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DYNAMICS OF DIVERSITY: MIXED STRATEGY SYSTEMS

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Abstract: This paper examines the effects of birth and death rates on the dynamics of diversity in systems without abiotic environmental changes using a two-level cellular automaton model. The systems examined combine species with high birth- and death- rates (hi/hi) and species with low birth- and death- rates (lo/lo). The resulting chaotic systems seem to possess pseudo-attractors even in the case of high number of interactions between species which was not true of more homogeneous systems previously examined. Overall the introduction of distinct types of species led to increased diversity and stability (though in a special sense) which may explain the association of these two characteristics in field observations. Most systems involved mixtures of hi/hi and lo/lo elements although 'pure' systems did occur, more commonly as lo/lo systems.

Introduction

In a previous paper (Dale & Hogeweg 1998), we introduced a two-level cellular automaton (CA) model of a simple ecosystem to investigate the dynamics of diversity. One important characteristic of this model is that it includes no extrinsic environmental changes, all variation being developed by the dynamics of the model species in competition for space. This same characteristic holds for the model to be presented in this paper. For studies involving gradients, see Boersma, van Schaik & Hogeweg (1993) and Colasanti & Grime (1993).

We accept Levin's (1992) argument that ecological interest lies in between-scale interactions, permitting our processes to operate at their own, independent, scales both within and between the two automata. The first automaton can be regarded as representing Eriksson's (1993) 'ecological' phenomena, for example, resource use patterns, effects of herbivores or even chance effects of recruitment. It also produces mesoscale patterns (cf. Hastings et al. 1983), including those recognised by Prentice & Leemans (1990). In their forest, small gaps were immediately filled by the dominant tree species, whereas large gaps permitted invasion by other species which were then replaced by the dominant tree species. Thus the existence, or otherwise of a 'pattern and process' cycle was entirely dependent on the size of the gaps.

Our results reflect the populations of species, and this implies some kind of averaging over the entire CA space with concomitant loss of detail concerning individuals or their immediate neighbourhood. The use of 'population' is thus a smoothing tool and it may subsume considerable variation. Note that Patil & Taillie (1982) regard diversity as a population property derived from information on species rarity. This suggests that diversity is another smoothing device which can hide much detailed variation. Examining in more detail the actual progress of our simulations provides an opportunity to identify the manner in which processes exhibit themselves in space and through time.

The second automaton may represent complementary 'historical' phenomena, speciation, extinction and biogeography acting through the pool of available species (cf. Taylor, Aarsen & Loehle 1990). It is also used to provide an influx of replicators but, unlike mutation, this influx is selective in form, since it is derived from whatever replicators have proven not to be disruptive and hence have been maintained in the memory. However, in principle these memorised replicators may mutate so that novel forms can enter whose disruptive qualities are untested. This would introduce the balance between creation and extinction of taxa which Balon (1993) has argued is an important long-term conservation objective. In the present study, however, the mutation rate was set to an extremely small value, thus reducing any evolutionary effects to a minimum.

Previous Results

Summarising our previous results, we found that diversity varied markedly through the simulations and could not be regarded as a characterising feature of the system. This implies that a simple description of an ecosystem based solely on the presence (or abundance) of species is inadequate to define the state, and will not enable the investigator to make predictions regarding the dynamics of the system.

We could identify 4 scenarios resulting in 3 patterns of diversity dynamics which are shown in Table 1. If each species interacted with many others (in our original model 'many' = 7 or more) or if the influx of propagules from outside was very large then the system apparently moved through all permutations of species combinations with no long-term stable components; we call this a **percolation** pattern. For the case of few interactions, the dispersal of the species was critical. With global dispersal an **invariant attractor** pattern is obtained which retains a core of species

Table 1. Characteristics of Dynamic Diversity Patterns – from Dale & Hogeweg (1998). n/a = not applicable.

System Type	State of Experimentally Controlled Processes		
	Dispersal	Connectivity	Propagule Influx
Invariant	Global	Low	Low
Core with Transients	Local	Low	Low
Percolation	n/a	High	Low
Percolation	n/a	n/a	High

constantly present and which is always difficult for other species to invade. This corresponds to a resistant system. With local dispersal we obtain the **core with transients** pattern where a very small number of constant species is present, but the system suffers repeated invasions, followed by recovery, thus providing an example of a resilient system.

The system previously modelled can be viewed in two ways. It could either represent a metapopulation of a single species, or a large number of species, each more or less equivalent, evenly spread through the parameter space. In both these cases, the species (or populations) in effect all adopt a similar strategy differing only in randomly assigned parameter values. Thus, in any specific simulation, all species were assumed to disperse globally (or locally), all species had high (or low) numbers of interactions with other species, all propagules were internally (or externally) generated. While possible, such coarsely homogeneous systems seem unlikely to occur in nature. Indeed, in evolving linguistic systems, Arita & Koyama (1998) found homogeneity was associated with reduced fitness and while the mechanisms of evolution are obviously not identical, a similar result might be expected in biological systems.

In this paper, I look at the effects of introducing two strongly contrasting species groups which differ in their strategies. Such a situation occurs when the species are separable into two distinct life-form groups, such as tree and forbs. Such a polarisation will not have a great effect in the isolationist case, so we restricted our attention to the percolation and core-with-transient cases. By concentrating on local dispersal, without external propagule influx, we can vary the degree of interaction of the species to cover the transition between core-with-transient and percolation systems. This enables us to identify if the polarisation delays or accelerates the change from one to the other.

The Polarising Dimension

Within the model we can identify various characteristics which might provide us with possibly interesting polarisation. These include:

- Mortality Rate
- Birth Rate
- Number of interactions with other species
- Capture of Space
- Global/local dispersal

Of these, it was simplest to investigate mortality and birth rates. However, changing either mortality rate or birth rate in isolation will lead to rather obvious results, and both need to be manipulated to maintain some kind of balance. Reducing mortality leads to longer lived individuals, so as a counter balance we reduced the birth rate (or rather the rate at which adjacent space is captured which might also be a result of reduced growth rates) for low death rate species. This prevents the ultimate complete takeover which would otherwise occur. For high death rate we retained the values used in our previous studies without any adjustment to birth rate.

Once this choice has been made we need to consider what combinations should be examined. Both high birth-low death and low birth-high death possibilities are uninteresting, the former leading to overwhelming dominance, the latter to extinction. So we need to examine only a polarisation between low birth-low death and high birth-high death cases. In practice, we established low death rate to be 1/4 of the high rate, which remained as in our previous model at 20%. Low birth rate was then similarly reduced to 1/4 of the high, and again the high rate remained unchanged from our previous model. This effect was introduced by permitting the individual to compete only 25% of the time for adjacent available space. Overall, these changes retain the parameter values within interesting ranges yet would seem sufficient for any effects to be easily noticeable.

Evidence of differences of this magnitude in the field can be found in Antonova, Elsukova & Lagunova (1998). They reported a two-phase cyclic pattern involving *Picea abies* and *Tilia cordata* in taiga and suggest that there are roughly 2 generations of *Picea* for each one of *Tilia*. Our assumption of a factor of four is clearly of the same order of magnitude.

We have therefore two groups of species distinguished by reproductive strategy. These are:

- High birth rate with high death rate (hi/hi)
- Low birth rate with Low death rate (lo/lo)

Initiation was then made by assigning 50% of the 160 species to the hi/hi class and the remainder to the lo/lo class, and in each case the usual further small variation was added to differentiate between species within a class. Thus we have a bimodal distribution with some variance around the two modes.

Analyses and Presentation of Results

The simulations are designed to provide information on the following questions.

- Is there likely to be interference from side effects of changing mortality and birth rates?

Changing mortality and birth rates is not without side effects and we have identified two which might have serious consequences. The first of these is that there will be a tendency for areas of bare ground adjacent to longer lived individuals to remain empty longer than they would in the previous automaton. This is a consequence of the ordering of activities within the algorithm, but we would argue that it is not unlikely in real vegetation. Occupation of an area adjacent to a long lived tree might be expected to be somewhat more difficult than occupation of an area more distant, although this remains a moot point since it can also be argued that more propagules would be available locally. It is difficult to see any solution unless a concurrent implementation of the simulation were constructed.

The second problem is rather less obvious, being more technical. Many of the systems we are examining could be expected to generate mesoscale patterns (Boerlijst & Hogeweg 1991) and the size of these patterns depends in part on the birth and death rates. We would expect that members of the lo/lo class would produce spatially bigger patterns than the hi/hi class. In order to speed up the simulation we normally employ a 100 x 100 automaton grid, but it may be that this is too small to allow the lo/lo species to develop their patterns fully. This could obviously interfere with the development of the lo/lo species interactions since these would be truncated at the edges of the automaton. We therefore also examined the effects of using a 160 x 160 automaton grid – an option permitted by the increasing computer power available to us which reduced the running times by a factor of 8 or more.

- Do the boundary between core-and-transient and percolation classes remain much the same or does polarisation provide acceleration or delay of the change from the former to the latter?

Polarisation provides us with a system lying between the metapopulation and multi-species cases considered in the previous paper. We can expect that separation into a small number of classes will be of greatest interest since the many-class partition would simply approach the multi-species case. If a partition into a small number of classes destabilises the system, by which we mean that it results in earlier onset of percolation, the possibilities for prediction in such systems are reduced. Conversely, if the polarisation stabilises the system, that is it delays the onset of percolation, we can expect that introducing more polarisation along other, largely uncorrelated, dimensions will further enhance the delay – and this of course means that the systems are more stable! Thus the separation of species into discrete and well separated types would enhance the overall stability of the system even in cases of high diversity. Note, though, that stability here is not constancy. The core-with-transient system exhibits resilience to invasion not resistance.

- Can stable mixtures of the two major types of species be found? Conversely, is it possible for a single type to dominate the structure maintenance?

Although the availability of well separated types of species might increase stability, this does not mean that both types have to be present at any specific time for this to occur. It is possible that the structure of the interactions could also lead to improved stability, independent of the existence of both the polarised types at a specific time.

Presentation of Simulation Output

The output from all the simulations is quite large so I have selected interesting ones. These results are presented graphically using two different formats for the illustrations.

The first format (Figs. 1 & 6) uses a trace through time of four aspects of the system. The commencement follows the cessation of the selection procedure for seeking high diversity and time runs down the page. The aspects are presented in four columns representing (from left to right)

- A transect across the horizontal centreline of the automaton grid, with samples taken every 10 iterations.
- A trace diagram showing the presence and absence of species through time as coloured lines.
- A cumulative representation of the number of species present.
- A series of snapshots of the automaton grid. The number used is 7 for a small automaton and 4.5 for a large one.

It should be remembered that in general the same colours do NOT indicate the same species in two different diagrams, although because of the genetic algorithm there can be some correlation. In all cases the simulation starts at the top of the page.

The second format shows the active interactions between species as a directed graph. The direction shown is that of positive interaction, with the arrow pointing towards the receiver, except in the case of a mutual pairwise interaction when NO arrow is drawn. In order to reduce the complexity of the diagrams, edges are introduced into the graph only if they have persisted for several iterations in the system. This means that transient species are largely ignored and the graph represents some local stability of interaction structure. The two strategies are distinguished by colouring the nodes, representing species, appropriately.

Results

The first important point is that the systems generated were even more diverse, in general, than those found in the previous study. Further, whereas in the previous study the most percolation systems were the most diverse, in the present study percolation systems were largely absent. Instead, core-with-transient systems remained apparent up to connectivities of 9 which markedly exceeds the critical level (7) for percolation systems in our previous study.

One mechanism for increasing diversity is the existence of mesoscale patterns. These might be in space or in time. Figure 1 shows that spatial segregation occurs and in fact acts to maintain high diversity. In the first column there is an obvious tendency for left and right segments to follow distinct paths at least in the middle of the time period. However, there did not seem to be any constraint on the size of mesoscale patterns where they developed.

Figs 2-4 show interaction diagrams between species together with information on the hi/hi and lo/lo components. Most such diagrams are of the first kind with multiple pathways of cyclic change. The other 2 forms, two distinct and disjunct cycles and a single cycle, are much rarer. With increasing levels of interactions, the complexity of these diagrams did tend to increase (see Fig. 5), but in most cases a percolation system was not obtained; that is a system where the graph is no longer planar and the degree of connectivity is extremely high. This remained true even when the connectivity reached a value of 9, considerably larger than the critical value of 7 identified in our previous study. Thus the introduction of polarisation appears to stabilise the system, while also permitting an increase in overall diversity.

Generally most systems incorporated both hi/hi and lo/lo elements in the cycles but homogeneous systems did occur.

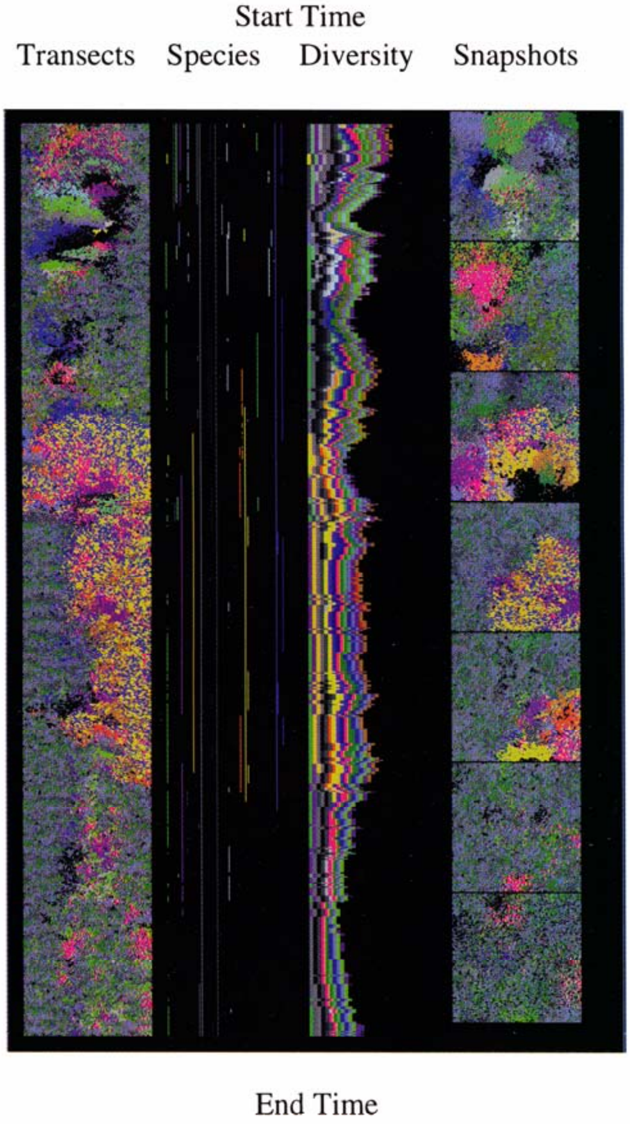

Figure 1. Trace Diagram for a 7-connected system showing initial high diversity maintained partially by spatial segregation in the middle period.

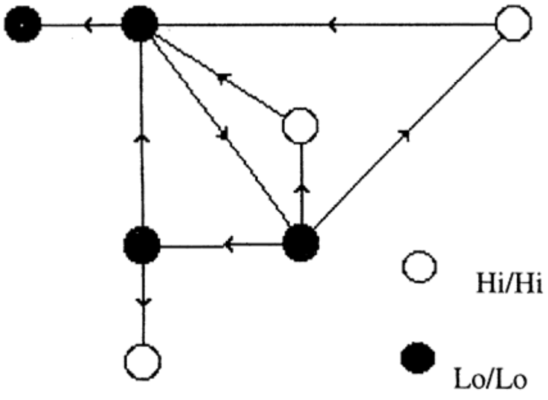

Figure 2. Interaction Diagram for a 4-connected system showing multiple superposed cycles. The nodes of the graph are shaded to show whether the species represented falls in the hi-hi class or the lo/lo class. Arrows indicate the direction of positive reinforcement. Lines without arrows are used where reinforcement is mutual.

As perhaps might be expected, homogeneous lo/lo systems were more common than hi/hi systems

Temporal mesoscale patterns can also be identified. Fig 6 illustrates the waves of invasion in the form of stripes of brown and white in the transect traces. These ripple structures show the passage of an invasion wave across the central line. The slope of these ripples indicates the speed of passage. While the larger ripples are visually more obvious, there also exist much finer grained patterns of this kind probably reflecting the passage of hi/hi patterns. It is also noteworthy that very few pure colour areas are visible, in most cases the composition being a mosaic. Examination of the snapshots suggests that this is commonplace although patches of different mosaics may coexist while unreflected in the median line. This suggests that examination of the texture of the patterns could provide characteristics reflecting the nature of the underlying system, at least in the short term. I am presently examining this possibility.

As a minor aside, at the lower levels of connectivity bare ground seemed to be present more commonly than in our previous studies. In Fig. 7, very high diversities are shown, matching or exceeding those of percolation systems, but even there the black patches representing bare ground can be seen, mostly in the lower right corner of the snapshots. Closer inspection of the local dynamics suggests that this is because the lo/lo species tended to form boundaries not easi-

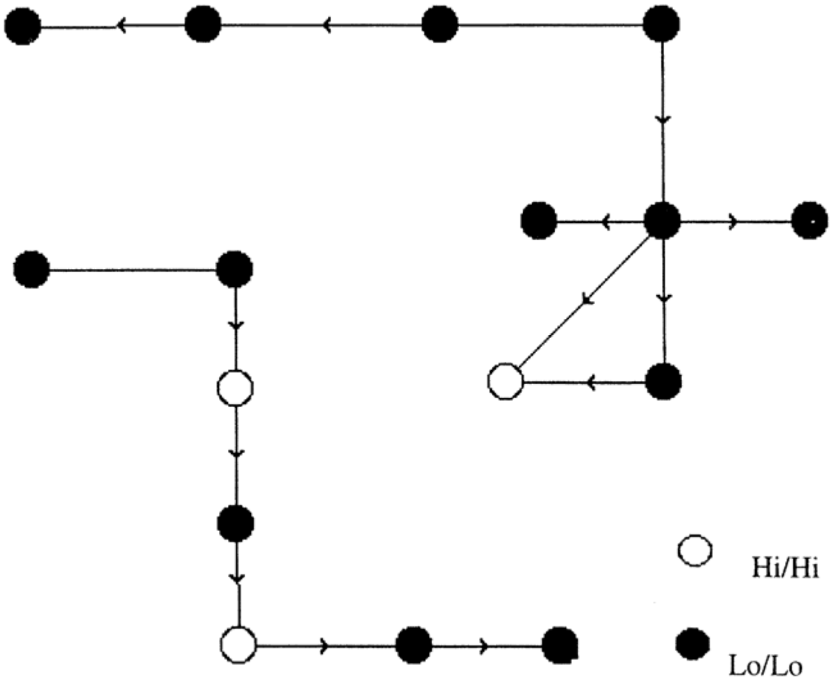

Figure 3. Interaction Diagram for 4-connected system showing 2 disjunct cycles. The nodes of the graph are shaded to show whether the species represented falls in the hi-hi class or the lo/lo class. Arrows indicate the direction of positive reinforcement. Lines without arrows are used where reinforcement is mutual.

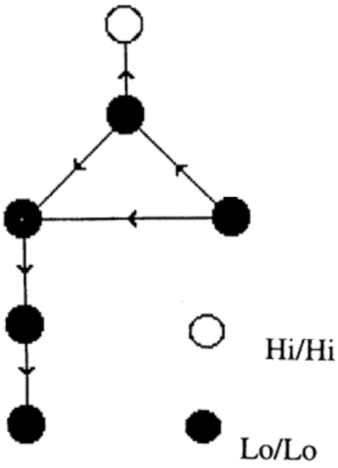

Figure 4. Interaction Diagram showing a single cycle for a 5-connected system. The nodes of the graph are shaded to show whether the species represented falls in the hi-hi class or the lo/lo class. Arrows indicate the direction of positive reinforcement. Lines without arrows are used where reinforcement is mutual.

ly penetrated by the hi/hi species. The short term invasion dynamics are of course a product of our specific choice of occupancy rules so that the prolonged persistence of bare ground could well be an artefact.

Discussion

The size of the automaton

Changing the size of the automaton did not apparently markedly affect the results obtained. Inspection of the output of many simulations did leave the impression that bare ground was perhaps more common and had a somewhat more prolonged lifetime than in our previous studies, although this was more apparent at low than at high connectivities for some reason. However, overall the effect did not assume any great significance and it may not be related to the size of the automaton.

Diversity and Polarisation

Overall it would seem that the diversity is generally increased by the introduction of the low/low strategy; i.e., high diversity is attained and maintained at lower levels of con-

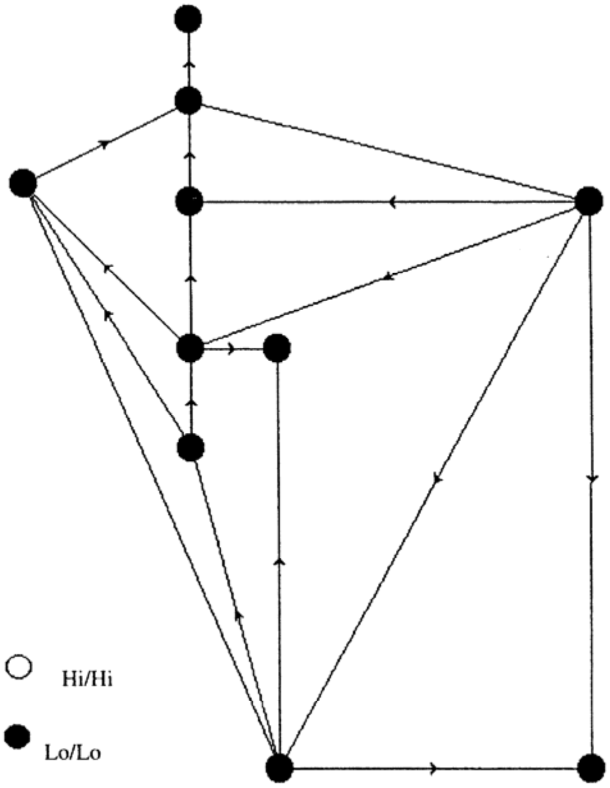

Figure 5. Interaction Diagram for a 9-connected system showing single strategy solution. All nodes of the graph are in the lo/lo class. Arrows indicate the direction of positive reinforcement. Lines without arrows are used where reinforcement is mutual.

nectivity than in unpolarised systems, yet the advent of a percolation system without fixed, stable species composition is delayed. The effects of changing the cardinality of species interactions is much less marked than in our previous studies. The larger connectivities did seem to produce higher diversities and more complex systems but at least some cases remained within illustratable limits, whereas previously, percolation systems were so complex as to be largely unpresentable graphically. Also the larger systems seem more stable, with convergence towards similar interaction graphs perhaps because there are more alternatives.

Cycles and strategies

The nature of the connection graph underlying the dynamic patterns is also of some interest, since it can indicate if such stability as exists is due to homogeneous or heterogeneous cycles; i.e., if cycles exist which contain ONLY hi/hi or lo/lo elements, or whether elements of both classes are present. In fact, we seem to have an increase in pairwise cycles and often these are heterogeneous. Even with the 9-connected cases, some relatively simple patterns of interaction were found though homogeneous was rarer than heterogeneous.

There seems to be no barrier to pairwise cycles, combining both strategies or admitting pure strategies. Longer cycles obviously have more opportunity to be heterogeneous and there seems to be some tendency for the species types to alternate around cycles, although this is difficult to characterise. In several cases, species form components of several cycles and unique assignment is not possible. The more likely situation met is one of 2 or more cycles connected to parasitic chains, often sharing one interaction. In a few cases, completely disjunct cycles are present.

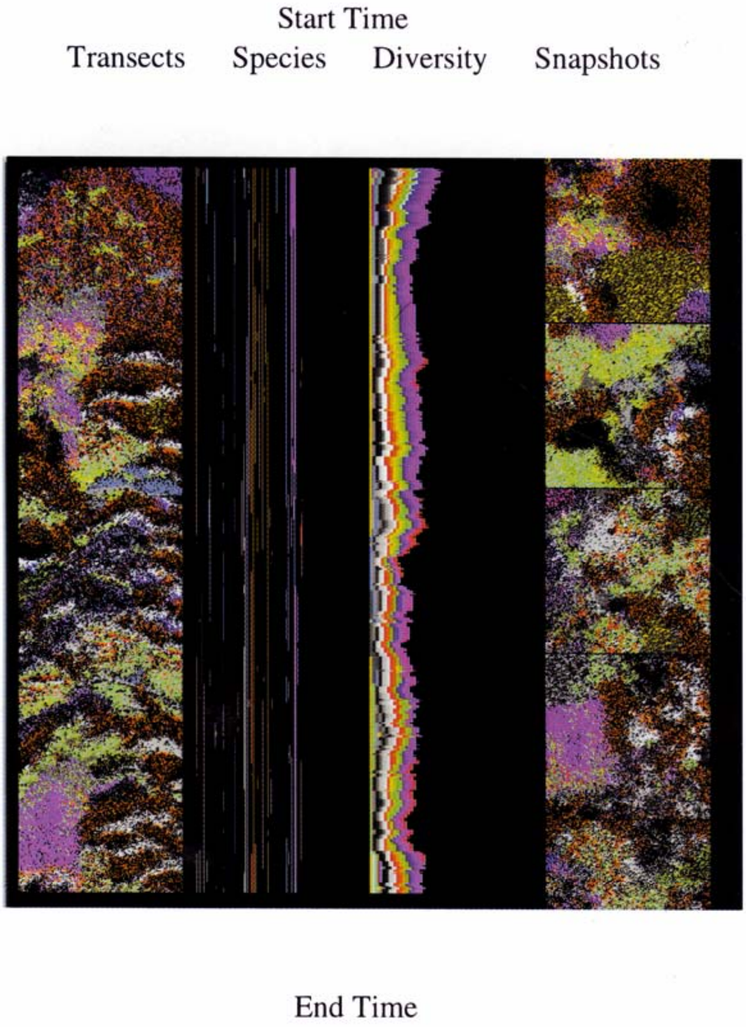

Figure 6. Trace for a core-with-transient 9-connected solution. Note herring-bone pattern ripple structures in Transect column.

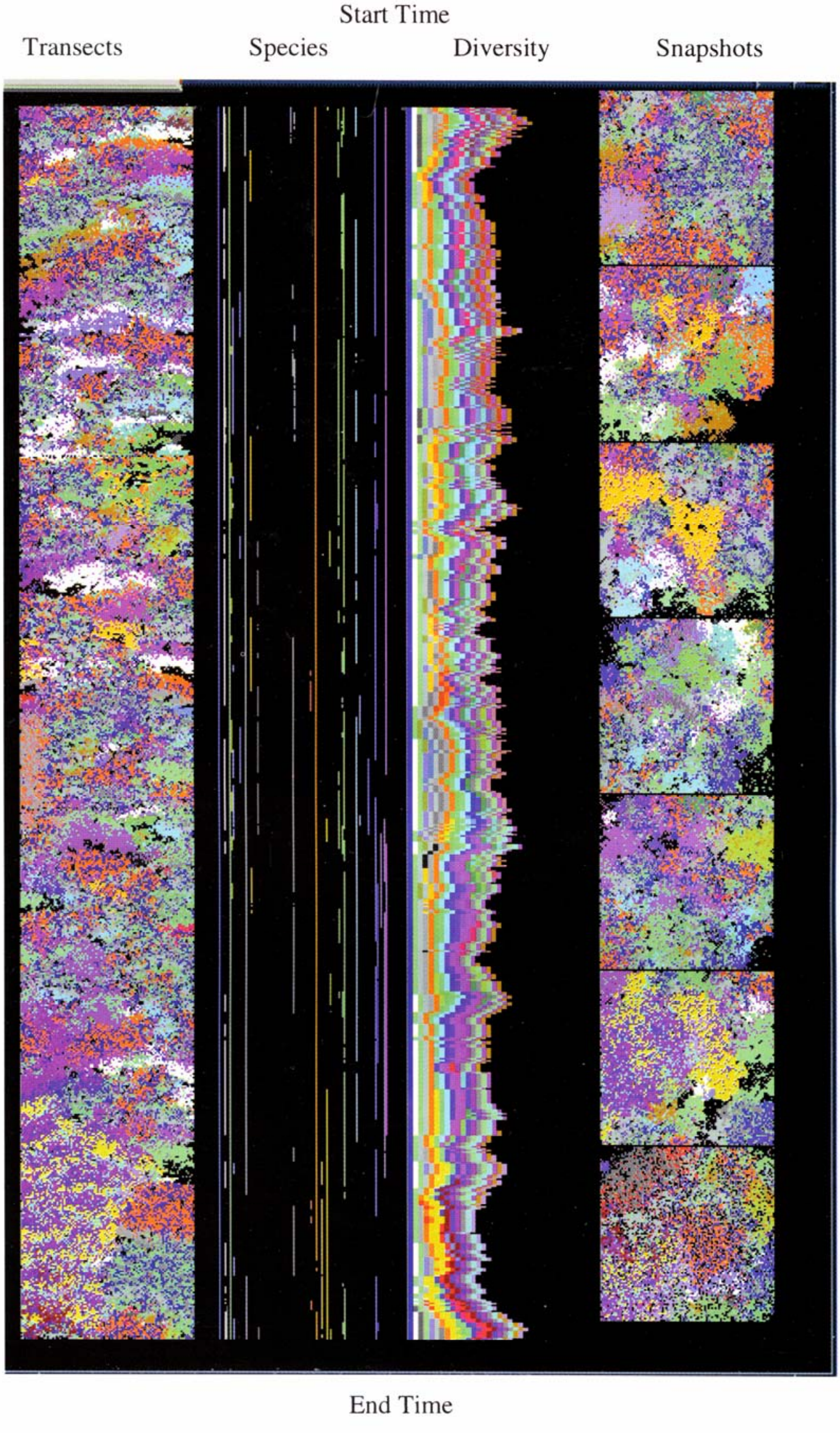

Figure 7. Highly Diverse Trace from a 5-connected system. The diversity here is as great or greater than many percolation systems in our previous study (Dale & Hogeweg 1998).

Ebbs, Floes and Scales

Inspection of snapshots and transect traces shows other interesting patterns in addition to the ripple structures noted above. In some cases, we can see spatial segregation in the trace where two (or more) patterns coexist for a time by maintaining separate areas. This is most interesting as it conflicts with the notions of climax theory in its original form and supports the polyclimax model even when environmental distinctions are not present.

Perhaps of even greater significance are the evolutionary implications of the temporal and spatial variations which develop. These are not restricted to biological systems, for Mayer & Rasmussen (1998) found a similar variety of time and space scales develop in chemical systems. Savill, Rohani & Hogeweg (1997) have examined the effects on evolution in circumstances where the environment is a product of microscale interactions resulting in mesoscale patterns, but here we do not have the spiral waves of relatively constant dimensions (cf. Boerlijst & Hogeweg 1991), but at best quasi-attractors stable for some relatively short period of time and perhaps restricted in spatial extent. Thus if the environment can be defined in terms of other competing organisms, which is a presupposition of much phytosociology, then this environment is constantly changing at the local level. To cope with this requires relatively fast adaptation at least within a limited range of possibilities.

Conclusions

It is not the intent of this paper to deny that changes in the abiotic environment will produce changes in the vegetation system. Environmental change is obviously a potent causal factor for inducing change in vegetation and locally enhancing diversity. However, the results do demonstrate that vegetation systems might produce very similar behaviour to that expected as a result of abiotic variation without environmental causation. This makes the identification of environmental causation a more difficult task, and not an automatic inference.

The other major conclusion is that polarisation of the species increases stability as well as diversity, at least for the core-with-transient system. We argued earlier that distinction of a small number of types along any single axis will be most potent, as distinguishing a large number of types returns us to the situation considered in the earlier paper. Adding further disjunctions along other, largely independent dimensions of strategy can be expected to further increase stability, and probably diversity too. Thus the relationship between diversity and stability becomes an emergent property, a consequence of evolutionary segregation. Further, there is likely to be variation in response to the degree of segregation actually attained; the more distinct, the greater both diversity and stability.

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