because of the sudden change from disconnected to connected, the system is highly sensitive to initial conditions at the phase change. Also, because of the extremely high variance the size and composition of patches in any two systems are likely to be quite different from one another.

The universality of graphs in the structure and behaviour of complex systems suggests that phase changes may play a role in system evolution. In particular it enables us to generalize the model proposed above for species evolution in a landscape to identify a potentially universal mechanism based on phase changes triggered by disturbances. We suggest that the inherent variability of phase changes in connectivity (Fig. 2b) provides a source of novelty in many systems (Green 1994b). Taken in the broadest sense, we can understand variation (c.f. mutation) to mean changes within a system's components or its connectivity. We can interpret selection as constraints that either prevent variation or else push it in a particular direction. Adopting the above idea, we suggest that many systems flip-flop backwards and forwards across a "chaotic edge" associated with a phase change in their structure or behaviour. This phase-shift mechanism (Fig. 5) works as follows:

Copyrighted Material

- The system can exist in either of two phases - a connected phase, wherein selection predominates; and a disconnected phase, wherein variation predominates.
- Most of the time the system rests in the connected phase. Selection maintains the system in a more or less steady state.
- External stimuli may disturb the system, forcing its structure to shift across the phase change. Whilst the system is in the disconnected phase, variation has free rein.
- Following a disturbance, connectivity gradually builds up again within the system until it reorganizes itself (“crystallizes”) into a new stable structure. Because of the variability associated with the phase change, this new structure is likely to be quite different from the structure prior to the disturbance.

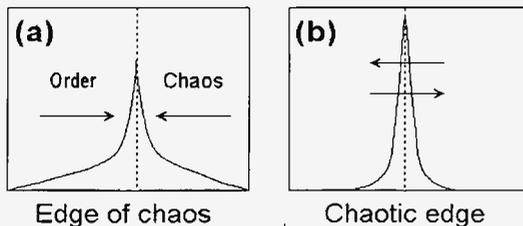


Figure 5: Contrasting the edge-of-chaos and phase-shift models of evolution in complex systems. The x-axis represents a connectivity “order” parameter appropriate to the system concerned. The spike represents the critical point where a phase change occurs. (a) In the edge-of-chaos model complex systems evolve to lie near or at the critical point (the spike) between ordered and chaotic phases. (b) In the phase shift model, which is described here, external stimuli flip the system across the chaotic edge into the phase where variation predominates. The system then gradually returns, crystallizing into a new structure or behaviour as it does so. See the text for further explanation.

Application of the Model to Evolution in Natural and Artificial Systems

In this section we look at a number of cases where the above model appears to apply.

Feedback Networks

Competition, predation, herbivory and other interactions among species are common types of connectivity within any ecosystem. One issue is to assess the effects of suites of interactions that can arise in

complex ecosystem (eg. rainforests). Levins (1970; 1977) introduced the idea of “loop analysis”: by knowing the sign of particular interactions we can trace whether feedback loops are positive (i.e. destabilizing) or negative (i.e. stabilizing). Theoretical studies of population dynamics indicate that random assemblages usually form non-viable systems (Tregonnig and Roberts 1979). That is, the interactions are highly likely to form positive feedback loops, which lead to the extinction of one or more species. In a system with few interactions, such instabilities are less likely to occur than in a richly connected one (May 1972; 1974). Thus gradually adding new species (eg. by migration) to a viable system increases the overall connectivity until the phase change occurs and positive feedback becomes inevitable. The system would then lose species and collapse back to a new, sub-critical state. Further immigrant species would then set the process off again.

Neural Function

Experimental evidence (eg. Freeman, 1975) implies that some neural systems exploit phase transitions as a source of novelty and flexibility, which allows them to continually adapt to new stimuli. In particular, brain function may involve changes in shifts in connectivity between neurons. Freeman (1992) has shown that, unlike current artificial neural networks, living neural systems (eg. cat’s brains) exploit chaos as a source of novelty in creating memory patterns. We suggest that the above novelty arises from the inherent unpredictability of connectivity patterns associated with phase transitions.

Socio-economics and Cultural Change

We expect that our model will be relevant to human social and economic systems. For instance, changes in communications, such as the introduction of the Internet, changes the patterns of connectivity between groups and individuals (Bossomaier and Green 1998). More generally, any new technology disturbs the prevailing socio-economic framework, which eventually settles down into a new pattern (Toffler 1970). The precise application of the theory to social systems awaits the development of models that define appropriate connectivity models for socio-economic systems. However some authors have pointed to empirical evidence suggesting that connectivity models may provide fresh insights. For instance Dunbar (1996) has pointed out that different forms of social interaction (speech versus grooming) led humans to have larger natural group sizes than apes or monkeys.

Copyrighted Material

Geomorphology

The notion of gradualism first arose in the context of geomorphology. In the early 1800s Lyell showed that geological change can be attributed to the action of erosion and other slow continual processes. In truth, however, geological change includes both gradual and catastrophic processes. For instance, volcanism builds mountains and lava plains, which erosion then shapes over time. Likewise erosion slowly shapes the course of streams, but intermittent floods can create new channels overnight.

Optimization

The notion of a fitness landscape, mentioned earlier in connection with species evolution, can be extended to optimization problems. We can imagine all possible solutions to a given problem as being mapped onto a hypothetical landscape (in some cases the existence of orthogonal parameters makes this possible literally), in which the elevation represents the value of the object function that we wish to maximize (or minimize). Optimization algorithms therefore seek to locate the hilltops (or valleys) in this solution landscape. The risk with simple hill-climbing, and other local optimization procedures, is that we may wind up stuck (say) on a minor foothill without finding the tallest mountaintop. To counteract this problem, many algorithms make use of the phase-change mechanism we have proposed here. For instance simulated annealing, uses a pseudo-temperature measure, which effectively allows solutions to drop downhill by a certain amount. At the start of the cooling schedule this temperature drop is large enough to allow the algorithm to wander anywhere in the landscape. In other words the solution landscape is fully connected. However as the cooling proceeds the system eventually passes a point where the connectivity breaks down and the algorithm becomes trapped on a particular hill. Likewise, the “great deluge” algorithm follows a random walk around the solution landscape, which it gradually floods until individual hills become isolated from one another.

In our own work on optimization, we have exploited the flip-flop, phase change mechanism more explicitly in the cellular genetic algorithm (see below).

Evolutionary Algorithms

Evolutionary Algorithms (EA's) are biologically inspired models for solving computationally hard problems. Evolutionary Algorithms are abstract models that typically ignore key features of biological and population dynamics. We argue that mimicking nature more closely leads to more robust algorithms.

The Cellular Genetic Algorithm (CGA) is a parallel

genetic algorithm that mimics adaptation in a landscape by mapping the population of solutions onto a pseudo landscape (Kirley et al. 1998). It raises the prospect of exploiting the population's spatial organisation to solve multi-objective and other novel problems. Our experiments show that random “disasters”, which clear space, can break down the connectivity, leading to isolated subpopulations whose genetic makeup rapidly drifts apart (Fig. 6). Intermediate rates of disturbance are essential to maintain a high diversity of genetically distinct individuals.

Conclusion

In essence the theory we have developed here proposes that many systems develop and change by a mechanism involving phase changes. Left to itself such a system will remain in a more or less constant state. However external events may disturb the system, flipping it into a different phase in which variation, rather than selection, dominates. The phase transition is an essentially chaotic phenomenon that perturbs the systems in unpredictable ways, and acts as a source of novelty. Following the phase change the system gradually drifts back into its original phase, but can settle into a completely new steady state.

This model differs from other theories that have been proposed. First, it differs from the kinds of critical collapse described by Bak and Chen (1991). In a critical collapse, a system collapses spontaneously when connectivity exceeds the critical threshold. In our model, the system is normally static. It is an external disturbance that triggers the change. The two theories describe different aspects of critical behaviour and are complementary. Most importantly, the system does not keep returning to its original state. Instead it

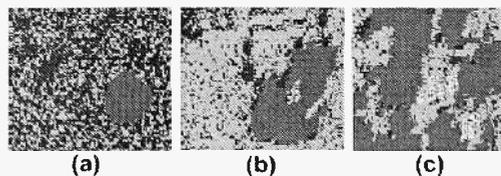


Figure 6: Exploiting connectivity phase shifts in the cellular genetic algorithm. Lighter colours indicate fitter individuals. Black indicates a disaster zone. (a) The landscape view at generation 3, after a disaster has struck. (b) Additional disasters have hit the landscape, patchy subpopulations are beginning to form. Parts of the disaster zone shown in (a) have been reclaimed. (c) The cumulative affect of many disasters across the landscape. (After Kirley et al. 1998).

Copyrighted Material

evolves via a sequence of disturbances and crashes.

The present theory differs too from the "edge of chaos" model. Rather than settling in the critical region, the phenomena we describe here exhibit jumps through the critical region. The systems do not settle and remain in a critical state. More generally, the two models were developed to describe different things. The edge of chaos model arose from considerations of the behaviour of automata, with the relevant critical region lying within the system's state space. In contrast the model developed here derives from considerations of system structure, such as the connectivity within a landscape.

In this account we have described a particular evolutionary mechanism. In itself, this is not a universal theory of evolution. Inevitably, our general theory is an abstraction. And in the abstraction some important details are lost. For instance we say nothing about the nature of the processes of selection and mutation. These details do matter. For example, in considering landscapes, these processes can also be affected by the spatial patterns and processes (Green 1997).

A truly universal theory would need to encompass all of the above issues, as well as many others besides. Nevertheless, we feel that the mechanisms we have identified point to the practicality of setting species evolution in the context of a general theory of evolutionary processes. Certainly recent reviews of evolutionary theory (eg. Depew and Weber, 1997) take on board work on complexity and related phenomena. Developing a general evolutionary theory is surely one of the great scientific challenges for the new Millennium.

References

Alvarez, L.W., Alvarez, W., Asaro, F. and Michel, H.V. 1980. Extraterrestrial Cause for the Cretaceous-Tertiary extinction. *Science* 208:1095-1108.

Bak, P. and Chen, K. 1991. Self-organized criticality. *Scientific American* 265:26-33.

Barber, H.N. 1970. Hybridization and the evolution of plants. *Taxon* 19:154-160.

Bossomaier, T.J. and Green, D.G. 1998. *Patterns in the Sand - Computers, Complexity and Life*. Sydney. Allen and Unwin.

Bossomaier, T.R.J. and Green, D.G. eds. 2000. *Complex Systems*. Cambridge University Press.

Briggs, B.G. 1986. Alpine Ranunculi of the Kosciusko Plateau: habitat change and hybridization. In B. Barlow, ed. *Flora and Fauna of Alpine Australasia - Ages and Origins*. 401-412. Canberra. CSIRO.

Davis, M.B. 1976. Pleistocene biogeography of temperate deciduous forests. *Geoscience and Man* 13:13-26.

Depew, D.J. and Weber, B.H. 1997. *Darwinism Evolving*. Cambridge Mass. MIT Press.

Dunbar, R. 1996. *Grooming, Gossip and the Evolution of Language*. London. Faber and Faber.

Eldredge, N. and Gould, S.J. 1972. Punctuated equilibria: an alternative to phyletic gradualism. In T.M. Schopf ed. *Models in Paleobiology*. San Francisco. Freeman, Cooper.

Erdos, P. and Renyi, A. 1960. On the evolution of random graphs. *Mat. Kutato. Int. Kozl.* 5:17-61.

Freeman, W.J., 1975. *Mass action in the nervous system*. New York, Academic Press.

Freeman, W. 1992. Tutorial on neurobiology: from single neurons to brain chaos. *International Journal of Bifurcation and Chaos* 2(3):451-482.

Green, D.G. 1982. Fire and stability in the postglacial forests of southwest Nova Scotia. *J. Biogeog.* 9:29-40.

Green, D.G. 1987. Pollen evidence for the postglacial origins of Nova Scotia's forests. *Can. J. Bot.* 65:1163-1179.

Green, D.G. 1989. Simulated effects of fire, dispersal and spatial pattern on competition within vegetation mosaics. *Vegetatio* 82:139-153.

Green, D.G. 1990. Landscapes, cataclysms and population explosions. *Mathematics and Computer Modelling* 13(6):75-82.

Green, D.G. 1992. Emergent behaviour in biological systems. In D. G. Green, and T. J. Bossomaier eds. *Complex Systems - From Biology to Computation*. 25-36. Amsterdam. IOS Press.

Green, D.G. 1994a. Connectivity and complexity in ecological systems. *Pacific Conservation Biol.* 1(3):194-200.

Green, D.G. 1994b. Connectivity and the evolution of biological systems. *J. Biological Systems* 2(1):91-103.

Green, D.G. 1994c. Evolution in complex systems. In R. Stonier and X. H. Yu eds. *In Complex Systems - mechanism of adaptation*, 25-31. Amsterdam. IOS Press. Reprinted as Green, D.G. 1995. *Evolution in complex systems*. Complexity International Vol. 2.

Green, D.G. 1997. Complexity in ecological systems. In . Klomp and I. Lunt eds. *Frontiers of Ecology - Making the Links*. N. 221-231, London. Elsevier.

Copyrighted Material

- Green, D.G. 1999. Self-Organization in complex systems. T.J. Bossomaier and D.G. Green eds. *Complex Systems*. 7-41. Cambridge University Press.
- Holland, J.H. 1995. *Hidden Order: How Adaptation Builds Complexity*. Ann Arbor. Univ. Michigan Press.
- Kauffman, E.G. and Walliser, O.H. 1990. Extinction Events in Earth History. *Lecture Notes in Earth Sciences*. Berlin. Springer-Verlag.
- Kauffman, S.A. 1992. *The Origins of Order: Self-Organization and Selection in Evolution*. Oxford. Oxford University Press.
- Kirley, M., Li, X. and Green, D.G. 1998. Investigation of a cellular genetic algorithm that mimics evolution in a landscape. In X. Yao et al. eds. *Simulated Evolution and Learning. SEAL 98. Lecture Notes in Artificial Intelligence, 1585*. 93-100. Berlin. Springer.
- Langton, C.G. ed. 1989. *Artificial Life*. Reading Massachusetts. Addison-Wesley.
- Langton, C.G. 1990. Computation at the edge of chaos: phase transitions and emergent computation, *Physica D* 42(1-3):12-37.
- Langton, C.G. 1992. Life on the edge of chaos. *Artificial Life II*, 41-91, New York, Addison-Wesley.
- Levin, D.A. 1970. Hybridization and evolution - a discussion. *Taxon* 19:167-171.
- Levins, R. 1970. Complex systems. *Towards a Theoretical Biology. 3. Drafts* Waddington, C. H. ed. 73-88, Edinburgh University Press, Edinburgh.
- Levins, R. 1977. The search for the macroscopic in ecosystems, In G. S. Innes ed. *New Directions in the Analysis of Ecological Systems II*. 213-222, La Jolla. Simulation Councils.
- May, R.M. 1974. *Stability and Complexity in Model Ecosystems*. Princeton. Princeton University Press.
- May, R.M. 1972. Will a large complex system be stable? *Nature* 238:413-414.
- Prigogine, I. 1980. *From Being to Becoming*. San Francisco. W. H. Freeman and Co.
- Raup D.M. 1986. Biological extinction in Earth history. *Science* 231:1528-1533.
- Raup, D.M. and Jablonski, D. 1986. *Patterns and Processes in the History of Life*. Berlin, Springer-Verlag.
- Toffler, A. 1970. *Future Shock*. New York. Bantam Books.
- Tregonning, K. and Roberts, A. 1979. Complex systems which evolve towards homeostasis, *Nature* 281:563-564.
- Webb, T. III 1979. The past 11,000 years of vegetational change in eastern North America. *BioScience* 31:501-506.