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THE FUNDAMENTAL NATURE OF VEGETATION DYNAMICS - A CHAOTIC SYNTHESIS

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Abstract: I consider determinism and randomness as fundamental components of vegetation dynamics. I attempt to resolve the dichotomy in ecological theory which, for vegetation, manifests itself as the Clements-Gleason controversy. I present a case study in which determinism and randomness appear to convolute and in which dynamics may be best described as deterministic chaos. Having presented a technical discussion of the topic elsewhere (Anand & Orlóci 1996), I now focus on the implications to ecological theory in general. I suggest that chaos provides the foundation for a unifying theory of vegetation dynamics in which classical theories reside as special cases.

Introductory remarks

The subject of this paper is dynamics in vegetation. By dynamics I mean specific compositional change in the community with time under impetus of some perturbation. Why use the term "vegetation dynamics" and not "succession"? I feel that the term "succession" and its qualifiers such as "primary", "secondary", etc., conjure a loosely defined set of events. A discussion of dynamics should begin free of any colouring of terms. The question to be asked is "what is the fundamental nature of vegetation dynamics?" Historically, the answer has led to contrasting ecological theories which emphasize either determinism or randomness. As we shall see in the next section, neither of these views seems realistic.

Clements-Gleason Dichotomy

I begin with the philosophical dichotomy of F. E. Clements and H. A. Gleason. Perhaps the most well-known formalization is by Clements (1916). He viewed vegetation as an organism which "arises, grows, matures, and dies." The mature state, the climatic "climax" formation is, according to him, "able to reproduce itself with essential fidelity". Significantly, Clements believed that dynamics in vegetation is a "complex but definite" process. It is a logical extension of these that vegetation dynamics is universal, progressive, and orderly. If Clements was in fact correct then, with sufficient knowledge of the ambient conditions, the process is predictable. The Clementsian view is of course predicated on his assumption that diverse pioneer communities eventually converge to a self-perpetuating monoclimax state, under the control of the regional climate. While Clements realized some limits to predictability, he still believed in the philosophy that there is design, purpose and unity in nature, that the plant association is unique and, in its totality, more than the sum of its individual components. Clements' view, being uncharacteristically poetic, was interpreted as being untestable and thus unscientific, yet Clements' logical intuition lead him to continue along this line.

On the other extreme lies Gleasonian view (1926) that "succession is an extraordinarily mobile phenomenon", and at the same time "not to be stated as fixed laws, but only as general principles of exceedingly broad nature". Gleason maintained that vegetation dynamics "need not ensue in any definitely predictable way" based on the belief that "every species is a law unto itself". To Gleason vegetation dynamics was individualistic, unpredictable, and under the strong influence of chance effects. This view gives an infinity of possibilities of describing vegetation dynamics, and thus cannot be tested either. However, it cannot be dismissed as being illogical.

Clearly, as presented, Clements and Gleason supported dramatically different views on the fundamental nature of vegetation dynamics and at such extremes of scale that they are incomparable. Indeed, Gleason's dynamics may be seen as the underlying stand-level turbulence owing mainly to chance events and Clements' as some broad deterministic wave. The mathematical ecologist, whose interest is to model, is tempted towards Clementsian determinism, because it offers regularity and thus a hope for mathematical tractability. These indeed may be considered prerequisite for modeling vegetation dynamics – a reasonable suggestion considering that under the Gleasonian alternative, modeling would be an impossible, futile endeavor. Should one really try to look for something which is thought not to exist?

After a century of study, it is clear that the view of intense determinism has dominated vegetation ecology. Numerous and various attempts at modeling vegetation dynamics, i.e., searching for regularity is evidence of this. Drury & Nisbet (1973), McIntosh (1980), Finegan (1984) van der Maarel (1988), and van Hulst (1992) provide reviews of the effort and, in my judgment, a chronicle of advancement of the philosophical dichotomy.

Table 1. Point cover estimates of 8 species, 1 species group and bare ground after severe fire and grazing. Legend: BG - bare ground; EN - *Empetrum nigrum;* CV - *Calluna vulgaris;* ET - *Erica tetralix*; MC - *Molinia caerula;* RA - *Rumex acetosella*; JS - *Juncus squarrosus*; CP - *Carex pilulifera*; OS - other species. Adapted from Lippe et. al. 1985.

Year	BG	EN	CV	ET	MC	CP	JS	RA	OS
1963	57.1	17.9	8.60	11.6	0.0	0.2	0.0	4.7	0.0
1964	44.0	25.0	13.7	12.2	0.0	1.1	0.2	3.9	0.0
1965	32.7	34.9	13.9	14.3	0.0	0.5	0.0	3.7	0.0
1966	27.5	36.8	20.0	14.1	0.1	0.9	0.2	0.3	0.1
1967	19.7	46.1	21.0	10.8	0.1	0.7	0.4	0.5	0.7
1968	10.7	54.2	22.2	10.6	0.7	0.6	0.4	0.0	0.5
1969	6.70	55.7	23.3	10.4	0.3	2.0	0.7	0.1	0.7
1970	5.80	61.1	23.7	6.90	0.2	1.2	0.7	0.2	0.3
1971	9.50	57.6	24.7	6.60	0.4	0.6	0.4	0.0	0.3
1972	8.40	62.1	23.7	3.60	0.3	1.2	0.1	0.0	0.6
1973	4.40	67.9	21.3	3.30	0.2	0.6	0.4	0.0	2.0
1974	8.50	58.1	25.8	4.70	0.6	1.3	0.7	0.0	0.4
1975	9.20	62.2	24.3	2.50	0.6	0.9	0.2	0.0	0.1
1976	9.90	58.2	24.9	3.70	0.6	1.1	0.7	0.0	1.0
1977	19.6	48.4	23.5	5.70	0.3	1.2	0.4	0.1	0.9
1978	12.1	58.1	22.7	4.80	0.4	0.4	0.0	0.2	1.3
1979	9.30	65.1	20.3	2.70	0.0	1.5	0.1	0.2	0.9
1980	7.30	68.2	21.5	1.20	0.5	1.0	0.1	0.1	0.2
1981	5.40	65.5	20.8	4.60	1.0	1.6	0.4	0.3	0.6

Upon closer inspection of the classics, we should realize that both Clements and Gleason had a lot more to say about the nature of vegetation dynamics than conventional reviews let us believe. For example, while Clements viewed the process as being completely deterministic, he admitted that "the most stable association is never in complete equilibrium". Despite his emphasis on chance as a mechanism and disorder as its manifestation, Gleason acknowledged the "development of vegetation" manifested as "continued and progressive change". A dichotomization of these two views may have been an honest misinterpretation, but doing so unjustly ignores the early malleable but critical statements. I believe that inherent in these ambiguities lie central ecological questions, which have yet to be resolved.

The Clements-Gleason dichotomy can be viewed as the fundamental dichotomy between determinism and disorder, holism and reductionism, and universality and individualism – things which pervade the "soft" science (Pielou 1980, Orlóci 1993) of ecology. I re-address these dichotomies with the objective of elaborating on possible unification. I give evidence in this paper that neither of the classical views captures natural dynamics accurately, that neither is wrong, as they stand, and neither can provide a basis for a general theory of vegetation dynamics. I show that both views are realistic, but incomplete, and surprising as it may sound, and notwithstanding Gleason's intentions to refute Clements, I propose that these two views are not mutually exclusive. We have in a recent paper (Anand & Orlóci 1996) actually initiated this discussion, but then focused on specific experimental results rather than implications in the context of the broad historical debate.

Case study

I have to convince you though that nature does fit into a convolution of order and chaos, which these two theories individually imply. If we are allowed no flexibility, inaccuracies even on this scale are a trivial matter. Of course, in reality we cannot look for a perfect fit, but rather work within reasonable (stochastic) bounds. This is in fact the tradition in statistical analyses of complex cases, where one teases out trends and acknowledges deviations from them. The question to be asked, however, is how valid this approach can be to modeling vegetation dynamics? I feel that there are situations where deviations from a trend line or state cannot be simply dismissed as aberrations, and that a predisposition towards simple (usually linear) deterministic models may not be justified. I illustrate the difficulty with a specific example (Table 1).

The first dichotomy to be resolved is whether dynamics should be viewed as the behaviour of individual populations (reductionist) or at the higher, community level (holistic). Fig. 1 shows complicated individual *population* –level dynamics. The populations have been classified into dominant and rare types. To consider the dynamics at the level of individual populations, that is, to take a reductionistic view, we have to somehow conceptualize many kinds of dynamics simultaneously. But how do we visualize a complicated 9-dimensional process? Our inability to do this immediately leads to doubts about the feasibility of a reductionistic view. Whether or not vegetation dynamics is driven by individual population dynamics is not the question. The question is whether interactions and feedback which are manifested at the community level should be an integral part of the reasoning.

This approach, however, must involve summarization because the medium is unworkably many-parted. It is not unusual to find that, while hundreds of species occur in the community, one, two, or perhaps 3, are chosen to build a model of dynamics. However, realistically, no one could or should suggest *a priori* importance of this kind. Summarization cannot be achieved by simply reducing the community to 2 or 3 species. It is true that multivariate statistical analyses in ecology are mainly techniques of summarization, however in these, summarization is achieved through simultaneous analysis of all species (Orlóci 1978). In our example, a parsimonious summarization is achieved by projecting the 9-D configuration into 2-dimensional space using eigenanalysis (Fig. 2; Anand & Orlóci 1996) . In doing so, we move from the population-level, to the community-level. The latter of course incorporates the former, and while a one-to-one correspondence is lost, the community-level mapping still retains an overwhelming portion of the original information.

Upon inspection of the total process at the community level, a 2-phase structure is immediately seen, which was not obvious from a population-level view (Fig.1) . Thus there is use in applying the community-level view. Anand & Orlóci (1996) have shown that in the early phase of dynamics, roughly years 1-8, a simple linear law rules. The rate of change of composition in this phase is relatively fast, which is not unusual (Shugart & Hett 1973; Orlóci 1993). But then suddenly at year 8 the process slows down, loses direction and passes into a path of random turns and twists. What does this mean? Is it normal that a process begins with clear linear determinism but then suddenly strikes out, ending in apparent chaos? Is this kind of dynamics best described as deterministic (Clementsian) or random (Gleasonian)? It seems at the outset as though neither theory will do on its

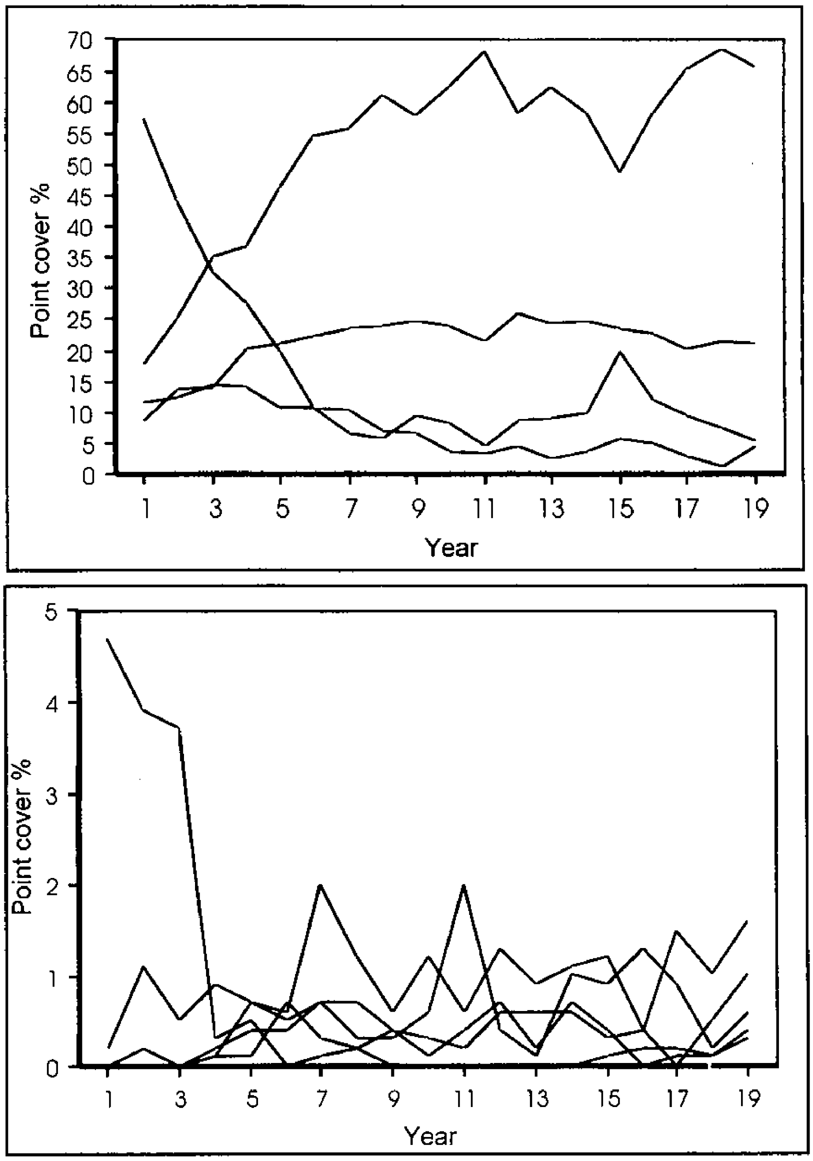

Figure 1. Population-level dynamics. Populations divided into dominant (top) and rare (bottom) types. Data in Table 1.

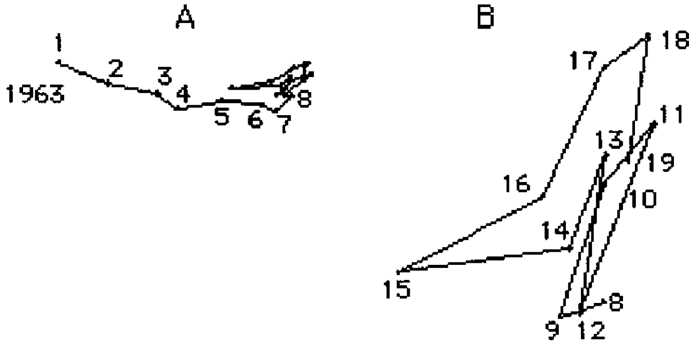

Figure 2. Community-level dynamics. Two-dimensional Eigenmapping of the 19-step recovery trajectory (A) from Atlantic heathland (Lippe et al. 1985) disturbed by fire and heavy grazing. Magnified section of last 11 steps (B) involves vertical distortion. The original data represent point-cover estimates of 7 species, one species group and bare ground. Step size is one year. Numerals indicate years elapsed. The mapping is 99% accurate, 95% on 1st axis (in A). Note linear early phase and nonlinear late phase. Break between phases coincides with point cover of bare ground dropping from 57% to less than 7%. Adapted from Anand & Orlóci (1996).

own, and as such a second dichotomy arises: determinism vs. randomness.

To begin the discussion of a simple model of determinism one has to first decide on what one means by determinism: how does one measure it? For this we need a model. Traditionally, models of determinism are simple and linear. Orlóci & Orlóci(1988), Orlóci et al. (1993), Anand & Orlóci (1996) measure the level of determinism in the process in terms of concordance with the fitted discrete-time stationary Markov chain. If the transition probabilities can be determined (for the method, consult Orlóci et al. [1993]), specific properties of the model make it a desirable choice to measure determinism. Feller (1965) points out that to define the model (specific path or chain of change), the initial conditions (the state of the community at year 1 in the example here) and the transition matrix **P** (which represents the replacement rates of populations from one year to the next) are needed. In the model any future state of the "community" $\mathbf{M}_t$ is determined by simply multiplying the state t-1 by the transition matrix **P**.

$$\mathbf{M}_t = \mathbf{M}_{t-1}\mathbf{P} \qquad (1)$$

Through iteration of (1), the Markov path from initial state to time point c is generated:

$$[\,\mathbf{M}_1, \mathbf{M}_2, \mathbf{M}_3, \dots, \mathbf{M}_c] \qquad (2)$$

The stationary Markov model has the property of convergence – irrespective of what the initial conditions are, as long as the transition matrix is the same, the community will converge on the same universal climax state; mathematically speaking, a point attractor exists. In fact, the initial state matters to all interested in succession, i.e., when the path upon which the stable point ("climax") is approached, since different initial conditions will specify different paths (Fig. 3). For me it is mainly the path which is of interest, since it represents the coenosere through which dynamics progresses. Predictability in stepwise progression and convergence make for a neat model of determinism, but also an unrealistic one for vegetation dynamics, for in Nature we do not expect to point attractors and pure determinism.

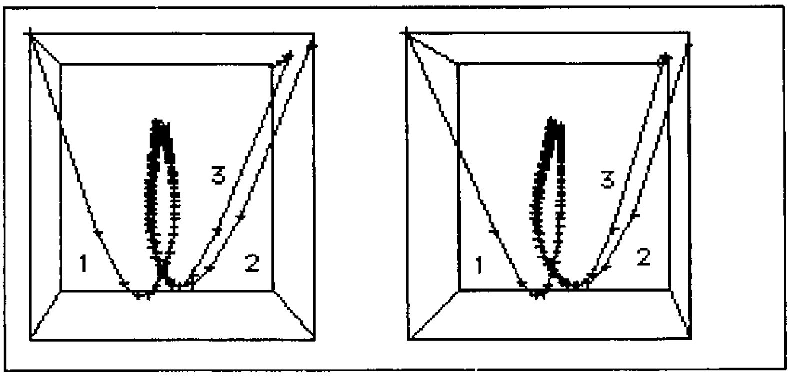

Figure 3. Convergence in the Markov model.

Markov modeling of succession and vegetation dynamics is much discussed (Horn 1974, 1975; van Hulst 1979; Binkely 1980; Acevedo 1981; Usher 1981; Lippe et. al. 1985; Orlóci & Orlóci 1988; Orlóci et. al. 1993), albeit with varying conclusions as to its value to accurately describe the natural process (e.g. compare results of Horn 1975, Lippe et al. 1985, and Orlóci et. al. 1993). Clearly, the model assumes Clementsian determinism : predictability and convergence to a monoclimax. Interestingly, Usher (1981) considers the Markov model to provide "a unifying concept in the dichotomous approach to succession". He claims that Markovian models can be viewed as incorporating Clements's view of orderly, predictable change, but also Gleason's views of reductionism by incorporating the fate of individual populations. While the fitted stationary Markov model may help to bridge the holistic/reductionstic view, it clearly makes no explicit provision for Gleason's chance mechanism.

The question may then be asked, how much Markovian determinism is observable in the recovering heathland? Anand & Orlóci (1996) give an answer to this question. They hold that the stationary Markov chain gives a reasonable fit. But are we satisfied with it as a model of the natural process? In other words, can we describe vegetation dynamics reasonably in terms of this simple, linear, purely deterministic contraption? The fact of the matter is that we cannot for good reasons: Firstly, we cannot ignore deviations from the pure Markov path altogether by considering any deviation to be unimportant noise (a hallmark of classical statistical analyses), when we see it quite important in the later phase. In fact "noise" is *definitive* of the later phase. Second, Anand & Orlóci (1996) have shown that determinism cannot simply be decomposed (Fig. 4). For example, we cannot say that there is less determinism in the process as a whole than in the early phase, since if we tested the proposition we would likely to find the opposite true (see also Schaffer et. al. 1986; Moss & Wiesenfeld 1995). We cannot ignore nonlinearity, since it seems to effect the process in ways which are not yet clear.

So, looking back on the natural process, we should ask, "Could the transition from linear phase to nonlinear phase be connected to simple generating rules?" Can we come up with a better model in which nonlinearity has a part to play? Knowing that determinism in the process is well captured by the Markov model, it makes sense to try to rework it. This is exactly what Anand & Orlóci (1996) have done by imposing small amounts of random noise (nonlinearity) on the stationary Markov model. What they found was that dynamics in the basic Markov model could change quite dramatically in the long term. Fig. 5 shows an example of this behaviour to demonstrate that striking qualitative nature of change. A homogeneous linear process is transformed to a two-phase process, early linear and late complex nonlinear.

It becomes quite reasonable to ask the question: is the explosive behaviour that we observe in this dynamics an inherent property of the process? The fact that it re-occurs in different samples and on different scales suggests that there may be some fundamental determinism in the process. Is it due to the accumulation of the small random effects which are not detectable in the early phase, but suddenly manifest

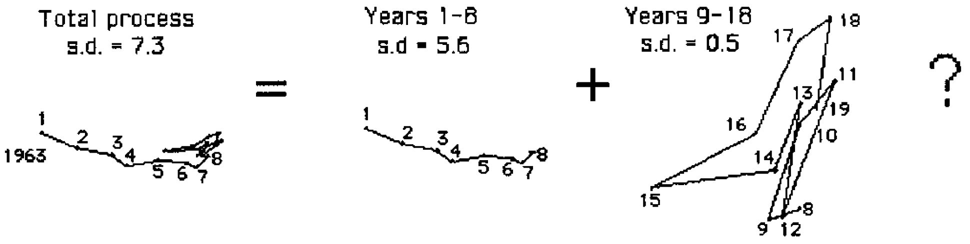

Figure 4. Decomposition of determinism in phases (after Anand & Orlóci, 1996). Concordance to the Markov model is reflected by the magnitude of s.d.

The term *concordance* describes the level of match between two structures. To define these structures we first compute the two c x c Euclidean distance matrices D_X and D_M corresponding to coenostate records $X_1, X_2, \ldots, X_c$ and the Markov scores records $M_1, M_2, \ldots, M_c$ such that $M_{t+1} = M_tP$ with $M_1 = X_1$. The coefficient

$$s^2(D_X;D_M) = \frac{\sum_{j<k}^{c}(d_{Xjk} - d_{Mjk})^2}{\sum_{j<k}^{c}(d_{Xjk} - d_{Mjk})}$$

is our definition of stress or discordance (Orlóci, Anand & He 1993), and the difference $1-s^2(D_X;D_M)$ is proportional to the level of concordance of the observed distance configuration and the model Markov distance configuration.

s.d. is determined from the equation $\text{s.d.} = \frac{s^2_{\text{observed}} - s^2_{\text{mean}}}{\text{s.d.}^{.5}_{s^2}}$

themselves qualitatively as a phase transition? This suggestion would not be out of line with Gleason's statement: "In addition to the imperfections of similarity [between vegetation states] caused by chance, and largely masked by them, are other variations of a cumulative nature".

Chaos

It is clear that mathematics and statistics cannot be easily applied to answer these questions. This is because the classical theory cannot readily handle the "complications" of Nature. Orlóci (1995) calls for a complete re-conceptualization of statistical ecology in order to deal with the reality of a complex natural medium. I believe that the answer to these questions and the theoretical synthesis we seek can be sought by considering chaos theory, exposed by Gleick (1987) at the level of popular science and by, for example, Çambel (1993) on a somewhat higher level.

Chaos theory represents a mathematical formalization of the view that determinism and disorder, simplicity and complexity, pattern and unpredictability need not and should not be considered mutually exclusive. It provides a promising framework in which to pose our questions about vegetation dynamics. We find that these things are in fact not easy to isolate. The theory allows us to look for underlying determinism in an apparently random and explosive process. The central concepts in chaos theory revolutionize our approach to modeling vegetation dynamics, and this is mainly due to the following discoveries about general systems:

1. sensitive dependence on initial conditions (Lorenz 1963). Minute changes in the local initial conditions can accumulate and have consequential effects in the long-term.
2. simplicity giving rise to complexity. This is probably most familiar to the reader in the discovery that complex and beautiful patterns can arise from very simple mathematical laws, and in Mandelbrot's (1983) introduction of fractal geometry which allows us to describe and classify these objects.
3. complexity giving rise to simplicity. The evolution of a fern leaf pattern is an example. This pattern in fractal diagrams arises by a completely random generation of points.

Tools which allow for the detection of deterministic chaos include:

1. Lyapunov exponents. These measure sensitive dependence on initial conditions, and may be considered a "test for chaoticity". The basis of this measure explained by Wolf et. al. (1985) is to measure the divergence of the trajectories of initially close points. If the divergence is high (exponent positive), then we say that the process is sensitively

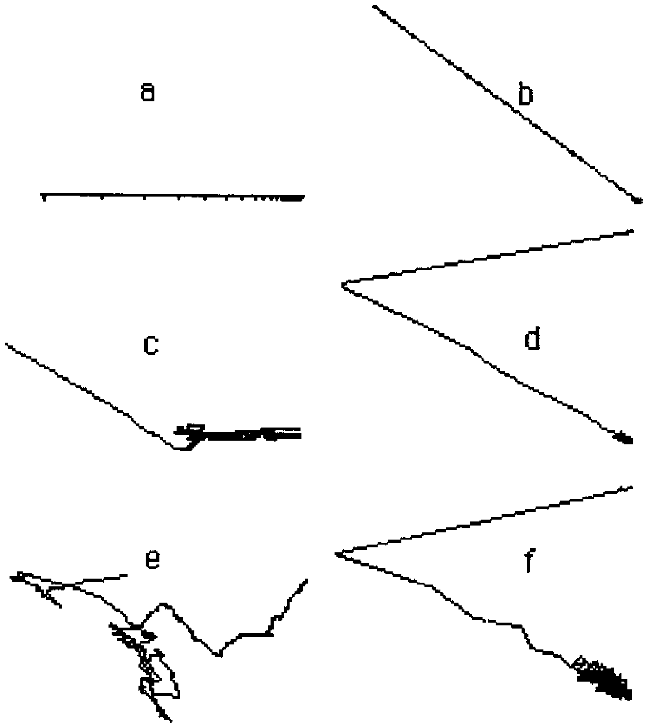

Figure 5. Phase space mappings of the Markov process (left) and reconstructed attractors (right). Chain length shown is 950 steps. Random perturbation levels: 0% (a,b), 15% (c,d), 25% (e,f). From Anand & Orlóci (1996).

dependent on initial conditions or chaotic (Peitgen et. al. 1992).

2. Fractal dimension. This measures structural complexity of a process and its attractor. Typically, the attractor of a chaotic process has high fractal dimension (Burrough 1983; Peitgen et. al. 1992).

To apply these tools we require far more observations than we could realistically expect from ecological studies (Berryman & Millstein 1989; Hastings et. al. 1993). This problem, however, may be resolved by relying on simulation as pointed out by Anand & Orlóci (1996). Indeed, in our application of the tools to simulated dynamics of the perturbed Markov chain we found that the process is measurably "chaotic" (positive Lyapunov exponent and high fractal dimension). By the accumulation of small but sustained random feedback effects the model vegetation path is shown to be sensitive to initial conditions, exhibits explosive behaviour, and tends towards a complex "strange" attractor which is fractal. And thus it is clear that, in the model, a combination of determinism and disorder gives rise to a special kind of determinism – deterministic chaos. In this, dynamics is predictable in the short-term, but unpredictable in the long term, not exactly repeatable, and yet stochastically bounded by a complex attractor.

Concluding remarks

It has already been pointed out that in the chaos-theoretical view of vegetation dynamics both Clementsian and Gleasonian theories are supported: Clementsian determinism by the existence of a clear two-phase structure dominated by linear determinism, and Gleason by the revelation of chaotic sensitive dependence on initial conditions as well as the significant role chance plays in the process. Indeed Gleason's remarks that "there is no exact repetition of the same vegetation from one community to the next" and that "observed heterogeneity may well be due to chance" are confirmed. Furthermore, Clements' striking and perhaps uncharacteristic statement, "in the thorough analysis of succession it becomes evident that the use of the term in both a concrete and an abstract sense tends to inexactness and uncertainty" also finds residence in the chaos-theoretical view. In summary, chaos theory provides just that flexible "dynamic connection" which Gleason found lacking in the classification of series of plant communities and thus forcing him to the conclusion that the plant community must be an individualistic phenomenon. Given all these, the chaos-theoretical view allows for much more flexibility in modeling vegetation dynamics which I feel has been constricted by dichotomous views of determinism/disorder, and holism/reductionism, in the past.

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