COENOSES 13(1):3-15, 1998
© C.E.T.A., Gorizia, Italy

ON THE DYNAMICS OF DIVERSITY

M. B. Dale[1] & P. Hogeweg[2]

1 Department of Environmental Studies, Griffith University, Nathan, Qld 4111 Australia and
Strie Pty. Ltd. 10/217 Hawken Drive, St. Lucia, Qld 4067, Australia.
2 Bioinformatica, University of Utrecht, Padualaan 8, 3584 CH, Utrecht, The Netherlands

Keywords: Diversity, Spatial patterns, Dynamics, Maximisation, Simulation, Multilevel cellular automata, Memory, Genetic algorithm, Management.

Abstract. Diversity has become a very popular measure for characterising the 'value' of ecosystems. In this paper we use a 2-level cellular automaton model to explore the stability of diversity measures in space and time, and to characterise those systems which have maximal diversity. We obtain three classes of system which consistently have high diversity, although for different reasons. We comment on the significance of these results for management and conservation, and note some implications for phytosociology.

> *The full area of ignorance is not mapped;*
> *we are at present only exploring the fringes.*
> J. D. Bernal

Introduction

Biodiversity has emerged as one of the key concepts of conservation (Hobbs, 1992). It is used by scientists, politicians and the general public, yet remains somewhat nebulous, for it is not clear that there is truly a single 'interpretive community' (cf. Carley & Palmquist, 1992) which actually agrees on its meaning. Statistically it is often related, even equated, with variance, although including categorical dimensions. It is supposed to cover variability ranging from genes to landscapes, from composition to structure and function, although quantifying this range remains impracticable. It has been credited (and discredited) with important roles in the maintenance of stability and a plethora of processes and conditions have been associated with its development, maintenance and control.

Yet while there has been recognition of the spatial variability of diversity, indeed this is of major importance to conservational arguments, there has been less study of its dynamics. Biodiversity seems, in most uses, to be a static phenomenon for all that its generation may depend on dynamic processes. A community is assigned "a diversity" and we are rarely enlightened as to the stability of this value through time. Yet the ambiguities of the relationship between diversity and stability which results from field studies, to mention only one area of interest, suggests that we need to know much more about how diversity is distributed in time. Furthermore we would like to be able to relate the emergent property of diversity to the individual properties of the various species composing the community, especially those important to population dynamics.

In this paper we use simulation models based on multilevel cellular automata to investigate the dynamics of diversity in certain simple cases. Simple because, of Zobel's (1992) 7 theories of coexistence, we use only three: non-equilibrium environment (nonstationarity) modelled as variation in fitness, regeneration niche based on availability of space and seed re-immigration as part of a more general memory structure. In particular, we assume that no static environmental heterogeneity is present, i.e., no resource variation in space, and that there are no extrinsic disturbances impinging on our system other than influx of propagules.

This is not as restrictive as it appears as there already exists some information on the effects of heterogeneity or patchiness (Czárán & Bartha 1992, Hassell, Comins & May 1994) and disturbance (e.g., Englemark, Bradshaw & Bergeron 1993) and both will involve interactions of spatial and temporal scale and intensity.

We shall also examine the patterns of relationships between organisms which lead to the development and maintenance of high diversity systems. Finally we comment on the import of our results to the use of diversity measures, in management, conservation and phytosociology.

Methods

Various modelling formalisms provide means for examining spatial and temporal variation (see Mayoh 1992). The theoretical model on which we shall base our experiments is that of the cellular automaton (CA). Essentially this comprises a rectangular grid of cells, which change their state on the basis of the states of neighbouring cells. For an introduction to the use of CA in ecology, see Hogeweg (1988).

In our model the states of the cells represent the occupancy of the cell with a single replicating entity of a certain kind or its being empty. The entities compete for space: replication can only occur into an empty cell. Furthermore their interactions are immediately through catalysis: the replicator receiving most catalysis from its neighbours wins the competition, rather than the species receiving least competition being successful (cf Hunter & Aarssen 1988, for possible positive interactions between plants). A complete description of the model is given in Hogeweg (1994), who used it in the context of prebiotic evolution. Here we examine its application in ecosystem-context. We will here present only a short outline of the model emphasising those features which are significant for our experiments.

Three points are of particular importance. Firstly, unlike Colasanti & Grime (1993), we have introduced no static environmental (resource) variation and, except in one case, there are no extrinsic disturbances. All variation is a product of the dynamics of the model itself. We do this to identify what is possible without such sources of variation. For resource gradients, Boersma, van Schaik & Hogeweg (1993; see also Czárán & Bartha 1992) have already shown that segregation into distinct types can occur even if the gradients are shallow.

However, the local nature of the cellular automaton provides local nonlinear competition for empty space. This can lead to the formation of spatial patterns when local rather than global mixing occurs. For example, Fig. 1 shows ring-like structures, and such have been reported in the field, and are often interpreted as representing centripetal growth patterns. On closer inspection these structures are found to be double spirals (not circles) whose size is **not** age-dependent (cf Boerlijst & Hogeweg 1991; Hassell, Comins & May 1994).

But we do not ignore environmental variation entirely. We have concentrated on stochastic variation in environmental variation, that is the short term local fluctuations. The importance of such variation is that it changes the fitness of each of the entities relative to each other. We can simulate this effect equally as well by changing the entities themselves, that is we replace a constant genetic basis for the entities and a varying environment by a varying genetic basis in a constant environment, a process called here mutation. For a more detailed study of the interaction of spatial patterns and evolution see Savill, Rohani & Hogeweg (1997).

Secondly, we use a multilevel automaton to make provision for long term effects operating at a different, slower, time scale. Note that the time scales of operation of both the levels are fixed; in reality variation might be expected if extrinsic sources of variation were impinging on the system but since we have none they can be ignored, which simplifies the modelling. Our 2-level model is then embedded in a genetic algorithm which seeks to maximise the diversity.

Thirdly, this is a theoretical study. The relationships between our model parameters and functions and corresponding real-world values and processes are many-to-many. Thus the correspondence is such that instantiation of our model for a particular ecosystem may be very difficult. For example, where the model specifies that 2 entities interact, a real example will of necessity have to determine the nature of the processes involved in that interaction and evaluate the requisite parameter values.

The multilevel automaton

The basic automaton we use has 2 levels, one dynamic and the other passive. Each individual automaton is based on a grid of 100 x 100 cells (sometimes 160 x 160 cells for display). The cells in our automata form a grid, the boundary of which is regarded as empty and absorbing.

The replicator automaton

This is the active automaton which contains random networks of self-replicating entities. It represents the visible spatial ecosystem. A maximum of 160 different entities is possible, each of which interacts with all other entities through competition for space, while it has specific catalytic interactions with a small subset of the other entities. The term connectivity is used to indicate the average number of other entities which each entity catalyses. For convenience we shall refer to entities as 'species' although it must be made clear that this is not the only possible interpretation; that is, our species are more of the philosophical than the taxonomic kind.

For each species existing in a cell we calculate its total catalytic potential as the sum of the catalysis from species in the surrounding neighbourhood - neighbourhood being the surrounding 8 cells. An **empty** cell is occupied (colonised) by the adjacent species with maximal catalytic potential, if any such adjacent species exists. Other possible rules could be introduced. For example occupancy of empty space could be based on stochastic selection from the catalytic potentials, or alternatively non-catalysed replication could be allowed. Experiments suggest that the results are not crucially dependent on the rule used, and the deterministic rule avoids introducing unnecessary variation.

An **occupied** cell has a given species-specific probability of becoming empty – i.e., of dying. There is also in the model provision for a probability of somatic mutation where one species is immediately replaced by another. This mutation provides us with a means of simulating a variable environment. Fitness may be regarded as the 'distance' between species optima and environmental state and instead of constant species in varying environment we have varying species in a constant environment.

Species may **disperse** over the automaton grid. We have examined only two possibilities for dispersal, local and global. Local dispersal, diffusion, involves the species moving randomly to an immediately adjacent cell. Global dispersal, stirring, permits the species to move to ANY other cell in this layer.

Finally **new** species can enter the replicator automaton from the storage automaton or through random influx. Such species may be of the same type as those already present or of a different type, thus representing an invasion of the system.

The storage automaton

The second automaton represents a passive long-term storage system. It represents ecologically such possibilities as seed banks in soil and/or also external sources of species. Note the ambiguity of interpretation, which would necessarily have to be resolved if the model were to be instantiated for a real system. However, for our present theoretical studies should resolution is NOT required. Unlike an attempt to model a real system for practical purposes, we do not have to separate the effects of all the processes, nor combine components of different processes into single model functions.

Using a neighbourhood defined on the replicator automaton, catalytic potentials are again calculated, and the species with highest potential can be transcribed from the storage layer to an empty cell in the replicator layer. There is no transcription in the other direction. Further, there are (almost) no deaths in the storage automaton so any species can reappear after extinction on the replicator, which simulates long distance dispersal possibilities. In fact, because of the way the genetic algorithm functions (see below), it is possible for a species to disappear entirely, though this is unusual.

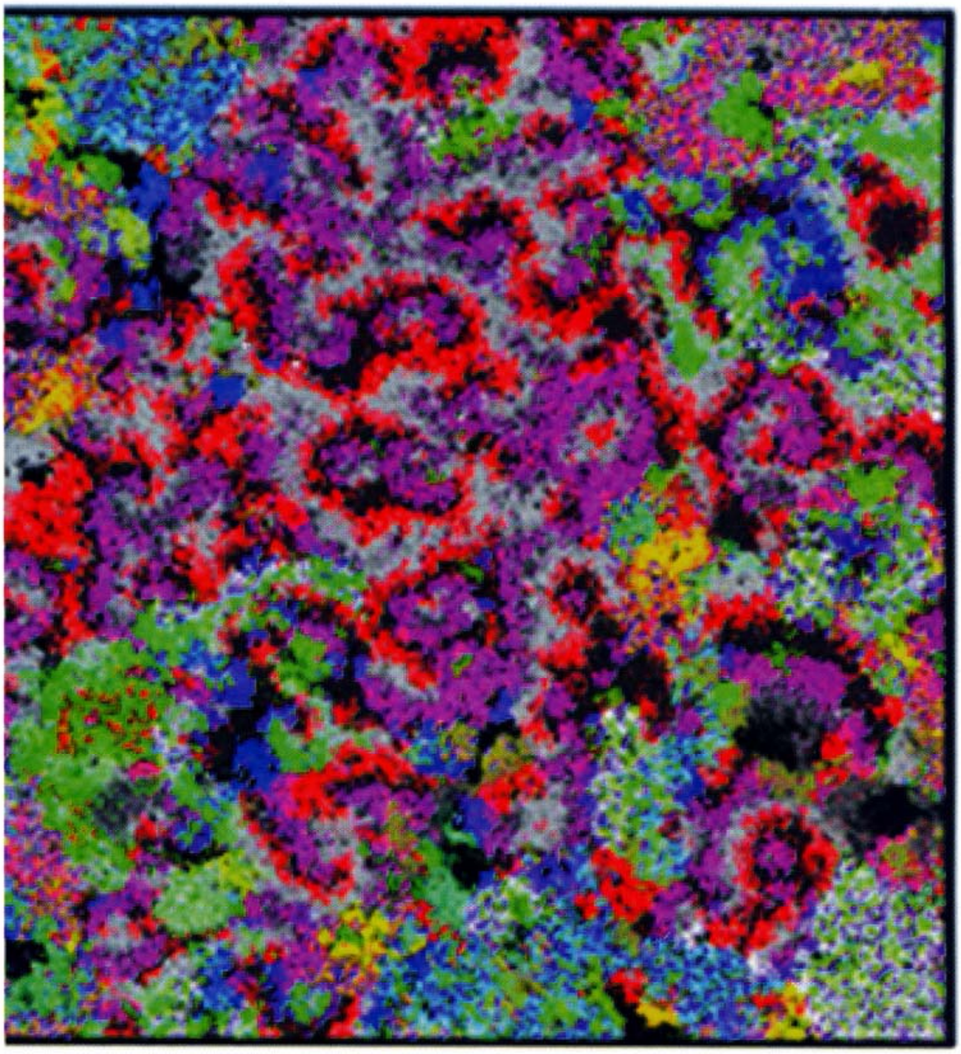

Figure 1. A snapshot of an automaton with colours indicating different species. The apparently circular patches are in fact double helices and their size does NOT change with time.

Genetic optimisation

We are not especially interested in random automata; in general they are unstable and of low diversity. In order to provide some more suitable objective we have chosen to seek for maximally diverse automata. To obtain such automata we employ a genetic algorithm.

Population

In our genetic algorithm we employ not 1 but 18 automata. This forms the population which is to be selected. Periodically we examine the population by calculating some evaluation function. We then reject members of the population with low values and replicate those members which have high values. During this replication process new species are added to the storage automaton, replacing existing ones in case of crowding. Moreover, we also permit 'crossing-over'; the 2-dimensional snapshots of 2 automata are broken in an identical manner and the complementary pieces are fused to form 2 new automata. This use of evolutionary mechanisms allows us to search the space of possible automata and identify those which maximise the chosen function.

Maximisation function

The function we use for evaluation is simply the number of different types of species (whose density exceeds a threshold) in the replicator automaton. This is the simplest and most obvious measure of diversity. More complex measures of diversity are certainly possible, with various entropic information measures the most obvious. However, here we are simply interested in identifying properties of systems which do maximise diversity. The threshold induces a slight smoothing effect and acts to reduce the instantaneous diversity.

As noted earlier, we could opt for an evaluation criterion based on something other than diversity. Although it is certainly one in which ecologists have shown considerable interest, diversity is not perhaps the most interesting property of the system. It might be more pertinent to examine stability or predictability in combination with diversity, or directly address population viabilities (Boyce 1992).

For conservation purposes we might consider Anderson, Hutson & Law's (1992) concept of permanence. Permanence means a set of species which can co-exist indefinitely. It is NOT equilibrium or asymptotic stability, since in these cases some orbits of convergence could involve extinction of some species whereas permanence implies that all orbits stay some finite distance from the extinction boundary. Goh (1992) has extended this and discusses q persistence where the orbits are always more than q distant from the extinction boundary. Our present results do contribute some information about stable configurations and invadability as side effects of diversity as will be seen later.

One other problem can occur if the investigator is prepared to provide constraints to determine the feasibility of a system. In such a case the program would need to first obtain some feasible solution before proceeding towards an optimal one, for our present random assignment would not guarantee feasibility. This would considerably complicate matters and in our simple system is unnecessary; in any case we hesitate to specify what is or is not feasible ecologically. To do so would necessitate much more detailed specification of many additional species properties possibly along the lines of Alatalo & Alatalo (1977). A possible means of coping is available through the use of a penalty function approach with feasibility as one component of the evaluation function.

Initialisation and operation

Evaluation and replication of the population takes place every 125 time steps which is also the timing for cross-over operations. We have not sought to identify optimal conditions for replication, which appears to be more efficient when applied to transient stages away from stable attractors. The selection of automata to kill or reproduce was made on the basis of the total number of species ($M=160$) and the number present at least 50 times (N); killing was based on $(M\text{-}N)^3$, reproduction on N^3.

For species, variation in death rate was provided by random uniform drawings in the range 0.15 - 0.25 while variation in catalysis was a uniform drawing in the range 80 - 125. There is evidence which suggests high death rate and low catalysis are 'advantageous' to a species, but we have not examined this in detail in the present study. Initial spatial allocation is random.

Selection under the genetic algorithm continued for 25000 time steps (200 crossover steps). After this the system was allowed to continue for at least 4000 more steps to assess its stability. The results presented below pertain to this terminal, unselected, stage.

Experiments

We have available 4 different levels of evolutionary system which might be examined, the ecosystems of replicators, meso-scale patterns formed, the population level and its variability and the stored information. In this study we shall be concerned only with the diversity of the individual replicators and the nature of systems which maximise this diversity. We examined three variables in this context.

Connectivity. As noted earlier each type of species interacts with a fixed average number of other species types. We can vary the amount of interaction by varying this degree of connectivity. It turns out that the behaviour of the system switches for high (>8) and low (≤8). connectivity (see below).

Dispersal. We have implemented 2 different dispersal regimes, local and global, using the same dispersal regime for all species in one simulation. These artificial extremes are chosen on purpose, to facilitate analysis. They indeed give rise to very different ecosystems.

Influx. Influx occurs as transfer between the storage layer and the replicating level or as random influx from the entire pool of species.

Results

Although our experiments cover 8 state combinations, the results show only 4 patterns, one of which is essentially a collapse to very few species in a non-diverse system. Since our interest is with high diversity we shall examine only the other three which we shall identify as 'invariant attractors', 'core-with-transients' and 'percolation' patterns. For these we first examine results showing various trace information representing the spatial and temporal variation in diversity. In these diagrams each colour represents a different species, with empty space being shown as black. The trace information is presented in 4 columns which we shall assume are numbered from left to right and with time on a vertical descending axis.

- Column 1 records a series of cross-sections or transects across the centre of the grid, taken every 6 time steps.
- Column 2 records the presence/absence of individual species throughout the course of the simulation.
- Column 3 shows the total number of species and their abundances in the replicator layer – the diversity.
- Column 4 shows 4 snapshots of the system, representing the spatial pattern of species present on each of 4 occasions.

In order to interpret these patterns we also use, where possible, a diagram showing the topology of the catalytic relationships between the species. This is of course a snapshot of the system at a particular time since the number and types of species present is potentially constantly in flux. For clarity our diagrams show the interactions of persistent species - there are usually a larger number of very transient species (existing for <5 steps) whose depiction would confuse the presentation.

Invariant attractors

This system occurs when there is global mixing, weak interaction, and low influx from the storage level. Up to 10 replicators are essentially constantly present. Commonly there is a cyclic catalytic structure with various parasitoid links coming from it. Fig. 2 shows a representative catalysis diagram and Fig. 3 the population fluctuations for the parasitoids and the cyclic species.

Diversity here does not vary much through time; the system remains largely constant in composition by effectively suppressing invasion by other species. The characteristic topology is one of simple cyclic structures with appended chains of parasitoids. However, it is surprisingly unstable in some other ways. If, for example, we remove the parasitoid labelled 37, then 67 outcompetes 30, the cycle breaks and the system collapses to a 2-species form. Stability is here clearly reliant on some delicate checks and balances!

Core and transient

Local mixing with weak interaction with low or high influx leads to a very different system containing a very few constant, but usually rare, species and a continuing series of invaders. These invaders enter the system, divert it to some possibly long transient series until a final return is made to the small constant core. Thus the specific species contributing to the diversity vary continually in time, and cumulatively diversity becomes very high. At any given time, however, it may be more or less diverse than the invariant attractor system.

Moreover, high diversity does not mean stability. We have examples where a rapid decline to a 2-species system follows closely after a peak diversity exceeding 30. Clearly, high diversity alone is, for this system, not an adequate predictor of persistence.

The trace in Fig. 4 and the topology in Figs. 5a,b,c shows an 8-connected system where we have long term storage with a low mutation rate in the replicator automaton. There is an early change from a blue dominated to a somewhat

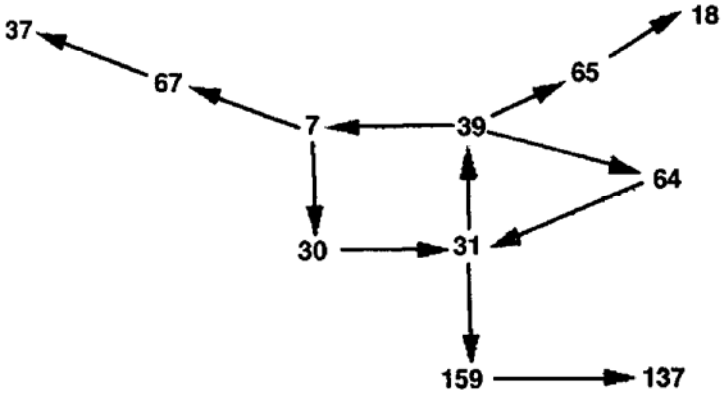

Figure 2. Linkage network showing facilitative interactions between species consistently present. Species occurring temporarily (less than 3 periods) are excluded. Arrows indicate the direction of the catalysis and line thickness indicates its strength.

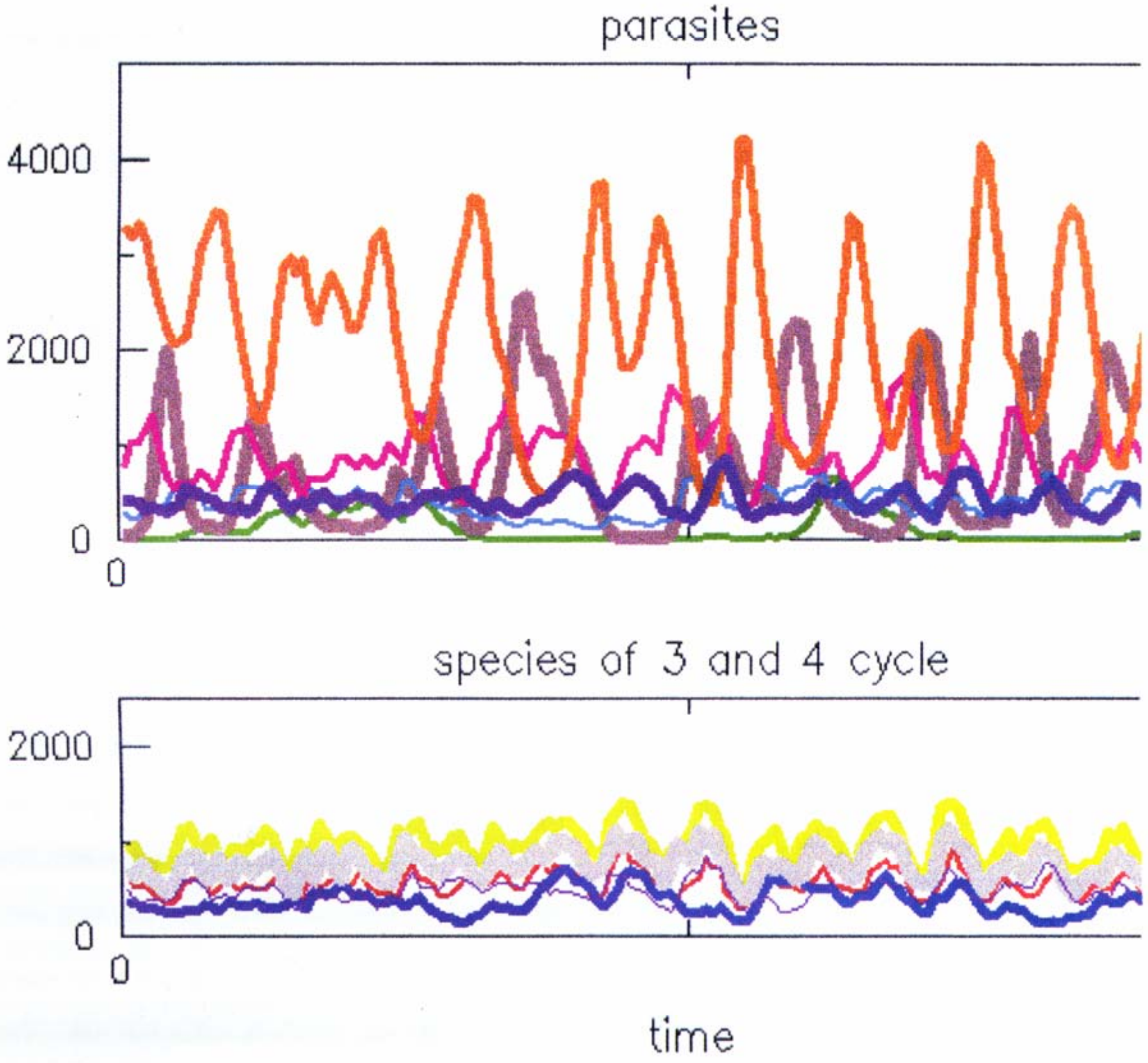

Figure 3. Dynamics of 'parasitoids' and Dynamics of core species for the Invariant Attractor. The episodic nature of the variation is similar to that observed in several population studies.

heterogeneous 'purple' one. The topology diagrams show the parallel changes in connectivity, with a transition through a complex cyclic structure to a simple one. But in general the diversity remains remarkably constant for long intervals although the species comprising it are continually changing. One set of species (17-57-117-25) remains present throughout although not necessarily in great abundance

We now suppress the storage layer, replacing it instead with a high mutation rate in the replicator layer. The interesting point (Fig. 6a) here is that there is a change from a purple-dominated to a blue-dominated system, **without** significant change in diversity. Indeed if this trace is continued, a reversal to purple-dominant occurs (fig 6b), followed later by yet another change to blue. We have here an ecosystem which, without environmental change or disturbance, can oscillate between two states. The change is a function only of interactions between the species.

The catalysis network diagrams (Fig. 7a,b,c) show the associated interconnections where it can be seen that one cycle (15-106-133-78) remains present while other cycles form and dissociate. Overall, though, we again have a diversity remaining relatively constant although the constituent species are changing.

More generally the characteristic topology for 'core-and-transient' systems is more complex than for invariant attractors, with multiple interlinked cyclic relationships. The transient invasions permit the formation of new cycles linked

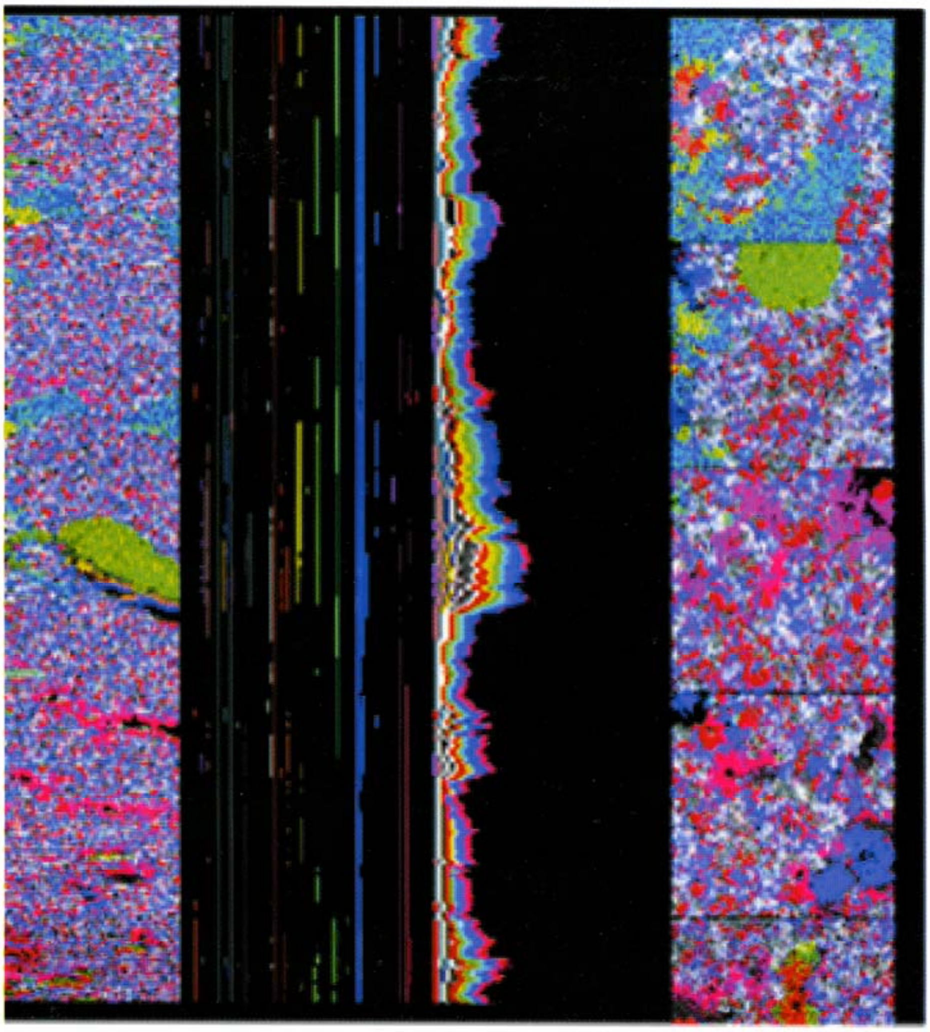

Figure 4. Trace 8-connected with storage layer. The vertical dimension represents time. Every species is allocated a distinguishing colour, which is constant over the 4 traces. For explanation of the 4 traces see text.

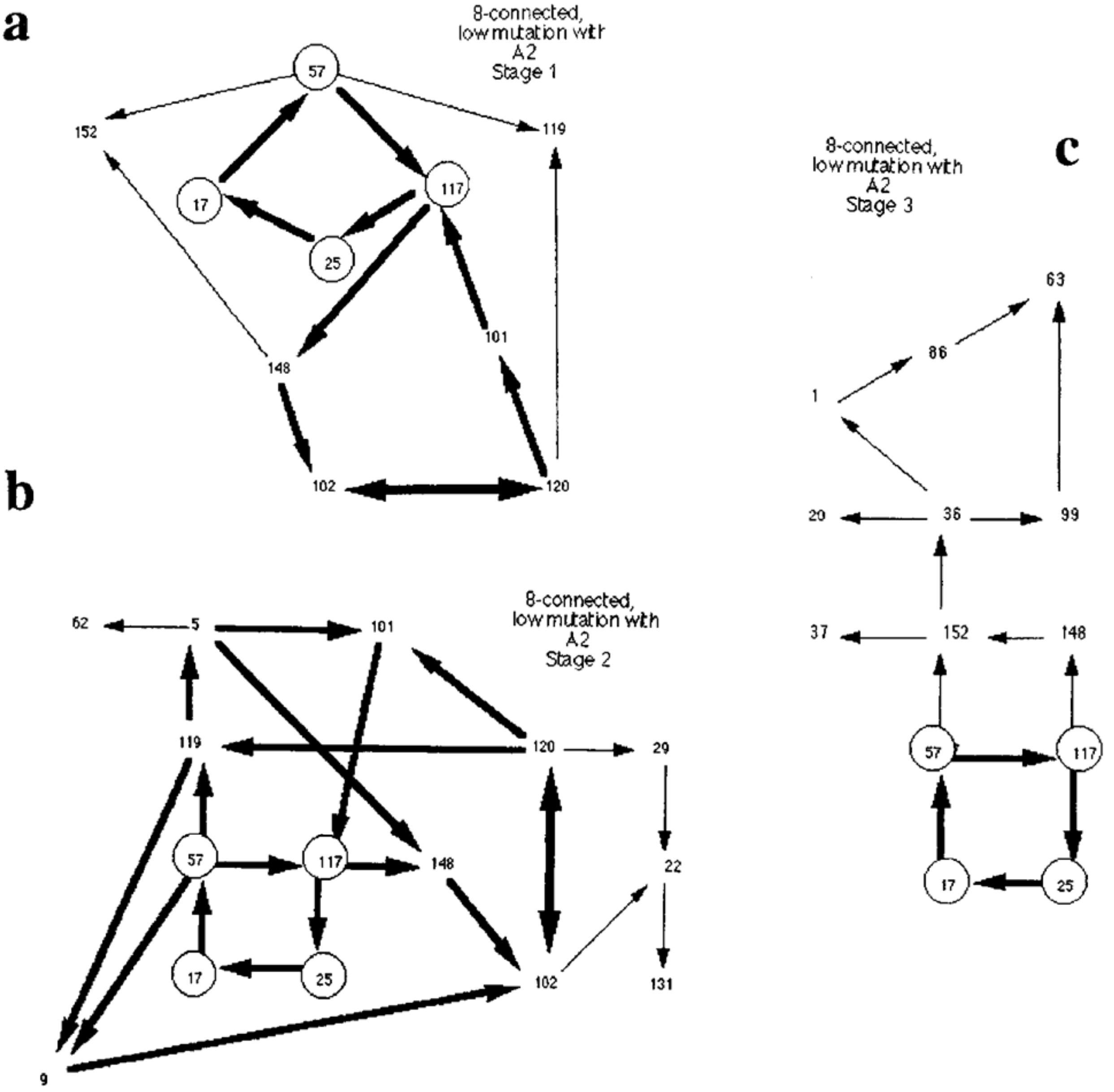

Figure 5. Associated Network at 3 stages. Note the large number of cycles.

in various ways to the persistent core cycle, but these additions are not, in the end, themselves persistent. Diversity in this system is more variable than in the invariant attractor case and furthermore the species which contribute to that diversity are themseves constantly changing apart from a small number of often quite rare but persistent ones.

Percolation

For the final case we show only the trace (Fig. 8); the topology is impossible to draw! If the connectivity is sufficiently high or the external influx is very large, dispersal becomes an insignificant factor. The system becomes a transient series wandering through the 160-dimensional space of species! No patterns are constant, no core species are constantly present. The diversity is mostly very high (30+) although it still fluctuates quite markedly.

In fact detailed observation suggests that occasionally small, local islands of stability do occur, forming pseudo-attractors, but these do not have a long lifetime (cf. Alvarez-Buylla & García-Barrios 1993). Thus when observing a system we can be misled by these temporary effects into believing that some persistant structure exists, especially if the time scale pertinent to the system is much slower than that of the human observers.

But note that there are 2 distinct possible causes for this situation of constant flux. High connectivity is commonly attributed to rain forests and this would provide reason for their high diversity. Large external influx is characteristic of the Great Barrier Reef which again has a high diversity. However, in certain monsoon forests of Northern Australia, which have the same species complement as the rain forests, it is probably the external influx of seeds which maintains diversity, rather than the interconnections (Russel-Smith & Lucas 1994). Thus knowledge of the species present is **not** a sufficient means of characterising the dynamics of the system.

Conclusions

As a theoretical model, our cellular automata provide a useful means of examining some topics. The model is not meant to mimic any particular ecosystem, but is meant to identify some general trends. As such our limited investigations do provide a basis for questioning certain popular notions regarding biodiversity.

What is perhaps most obvious here is that measuring diversity without knowledge of the generating processes tells

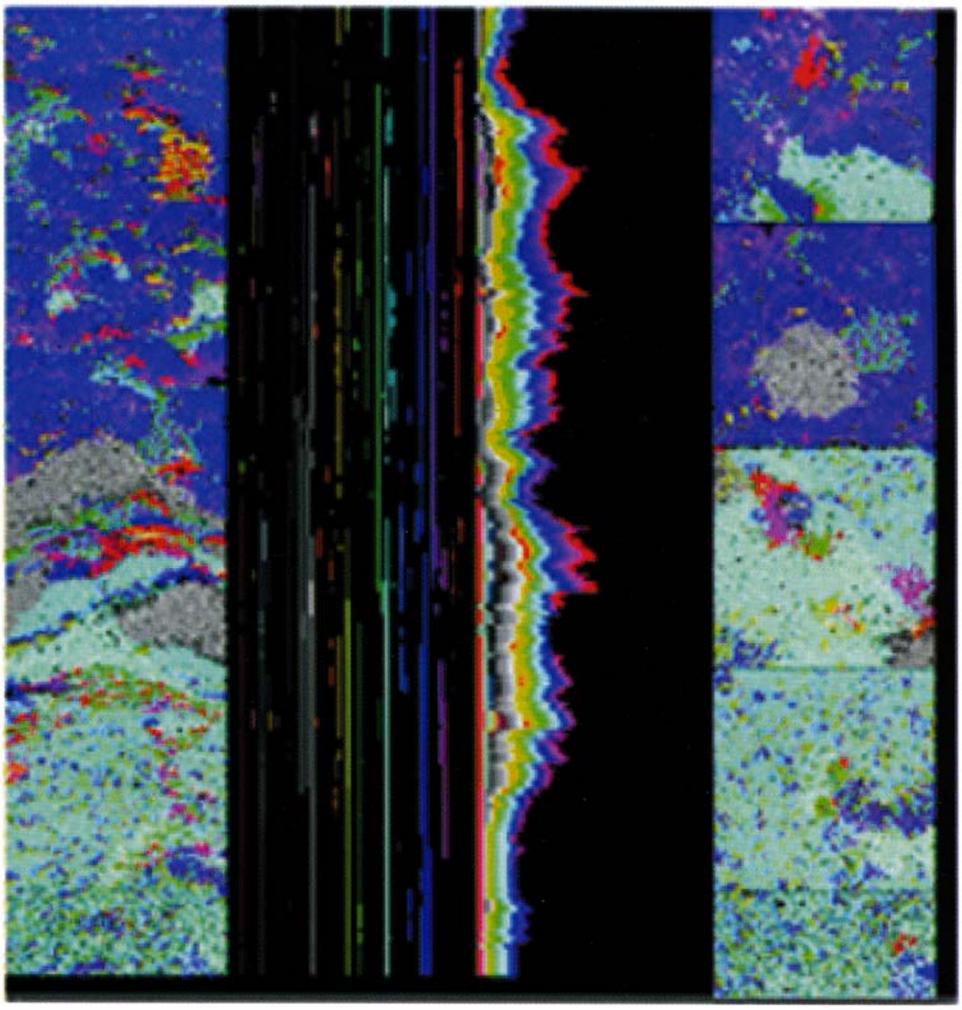

Figure 6. Trace 8-connected no storage layer but high mutation. (Above and next page).

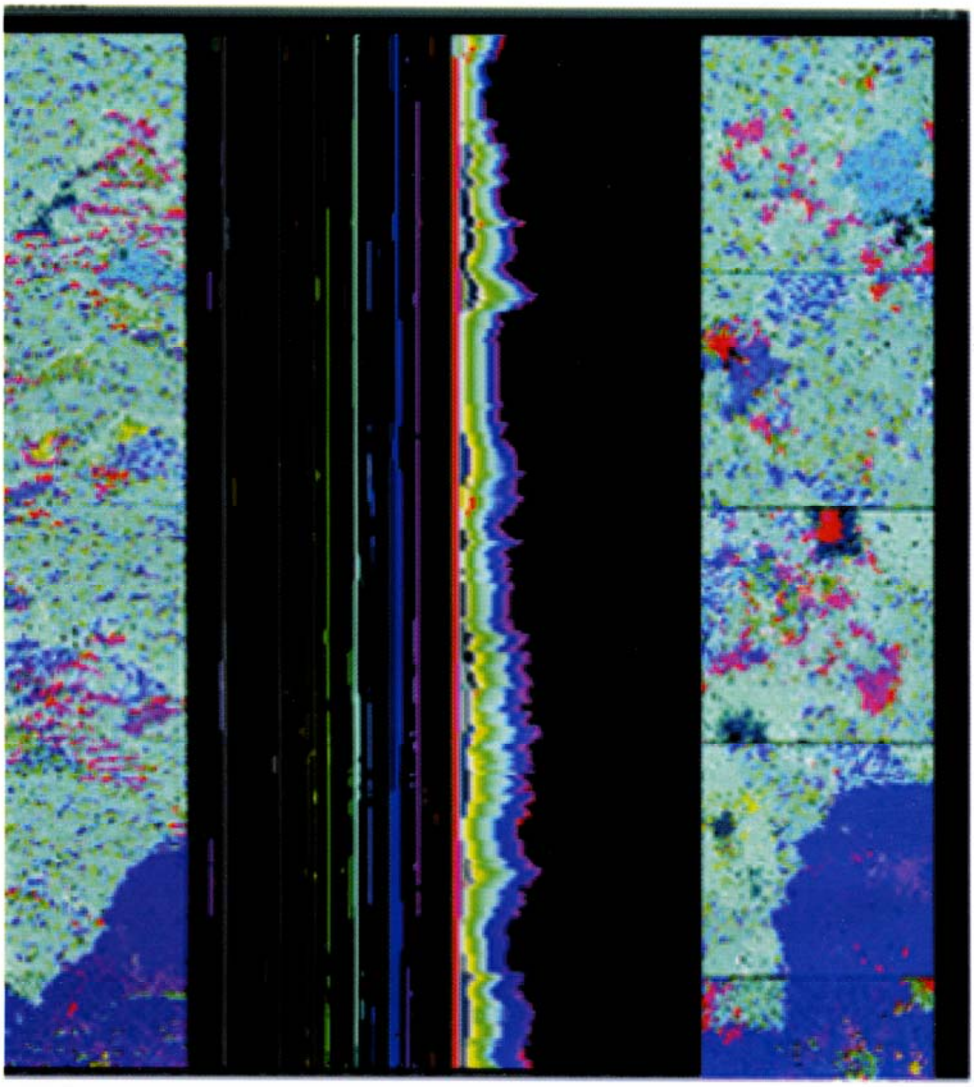

Figure 6b.

us very little about the system, or about its stability. We need to know much more fundamental characteristics of a system and the species composing it before the emergent property of diversity is useful and then it is likely unnecessary! Only if we know the system to belong to the invariant attractor class is a single measurement of diversity meaningful, for then invaders are few and the system generally stable. However, for conservation, knowing that a system is an invariant attractor allows us to effectively decide to do nothing except prevent major disturbances - natural invasion is unlikely.

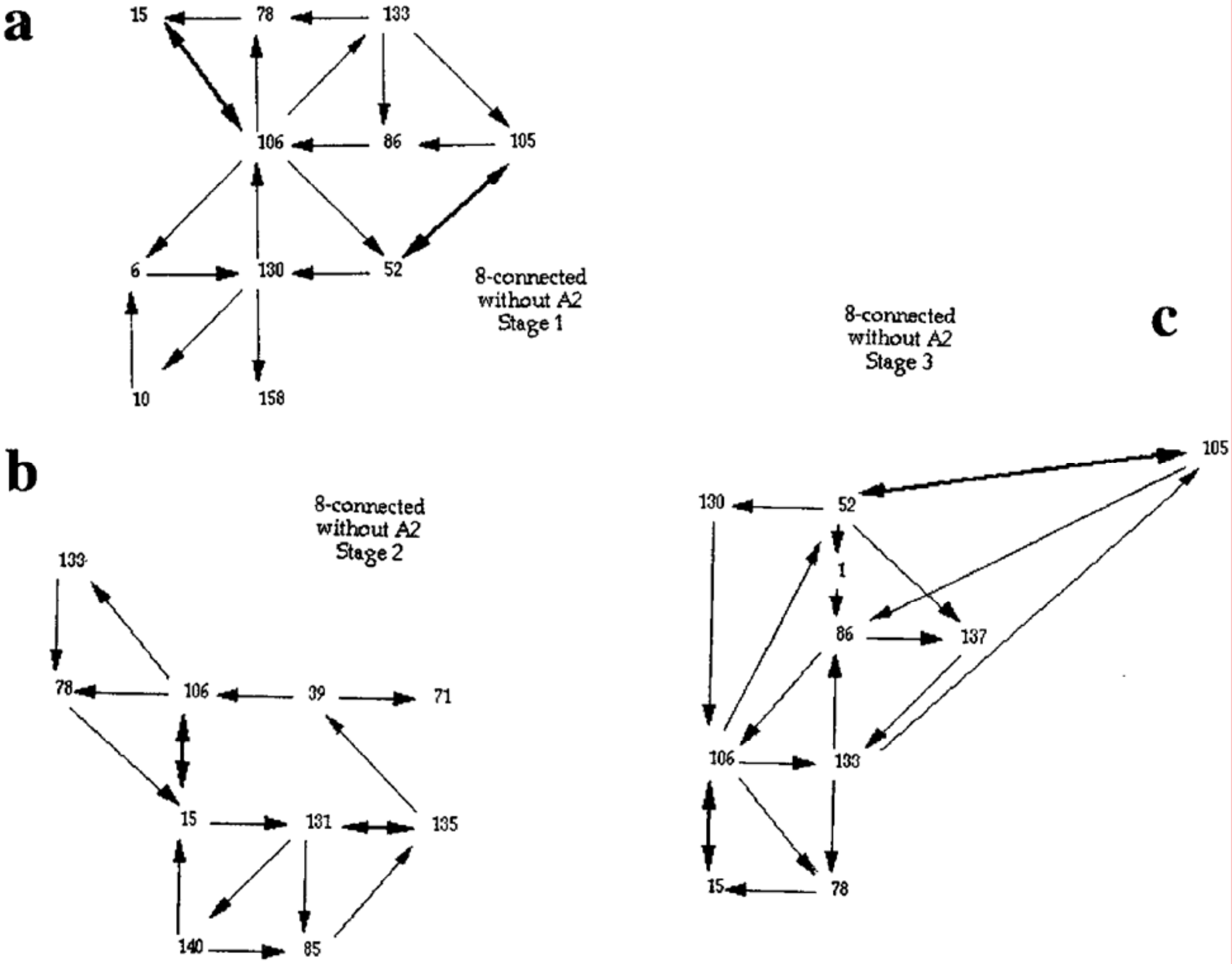

Figure 7. Associated Network at 3 stages.

We must also be careful when considering sustainability, especially if we are proposing an intrusive impact, such as the introduction of grazing animals and the removal of potential predators. The example of excising species 37 shows that all the species may be required to maintain the system and we cannot arbitrarily decide that something is a 'pest' to be eradicated. However, if we seek to maintain the system, we would generally try and remove exotic invaders.

For a percolation system everything is unstable, and, although a high diversity is maintained, the species contributing to it are forever in flux. But a common species complement is insufficient grounds for attributing this diversity to a single cause, as indicated previously. For conservation all we can do is obtain the largest possible area or else provide the external sources. But we must remember that no suite of species is actually being conserved. Attempting to do so could in fact lead to loss of diversity at a later time.

The most interesting case is the core-with-transient. Here diversity fluctuates quite widely, and this is associated with the development of meso-scale patterns. In such systems the spatial patterns are of critical significance. Such patterns can develop in a homogeneous environment, although it is known that differential predation can produce such patterns too (Pacala & Crawley 1992). Conservation of these systems involves recognition of the importance of the spatial patterning and the maintenance of areas sufficiently large for it to occur.

The core with transient case also showed the possibility of changes occurring in systems from internal causes and without any associated environmental change or disturbance impact. This is not to say that environmental control and disturbance effects are negligible. Instead, it means that we cannot **assume** any observed changes have external causes - beware, then, ordinations with environmental intent. It also means that we cannot interpret change simply in terms of a directed succession. The transient phases can be quite long, yet return to the core condition is still inevitable.

How does diversity fare as a measure of 'ecosystem health'? Unfortunately not so well. Activities inimicable to the survival of the system may well decrease diversity, but such decreases can also occur quite naturally. In a core-with-transient system we might examine the continuity of the core species to determine if an impact is damaging; with a percolation system even this is not available and some other measures are needed - local predictability perhaps? Further,

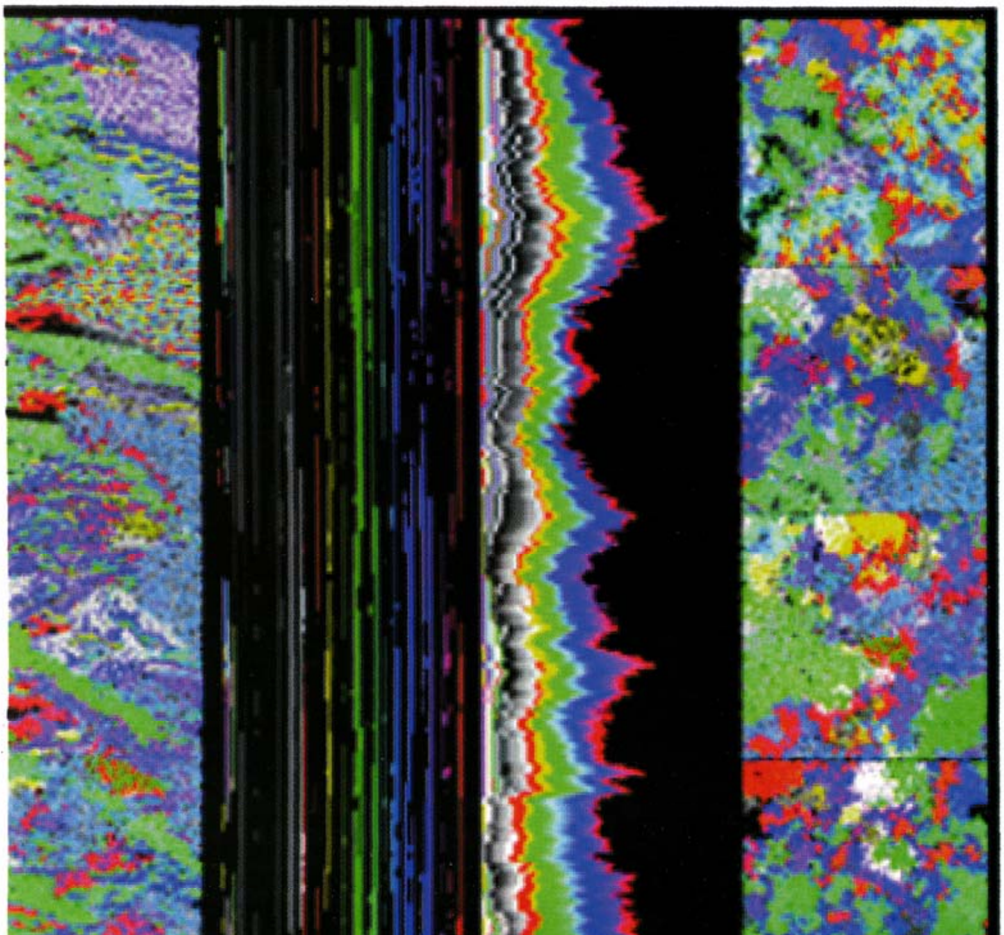

Figure 8. Trace of a Percolation System showing absence of constant species and highly variable diversity.

high diversity can be maintained by constant flux so that attempting to 'conserve' a specific high diversity phase of the system dynamics can lead to a suppression of the, otherwise natural, entry of further species. In part this is due to incompatibilities between scale of the human observation and the scale of changes in the system, which remain unrecognised by the human system assessing conservation value.

There are also some implications for those who would have us set up a universal classification system. Clearly, of our three types, only the invariant attractor systems lend themselves to such a treatment. In a percolation system there is no constancy and hence no classes, while core-with-transient systems will almost always contain a large number of species which are chance occurrences to confuse the issue. These will often, though not necessarily, be rare so that identifying 'rare' (faithful?) species provides no solutions.

We noted above that knowledge of the species alone is itself insufficient to characterise the dynamics. This does not mean that local typologies may not be useful in identifying and demarcating spatio-temporal patterns, only that these cannot be presumed to have any continuing utility. This has some marked consequences for management which is commonly based on the recognition of distinct areas which are in some sense disjunct through time. It also has major significance for those phytosociological schools which presume static species lists to be sufficient for prediction.

References

Alatalo, P. & Alatalo, R. 1977. Components of diversity: multivariate analysis with interaction. Ecology 58: 900-906.

Anderson H. M., Hutson, V. & Law, R. 1992. On the conditions for permanence of species in ecological communities. Amer. Nat. 139: 663-668.

Alvarez-Buylla, E. R. & García-Barrios, R. 1993. Models of patch dynamics in tropical forests. Trends Ecol. & Evol. 8: 201-204.

Boerlijst, M. C. & Hogeweg, P. 1991. Spiral wave structure in prebiotic evolution: hypercycles stable against parasites. Physica D 48: 17-28

Boersma, M., van Schaik, C. P. & Hogeweg, P. 1993. Nutrient gradients and spatial structure in tropical forests: a model study. Ecol. Model. 55: 219-240

Boyce, M. S. 1992. Population viability analysis. Annual Rev. Ecol. System. 23: 481-508

Carley, K. & Palmquist, M. 1992. Extracting, representing and analyzing mental models. Social Forces 70: 601-636

Colasanti, R. L. & Grime, J. P. 1993. Resource dynamics and vegetation processes: a deterministic model using two-dimensional cellular automata. Functional Ecol. 7: 169-176.

Czárán, T. & Bartha, S. 1992. Spatiotemporal dynamic models of plant populations and communities. Trends Ecol. Evol. 7: 38-41

Englemark, O., Bradshaw, R. & Bergeron, Y. 1993. Disturbance dynamics in boreal forest: Introduction. J. Veg. Sci. 4: 730-732

Goh, B-S. 1992. "Management and Analysis of Biological Populations", Elsevier, Amsterdam.

Hassell, M. P., Comins, H. N. & May, R. M. 1994. Species coexistence and self-organizing spatial dynamics. Nature 370: 290-292

Hobbs, R. J. (ed) 1992. "Biodiversity in Mediterranean Ecosystems in Australia", Surrey Beatty & Sons, P/L., Chipping Norton, NSW.

Hogeweg, P. 1988. Cellular automata as paradigm for ecological modelling. Applied Math Comp. 27:81-100

Hogeweg, P. 1994. Multilevel evolution: replicators and the evolution of diversity. Physica D 75: 275-291

Hunter, A. E. & Aarssen, L. W. 1988. Plants helping plants. BioSci. 38: 34-40

Mayoh, B. 1992. Templates, fragments and skins. In: G. Rozenberg & A. Salomaa (eds.) "Lindenmayer Systems: Impacts of Theoretical Computer Science, Computer Graphics and Developmental Biology", Springer-Verlag, Berlin. pp. 497-514

Pacala, S. W. & Crawley, M. J. 1992. Herbivory and plant diversity. Amer. Nat. 140: 243-260.

Russel-Smith, J. & Lucas, D. E. 1994. Regeneration of monsoon rain forest in Northern Australia: the dormant seed bank. J. Veg. Sci. 5: 161-168

Savill, N. J., Rohani, P. & Hogeweg, P. 1997. Self-reinforcing spatial patterns enslave evolution in a host-parasitoid system. J. theoret. Biol. 188: 11-20

Zobel, M. 1992. Plant species co-existence – the role of historical, evolutionary and ecological factors. Oikos 65: 314-320