ESSAY REVIEW

Chaos, cycles and spatiotemporal dynamics in plant ecology

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Summary

1 We review the problems concerned with describing ecological variability and explain why nonlinear systems theory and chaos may be of relevance for understanding pattern and change in ecosystems.

2 The basic concepts of chaos are considered briefly, where possible in the context of plant ecology. We outline the period doubling route to chaos and associated concepts of bifurcation, universality, sensitivity to initial conditions, dimensionality, attractors and Lyapunov exponents.

3 Examples are selected from the literature to illustrate how nonlinear models and time series analysis have already contributed to research in plant ecology.

4 Key methods used to detect the presence of chaos in ecological time series, including determination of the ‘return map,’ the Lyapunov exponent, the technique of nonlinear prediction and the method of surrogate data, are surveyed. We discuss how small sample-size, as typically acquired in field-studies, can act as a formidable limitation in such approaches.

5 Models of plant communities, which emphasize the importance of spatiotemporal dynamics, are outlined. The concept of deterministic chaos is shown to be useful in this setting also.

Keywords: chaos, nonlinear model, plant dynamics, spatial model, time series

Introduction

The study of nonlinear dynamic systems has become a rapidly expanding research discipline that has blossomed over the last decade. While its applications in the hard sciences are firmly established, it is only recently that the mathematical theory has become useful for ecologists on more than just an abstract level. In fact, whether or not the esoteric mathematics has relevance to the study of biological populations has been a subject of debate for almost 20 years (Hassell et al. 1976). Resistance to these techniques stems largely from the demanding theoretical concepts of chaos and its associated intimidating technical jargon (e.g. strange attractors, crises, repellors, transients and numerous other exotic mathematical objects), all of which are quite foreign to most field ecologists and generally outside their training. A number of ecologists reasonably question whether these methods will really help them in their quest to understand ecological communities or whether they are just another case of ‘physics envy.’ In the present paper we attempt to review why the study of not only chaos, but all forms of variability, has always been and will always be, important in ecology.

In particular, we will discuss some of the specific ways in which chaos theory can be applied to plant ecology, an area that in our view has been somewhat neglected to date. Until recently, conventional wisdom dictated that chaotic and cyclical population dynamics are unlikely to be found in plant communities (Crawley 1990). We will argue that this evaluation might well be outdated. For too long now the almost mythical notion of stable equilibrium (Connell & Sousa 1983), in the form of a competitive succession leading towards an equilibrium climax state, has been the dominant mode of thought in plant ecology, at the expense of other mechanisms which emphasize the importance of disturbance, change and variability. This is a viewpoint that is only now beginning to emerge and be taken seriously, as for instance by Dodd et al. (1995) in their long-term study of the plant communities in the Park Grass Experiment at Rothamsted, England. Although these plots are con-
Considered as possibly the best candidates anywhere in terms of being stable equilibrium plant communities, Dodd et al. (1995) suggest 'that the existence of outbreaks in a significant number of species calls for a re-evaluation of the concept of stable plant communities.'

In terms of understanding variability and non-equilibrium conditions, the theory of nonlinear dynamics has much to contribute to plant ecology, and we suspect that the rather cautious earlier assessments may have underestimated the true exploratory value of these techniques. In fact, one of the most exciting and challenging areas in mathematical physics, the spatiotemporal dynamics of nonlinear systems, is currently proving to be valuable for understanding spatial plant dynamics where processes such as the natural mosaic cycle (Watt 1947) and habitat fragmentation (Tilman et al. 1994; Stone 1995) all operate in a complex manner over different scales in both space and time (Rand 1994; Hendry & McGlade 1995).

**Historical diversion**

There are countless examples of how biological studies have enriched the mathematical and physical sciences (or vice versa). For instance, we need only recall the discovery of Brownian motion last century by the distinguished botanist Robert Brown, and its subsequent development by Einstein in his famous 1905 paper. There are many similar examples which have as a common thread, the goal of describing with scientific rigour the change and variability that occurs at different scales in the natural world. We emphasize that it is only over the last century that ideas of chance and probability theory have been fully exploited to explain variability. Prior to this, Science was by and large mesmerized by a deterministic world view, handed down in the form of Newton's laws. Once the step was made, however, and the full weight of the role of chance was recognized, major disciplines in Science were sometimes completely reappraised (as for example, the physics of quantum mechanics).

Yule (1927) was one of several important statisticians influential in promoting this new world view earlier this century. He attempted to model the rises and falls in long-term records of natural events, and was particularly interested in modelling the apparently periodic sunspot activity. The latter phenomenon had for long been considered responsible for the cycling of famines, agricultural production, trade and economic conditions around the globe. More recently, ecology's classic prey–predator hare–lynx cycle as well as the germination patterns in the Yukon white spruce, have been intimately linked with sunspot activity (Sinclair et al. 1993). The sunspot cycle was considered essentially deterministic and periodic with a 10-year cycle (Fig. 1a) until Yule and his colleagues challenged the idea (Fig. 1b). By demonstrating that the apparently regular periodicity of sunspot cycles might in reality be nothing more than an averaged sum of random events with characteristics rather like 'Brownian motion,' Yule caused something of a shock in the scientific community. For some, this smashed the hope that Nature's regular cycles could be understood or predicted mechanistically. The illusory appearance of cycles and other regularity in time series might only be a form of 'order in chance.'

Just as the probabilistic outlook was gaining wide, if not total, acceptance by the scientific community, and were beginning to be considered fundamental for understanding nearly all aspects of the universe right down to the smallest elementary particle, the tables turned suddenly with the development of chaos theory. In the early 1970s Robert May demonstrated that the highly irregular fluctuations we see so often in the natural world, and which have all the hallmarks of randomness, can paradoxically be generated by very simple deterministic models. Processes that to the naked eye seem random, might in reality be strongly deterministic and, upon close inspection, exhibit a form or 'order in chaos.' Not only can cyclical occurrences be explained by uncomplicated mechanistic models, but so too can seemingly random phenomena.

Given these major paradigm shifts in the hard sciences, in which physicists and mathematicians alike struggled to describe change and variability, it is little wonder that ecologists have been facing similar technical problems with their own work. In the course of this article we hope to explore in more detail how ideas connected with chaos theory and nonlinear dynamics may have relevance for characterizing the variability found in plant communities.

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Fig. 1 (a) Wolfer's data portraying observed sunspot activity over the years 1750–1920. (b) The simulation of sunspot activity by Yule's 'random' autoregressive model. Both graphs appear in Yule (1927).
What is chaos?

For the unfamiliar reader, we begin by very briefly describing a particular case of chaos emerging from a well known biological equation. Those seeking a fuller exposition of basic concepts are advised to read more comprehensive reviews such as Hastings et al. (1993) and May (1976, 1986). Consider then the nonlinear and density-dependent logistic equation:

\[ N_{t+1} = F(N_t) = rN_t(1 - N_t) \]  

(1)

where \( N_t \) might represent the biomass of a population in the \( t \)th generation, and \( r \) its natural rate of increase. The equation states that the population next generation \( (N_{t+1}) \) is some nonlinear function \( F \) (which in this case is quadratic) of the current population \( (N_t) \). The above difference equation is representative of the more commonly utilized continuous time logistic equation which has had a variety of applications in plant ecology (e.g. Lomnicki & Symonides (1990) modelled the pokeweed \textit{Phytolacca americana}, Room & Julien (1994) the clonal weed \textit{Salvinia molesta}; and Tilman (1994) describes a forest patch-model).

The time evolution of eqn 1 is found by iterating the equation from an initial population \( N_1 > 0 \), to yield the sequence:

\[ N_1 \rightarrow N_2 = F(N_1) \rightarrow N_3 = F(N_2) \rightarrow N_4 \]

\[ = F(N_3) \rightarrow \ldots \]

It is natural to ask whether the model population, if examined over a long enough interval of time, eventually reaches some equilibrium level. To check such an occurrence, one notes that the population can only reach equilibrium at some generation \( t \), if \( N_{t+1} = N_t \), i.e. when the current population is the same as in the next generation, and for that matter every generation following. It is a simple matter to calculate this equilibrium \( N^* \), by setting \( N^* = N_{t+1} = N_t \), into eqn 1:

\[ N^* = rN^*(1 - N^*) \]

Solving the above equation one obtains the nontrivial equilibrium \( N^* = 1 - 1/r \).

Further mathematical analysis (but outside the scope of this article) reveals that the equilibrium \( N^* \) will only be stable whenever the growth rate \( r \) lies in the interval \( 1 < r < 3 \). Figure 2a displays the growth of the population when \( r = 2.8 \) and the way it is 'attracted' to the stable equilibrium point. If followed in time, the population eventually converges to the equilibrium.

It becomes interesting to ask what might happen should the growth rate \( r \) be raised beyond the equilibrium's boundary of stability \( r = 3^2 \) ? Fig. 2 displays some of the different dynamic behaviour possible as the population's growth rates increase. For \( r = 3.2 \), the equation oscillates between two points (Fig. 2b), indicating that the single equilibrium \( N^* \) is no longer stable, but has been replaced by a stable two-cycle. As the growth rate increases further beyond \( r = 3.5 \), the two-cycle becomes unstable and replaced by a stable four-cycle (Fig. 2c). Similar 'period-doublings' follow with increasing rapidity as \( r \) increases geometrically giving cycles of period 1, 2, 4, 8, 16 ... . When \( r \) approaches a critical value \( r_c = 3.57 \), the period of the cycle approaches infinity. Chaos sets in exactly at the critical value \( r = r_c \), and irregular non-cyclical behaviour that might seem random to the eye ensues when \( r \) is increased beyond this value (Fig. 2d,e, \( r = 3.77 \)). A summary picture of the dynamics of eqn 1 is given in the associated bifurcation diagram (Fig. 3 and legend) which displays the equation's attracting equilibrium, periodic and chaotic solutions, as the parameter \( r \) is varied. Even more unusual 'period-halving' dynamics are possible for variants of this simple model, if the equation is modi-
Some technical characteristics of chaos

The majority of articles in the ecological literature concerned with either the theory or application of chaos only require a knowledge of surprisingly few additional concepts. We list some important ones below.

1 In population dynamics, the presence of a density-dependent growth rate is generally considered to be a necessary (although not sufficient) precondition for chaos. Density-dependence simply means that the per capita growth rate of a population depends crucially on current population abundance. Thus the controversy over whether populations are density-dependent or independent (Antonovics & Levin 1980; Hubbell et al. 1990) is linked to the controversy of whether population dynamics are chaotic.

2 A chaotic process must exhibit sensitivity to initial conditions with nearby trajectories diverging exponentially. Suppose at the beginning of a study, two populations $N$ and $N'$ are almost identical in biomass (i.e. similar initial conditions), and differ only by an amount $N - N' = \delta \ll 1$. If both populations are governed by eqn 1, then sensitivity to initial conditions means that the measured difference in biomass between the two populations will grow exponentially with time. Using mathematical notation, the difference at time $t$ between the two populations will be approximated by $\delta t = \delta e^{\lambda t}$, where $\lambda$ is a constant representing the Lyapunov exponent. (A more formal definition of the Lyapunov exponent can be found in Wolf et al. 1985). We sketch here only the general principle.) Sensitivity to initial conditions implies that the Lyapunov exponent must be positive ($\lambda > 0$). This ensures that the trajectories of populations with similar initial conditions rapidly get further and further apart from each other.

An important corollary to the above is that the behaviour of chaotic systems should be predictable in the short term but any attempt to make long-term predictions will only prove futile. When forecasting the behaviour of a chaotic system, the positive Lyapunov exponent ensures that prediction errors are magnified exponentially. Long-range predictability rapidly deteriorates when errors build up multiplicatively as forecasts extend further and further into the future.

3 Chaotic systems are stable in the sense that population trajectories will not exhibit irreversible exponential runaway growth. Instead, populations converge with time onto what is known in technical parlance as an 'attractor', and they fluctuate irregularly between the bounds set by the size of the 'attractor'. When plotted graphically, it is sometimes possible to see visually the population trajectory 'stretching and folding' as it wanders through the attractor. After a period of 'stretching' (exponential growth) the population trajectory 'folds' in phase space reducing population levels, thereby compensating for any bursts of runaway growth. The process of stretching and folding ensures the population trajectory remains bounded and prevents the occurrence of unstable and unmitigated exponential growth.

4 Stochastic (random) systems are considered to have infinite dimension, and a representative population trajectory might wander unpredictably in space and time as if having infinite degrees of freedom. A deterministic system, in contrast, is of finite dimension. In fact the dimension of the system is indicative of the number of equations required to reconstruct an accurate model of its dynamics. Thus low-dimensionality is considered good evidence for determinism.
The fluctuations in time series

Identifying the nature of irregular fluctuations in time series is a common problem faced by ecologists which as yet, has no simple solution. Consider for example, the fluctuations in Fig. 2(e). It seems impossible by the naked eye, and even by many well known statistical tests, to determine whether the time series is:

(a) entirely of random origin;
(b) the product of some low-dimensional chaotic process;
(c) a combination of both (a) and (b).

In actual fact the data was produced by iterating the simple logistic equation (eqn 1) in the chaotic regime.

On the other hand, it may be wrong to diagnose instantly fluctuations which appear ‘more or less’ cyclical, as strictly periodic for at least two reasons:

(a) As Yule demonstrated, cycles that are ‘nearly’ periodic can originate from a random process. Figure 1(a) graphs 175 years of sunspot activity (Wolfer’s numbers) where the approximate 10-year cycle is easily observable. However, Fig. 1(b) displays a time series produced by Yule (1927) that is nothing more than a linear autoregressive random process. It is difficult to differentiate between the real time series and the random process.

(b) A chaotic process can often create the illusion of periodicity too. Measles epidemics peak annually, usually at the beginning of the school year when susceptible children become exposed and easily infected. Despite the natural periodicity of the epidemic, its dynamics were nevertheless thought to be chaotic by Sugihara & May (1990), even though simultaneously locked to a seasonal cycle.

All of the above combinations should leave anyone intending to analyse a time series with the feeling of confusion. The recent interest in ecological time series analysis arose exactly for this reason, and as will be explained shortly, some advanced methods for identifying ecological signals are currently being refined.

Phytoplankton blooms: a case study

The dynamics of phytoplankton in aquatic ecosystems makes an interesting case study since these algae frequently exhibit erratic and explosive ‘boom and bust’ growth (large $r$ in eqn 1) and share many features associated with deterministic chaos (Ascioti et al. 1993). Figure 4 displays a 20-year time series (1970–90) detailing the yearly algae bloom of *Pyrrophyta* spp. observed in Lake Kinneret (Israel). The development of the phytoplankton bloom is directly correlated with the timing and duration of the mixing period in this warm monomictic lake (Pollingher & Zemel 1981). The time series exhibits features that could be associated with: (a) low-dimensional chaos characterized by bursts of rapid and intense nonlinear phytoplankton growth; (b) a noisy deterministic (limit) cycle, i.e. stochastic fluctuations (say the outcome of either measurement error or environmental noise) superimposed upon a periodic signal; (c) some possible combination of both (a) and (b).

Given that phytoplankton blooms control a significant portion of the world’s primary productivity, and are also often detrimental to general water quality, ecologists are particularly interested in understanding the circumstances by which these events are triggered (Beltrami & Carrol 1994). Should a bloom’s dynamics be substantially governed by low-dimensional deterministic chaos, then in theory the complex fluctuations can be modelled by simple mathematical equations possibly of a form similar to eqn 1. As we will explain, in practice the situation is not so simple and at the present time we know of no study that has carried out such a program with success, either for phytoplankton blooms or any other natural phenomenon.

Why is chaos important?

Why are scientists so eager to learn whether the fluctuating dynamics of the system they are studying might be deterministic in origin rather than the outcome of a random process? For plant ecologists, the question is connected to the vexing problem of whether communities are structured or whether they completely lack organization and are nothing more than chance arrangements. The issue can be traced at least as far back as Gleason (1926), who regarded communities as ‘accidents’ – loose assemblages of species that arise and are influenced more by the physical environment than by species interactions. In his own words, a (plant) community ‘is not an organism, scarcely even a vegetational unit, but merely a coincidence.’ The plant association is ‘merely a fortuitous juxtaposition of plant individuals’ (quoted in Watt 1947). This became known as Gleason’s individualistic hypothesis.
In contrast, Clements's (1936) notion of succession suggests that in the absence of disturbance, plant communities will eventually reach a predictable ‘climax’ equilibrium state that is stable and will be maintained over time. The organized structure of a climax community is thus the antithesis of Gleason’s vision of a loose assemblage of species. Separating out non-random patterns in analyses of spatial distributions has thus been of concern for plant ecologists, and a great variety of statistical tests have been employed for just this purpose. However, the assumptions underlying most of these tests are often quite rigid and most cannot adequately deal with the irregular chaotic signals arising from nonlinear dynamic processes.

There are many advantages of knowing whether the fluctuations of a system are deterministic rather than random. Most importantly, it tells us that there is some underlying mechanistic process which is worth our while elucidating. For example, Tilman & Wedin (1991) show how the inhibitory effect of plant litter on the perennial grass *Agrostis scabra*, is a mechanism that might explain the plant’s observed oscillations and the sporadic but pronounced crashes in growth. A nonlinear (chaotic) model of the plant–litter interaction served to cast light on the dynamics even further.

If a data set is found to be governed largely by deterministic chaos, key dynamic parameters of the system under study should be extractable, and at least in principle, reasonably good short-term future predictions are possible (Sugihara & May 1990). Because of the intrinsic determinism, the quality of predictions should be better than those provided by traditional time series techniques. Thus the ability to discriminate between deterministic signal and noise is not merely of academic interest, for it should open the doors to numerous practical applications.

If the signal is truly chaotic and of low-dimension then the theory states that only a small number of equations are required to model the system precisely. With this motivation, Nicolis & Nicolis (1984) and Tsonis & Elsner (1988) attempted to analyse several important time series of climatic data. They claimed to identify intrinsic deterministic properties within the data set that should allow the salient features of a climate system to be described by a simple model involving only four to eight coupled ordinary differential equations. These are remarkable findings which, if true, should have the potential to revolutionize the whole science of meteorology. Unfortunately, both the methods and results of these studies are controversial and according to some evaluations, should at this stage be considered speculative (Procaccia 1988).

The possibility that the climate signal is chaotic would certainly have ecological ramifications. The climate system might be viewed as a forcing function that effectively acts to drive many ecosystems. Since there is now growing evidence that at least some major climate signals are chaotic (e.g. the El-Niño mechanism; Tziperman et al. 1994), it would therefore seem reasonable that these signals manifest themselves in a chaotic way at the ecosystem level as well. More than that, one cannot ignore the known ecosystem-climate feedback loop, which makes the separation of cause from effect sometimes impossible. In the light of this, it might be wrong to refer to the climate signal as a forcing function, if ecosystem response plays an equally important role in shaping the overall ecosystem-climate dynamics. This symbiotic feedback mechanism is, after all, the essence of the Gaia hypothesis and indeed, Lovelock’s model of a daisyworld provides a novel case of a chaotic ecosystem–climate interaction (Zeng et al. 1990).

Cycles and chaos in plant communities

There have already been a number of serious attempts to utilize and incorporate ideas from nonlinear dynamics and chaos theory into the realm of plant ecology. One of the most visual and impressive field studies of cycles and potential chaos can be found in Symonides et al. (1986). They provide an example of a natural plant population, *Erophila verna*, which exhibits two year cycles in the field, apparently because of its over-compensating nonlinear density dependence in fecundity. The cycles were of an extreme nature, jumping between densities of 1–2 individuals and 55–65 individuals per 0.01 m² (very similar to Fig. 5d), but nevertheless predicted by a simple, empirically derived, iterative model qualitatively similar to eqn 1. Germination conditions tended to promote the model’s propensity for cycling in a manner that conforms with the period-doubling route to chaos (see Fig. 5 and discussion below). Indeed, local germination levels were found to be of sufficient magnitude to induce chaotic dynamics.

Silander & Pacala (1990) and Thrall et al. (1989) have presented a number of valuable studies which attempt to determine the conditions for oscillatory and chaotic dynamics in annual plants. Such behaviour, they argued, would be more likely to arise in annuals that have low seed dormancy, high seed survivorship, minimum plant-size thresholds for seed production, large fruited individuals with many large seeds, or grow in locations with high soil fertility. Their models demonstrate a range of dynamic behaviour for annual plants from stable positive equilibrium with damped oscillations, to sustained oscillations, to apparent chaos. One of the more interesting findings of their detailed modelling exercise is that seed dormancy (and its associated time lags) acts as a control on chaos, tending to cause a plant population which would otherwise appear oscillatory, to have a locally stable equilibrium. Nevertheless, they conclude that ‘contrary to Watkinson (1980) and Crawley & May (1987), oscillatory dynamics may be a com-
mon feature of some annual plants' (Silander & Pacala 1990).

The oscillatory nature of populations of the perennial herb Viola fulvibratula was examined in a nonlinear model by Solbrig et al. (1988), which allowed for the possibility of a realistically sized seed bank and made use of field data for calibrating all parameters. Because of the combined effect of nonlinear density dependent seedling survival and the incorporation of a time lag for seedlings as they grow into adults, the model population exhibited oscillatory rather than equilibrium behaviour. Although Solbrig et al. (1988) do not discuss the possibility of chaos, their predictions concerning the widespread occurrence of these oscillations are of obvious relevance: 'If the greater effect of density on seedling and young age classes, which has been documented repeatedly, results in the observed oscillations and if we have correctly simulated density, then the oscillations that we record should be the rule in equilibrium plant populations and we should be able to observe them in nature.' That oscillations might be the rule for some plant communities is a prediction that breaks with

![Graphical model of E. verna](image)

Fig. 5 Symonides et al. (1986) graphical model of E. verna examines seeds per plot in the t + 1th generation (i.e. \( N_{t+1} \)) as a function of seedling density in the tth generation. The latter variable can be expressed as \( N_t \) where is the fraction of seeds that successfully germinate. The return maps on the left (a,c,e) are obtained from plotting \( N_{t+1} \) vs. \( N_t \), (i.e. seeds/plot vs. seedling density). The point where the 45 degree line meets the return map, indicates the equilibrium \( N_{t+1} = N_t \), which is only stable in model (a). The dynamics in (b,d,f) are derived by iterating the respective graphical return map for five generations. (a,b) germination = 5%; (c,d) germination = 1%; (e,f) germination = 2%. Reprinted with permission from Symonides et al., Oecologia 71, 156–158.

The classic example of the spruce budworm system provides another interesting case study of how the interconnectedness of ecosystem components may lead to oscillatory and chaotic dynamics. In these systems, coniferous forests are periodically subjected to severe but infrequent (~ every 40 years) defoliation by outbreaks of an insect pest, the spruce budworm. Holling (1973) detailed the dynamics of two east Canadian forests in which balsam fir is usually the dominant tree species. It is also the most susceptible to the destructive spruce budworm. Spruce and white birch are less abundant, with the former less susceptible to the budworm than the fir, and the latter never being attacked. During a budworm outbreak, there is major destruction of Balsam fir (young individuals are less damaged), and the spruce and white birch come to dominate. In between outbreaks the budworm is exceedingly rare, probably being limited by natural enemies, thereby allowing the forest to recover producing stands of mature and overmature trees of all three species. If budworm outbreaks did not take place, the balsam fir would competitively exclude spruce and birch, and ultimately dominate the entire forest. Thus the budworm outbreaks are essential features in maintaining the persistence of this ecosystem. While the sporadic irruptions of the budworm might leave the impression that the forest community is an unstable system, paradoxically it is because of these periods of defoliation that the forest system has enormous resilience. May (1977) has used a nonlinear model to explore the dynamics of the budworm population showing how such a system might, under the right conditions, jump between two alternative states. Despite the success of the model, there have been a number of recent studies which argue that ‘the existence of such alternative states . . . remain poorly researched’ (Grover & Lawton 1994) and which suggest that these sorts of two-state models might need further biological refinement (Royama 1992). Nevertheless May’s model has other points of interest that are often overlooked. For example, when examined as a difference equation, chaotic population oscillations (as opposed to multiple stable states) are easily sustained (Stone, L. personal observation).

A more recent demonstration of the easily induced chaotic dynamics in the growth of insect pests was provided by Cavalieri & Kocak (1994) in their study of the European corn borer. In their model simulations, Cavalieri and Kocak found that the dynamics of these pests can enter a chaotic state with relative ease after small changes in parameters that are affected by weather. When chaotic, the simulated European corn borer population reaches higher levels of abundance than in an equilibrium or (periodic) oscillatory scenario. The erratic chaotic behaviour of their model has many characteristics in common with real field-data that has been gathered for these pests.

The effects of chaos may arise at a variety of different ecological and biological scales and not just at the population or community level. Lutte & Beck (1992) demonstrate how the endogenous rhythm of the photosynthetic process itself might jump to a chaotic state in certain environmental scenarios. They examined net CO2 exchange in the Crassulacean-acid-metabolism (CAM) plant, Kalanchoe daigremontiana under laboratory conditions. When irradiance or temperature were raised above a critical level, irregular oscillations were noted. In an attempt to understand the cause of the unusual dynamics, Lutte & Beck modelled the CAM network using a system of coupled nonlinear differential equations. In keeping with the experimental results, the simulation model showed a similar transition to oscillatory behaviour and then to chaos as irradiance was increased. The model also displayed a very sharp transition from order to chaos when ambient temperature was increased by only a few tenths of a degree. The CAM cycle, with its two different routes to chaos (via temperature and via irradiance), was explained as an outcome of the interaction of two intrinsic stable oscillations in the influx–efflux dynamics of the plant vacuole in a manner that operates rather like the physicist’s ‘double-pendulum.’

Methods to detect chaos

All of these examples indicate the possible presence of chaotic dynamics in real plant systems. However, proving unambiguously that this is the case, is a difficult if not impossible methodological task. A number of ingenious methods have been put forward as tests for chaos, but as yet, no technique has been devised that provides incontestable proof. We briefly outline four popular methods, all useful for probing for chaos and nonlinearity in ecosystem analyses, and then discuss their major limitation—the small sample size of field studies.

DETERMINING THE ‘RETURN MAP’

There is a very simple yet reasonable tool for ecologists who suspect the presence of a density-dependent relation in their data sets of the form: \( N_{t+1} = F(N_t) \) (such as found in eqn 1). It requires only plotting the variables \( N_{t+1} \) vs. \( N_t \). Any strong linear or nonlinear relationship arising from the potential presence of the function \( F \), should be immediately apparent to the eye. Once the form of the so called ‘return map’ \( F \) is identified, then it is possible to probe further for mechanisms that produce oscillations or chaos.

In Fig. 5 we reproduce the work of Symonides et al. (1986) who plotted the total viable seed production per plot (y-axis) against initial seedling density (x-axis). There are 11 points in total which suggest a ‘humped’ density-dependent curve for the function \( F \). Iterating this map leads to the dynamics displayed in (b) (d), and (f) which represent germination rates of...
0.5%, 1%, and 2%, respectively. Note how the period doubling route to chaos is observed with cycles of period 1, 2 and possibly 4. The actual plant dynamics very closely resembled that displayed in (d), with 1% germination rate although rates of up to 3% were observed in some field plots. Interestingly, the return map in Fig. 5 suggests that levels of germination of 2% (possibly even less), might produce chaotic dynamics.

**Calculating the Lyapunov Exponent**

A number of techniques have emerged which are designed to estimate the Lyapunov exponent (see above) of a time series (Wolf et al. 1985; Ellner 1991). If the Lyapunov exponent proves positive, then it seems reasonable to take this as evidence of chaos. These techniques take advantage of the fact that for a chaotic system, trajectories with very similar (but not the same) initial conditions should diverge exponentially at a rate determined by the Lyapunov exponent. With the aid of a computer it is possible to subdivide a long time series into a large number of small segments. The computer then isolates segments which are nearby and determines whether their trajectories diverge in time from one another exponentially. If so, it is possible to calculate the rate of separation and so obtain the Lyapunov exponent.

**Nonlinear Prediction**

Nonlinear prediction methods attempt to probe for short-term predictability in time series. The underlying idea is that, low-dimensional chaos should have better short-term predictability than a random process (Farmer & Sidorovich 1987; Sugihara & May 1990). The technique is often successful even if a chaotic data set is contaminated by noise. To sketch one common method, suppose the time series under analysis consists of N data points \( \{y_i\} \). For each point \( y_i \) in the time series, a computer algorithm attempts to predict the following point \( y_{i+1} \). The prediction so obtained, is then compared to the actual known value \( y_{i+1} \) and the error of the prediction, \( e_i \), can be deduced. The end product is thus a set of forecasts for one time-step \( (T = 1) \) into the future, as well as error terms \( \{e_i\} \).

The correlation coefficient \( r \) between the forecasts and the observed values may then be computed. The whole process is repeated for predictions two steps \( (T = 2) \) into the future and then for \( T = 3, 4 \ldots k \) steps into the future (where \( k \) is some predefined integer) so that the scaling of the correlation coefficient \( r \), and the error terms can be examined.

If there is some form of sensitivity to initial conditions then prediction errors should grow exponentially with \( T \) (the number of steps forecast into the future), while the correlation coefficient \( r \) should fall dramatically. For a stochastic process, on the other hand, the correlation coefficient and prediction errors will scale very differently to this pattern. It is these different scaling patterns that allow the differentiation of chaos from noise. This is essentially the argument used by Sugihara & May (1990) when they attempted to provide evidence for chaotic dynamics in real epidemiological data sets and phytoplankton bloom time series (see also Tsonis & Elsner 1992). In practice, the method can become problematical since complex noise sources also appear to have several of the signatures attributed to chaos, and are capable of fooling the best tests available (see e.g. Ellner 1991; Stone 1992). The problem is exacerbated even further if the time series under analysis is poorly sampled or lacks a sufficient number of data points, as we discuss shortly.

**Surrogate Data Tests for Nonlinearity**

The method of surrogate data, as conceived by Theiler et al. (1992), starts by recognizing the difficulty, if not impossibility, of convincingly demonstrating chaotic dynamics by any of the methods suggested to date. Instead Theiler et al. are less ambitious, and only attempt to seek out strong evidence for the nonlinearity of a time series. While this necessarily leads to a weaker statement about the underlying time series dynamics, it has the advantage of providing statistically significant results that cannot be misleading.

A null hypothesis is first posited stating that the observed time series has been generated from some type of linear Gaussian process (LGP) and is therefore random. One then tests the null hypothesis by comparing the observed time series to a large number of surrogate time series that are known to be ‘random’. Each of the surrogate time series is generated on the computer by a true LGP random process, and is thus guaranteed to be random by construction. As well, each surrogate time series is generated so that it simultaneously inherits important qualities of the observed time series (e.g. an identical frequency spectrum). (As a visual example, a typical surrogate for the actual sunspot data in Fig. 1a might be Yule’s random autoregressive model in Fig. 1b. Not only does the surrogate appear almost identical to the observed data set, but it has the same frequency spectrum.) The null hypothesis is then tested by checking whether the observed time series has identical statistical characteristics to the set of proxy time series which are truly null. If nothing exceptional is found, the null hypothesis that the observed time series is a random process cannot be rejected.

**Sample size – the limiting factor**

The inescapable problem with all of the above methods is that the number of data points in the time series under analysis must be very large for reliable assessments. Clearly a 10-year time series comprising 10 annual measurements of plant abundance would tell us very little about plant dynamics. Indeed it
would be extremely difficult to deduce whether the data displayed a linear trend or was instead cyclical. It would be harder still to decide whether the annual fluctuations in the data set were chaotic.

Eckmann & Ruelle (1992), both highly respected theoretical physicists, have argued that there will always be fundamental limitations for estimating dimensions and Lyapunov exponents. According to their calculations, the accurate estimation of a Lyapunov exponent in a time series requires approximately \( N = 100000 \) data points in a system with dimension \( (d = 5) \), and more than \( N = 1000 \) data points for \( d = 3 \). Such data sets are truly large, and we know of no ecological time series that comes close to these lengths. Most ecologists would treat a time series of 100 data points simply as a treasure.

Despite the depressing assessments of Eckmann & Ruelle (1992), tests on known chaotic and random data sets, have shown that in practice all of the above methods are reasonably faithful for time series of the order of 500 data points. Since several noteworthy ecological time series (usually epidemiological) of this size are available, they have made interesting test-cases. Although claims have been made for methods with far less stringent data requirements, we feel that many of these claims should be treated against a background of caution.

In all, this is particularly bad news for plant ecologists whose data sets usually consist of annual measurements taken typically over a few years. Some of the best 'long-term' data sets only comprise of some 40–60 measurements (e.g. Watt 1981; Dodd et al. 1995), which immediately points to where future research directions might lie both in field work and methodological areas. For the former, we presume that GIS (geographical information systems) and satellite remote sensing will provide very large, quality data sets in the not too distant future.

**Spatiotemporal dynamics**

Until now we have focused on a variety of ways in which plant populations might fluctuate in time. But this in itself reveals only a fraction of the whole ecological picture, for in the study of plant communities, interest also centres on patterns that occur over the entire spatial landscape. Tradition has it that the spatiotemporal dynamics of plant communities are fairly simple, and largely accord with the classical climax theory in which a fixed and predictable community structure determined by competitive equilibrium, will always eventually be attained (Clements 1936). After a disturbance the plant community is predicted to pass through a series of successional states, each with differing species composition, until the climax equilibrium state is reached. Watt (1947), however, challenged the climax theory, arguing that more emphasis needs to be placed on the highly dynamic nature of plant communities rather than focusing on abstract notions of stable equilibria (see e.g. Connell & Sousa 1983). According to Watt, the community is not spatially homogeneous and is best understood by breaking it down to a set of localized patches. The patches, or phases as Watt sometimes terms them, consist of aggregates of individuals and of species, and change dynamically often cycling in a progression of states (e.g. pioneer \( \rightarrow \) building \( \rightarrow \) mature \( \rightarrow \) degenerate). They 'form a mosaic and together constitute the community ... the patches are dynamically related to each other. Out of this arises that orderly change which accounts for the persistence of the pattern in the plant community.'

Watt describes seven communities which never appear to reach an equilibrium climax state; instead each shows unusual cyclical development amongst its constituent mosaic of patches. The patches cycle in a regular pattern affecting adjacent patches in a dynamic way thus forming a 'resultant regeneration complex as a community of diverse phases [or patches] forming a space-time pattern. Although there is change in time at a given place, the whole community remains essentially the same; the thing that persists unchanged is the process and manifestation in the sequence of phases.' In contrast, a single patch itself is not stable over long periods of time. Furthermore, because of the cyclical process of the patches, Watt shows that it is sometimes possible to observe the time-sequence of change at a given patch, recorded in the spatial distribution.

Sprugel (1976) and Sprugel & Bormann (1981) found the mosaic cycle concept very useful in their study of *Abies balsamea* (balsam fir) forests in the north-eastern United States. The wind-induced cycles of death, regeneration, and maturation appear to move constantly through these forests predictably at intervals of some 60 years. These repeating spatial waves (Fig. 6) are difficult to explain by usual notions of climax equilibrium but readily conform with Watt's theory of phases. Sprugel hypothesized that prevailing

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**Fig. 6** A typical cross section through a regeneration wave in the balsam fir forests described by Sprugel & Bormann (1981). The wave pattern dynamics leaves bands of dead trees interspersed with bands of regenerating and mature firs. Reprinted with permission from Sprugel & Bormann (1981), *Science* 211, 390–393. Copyright 1981 American Association for the Advancement of Science.
wind disturbances increase death amongst exposed trees located at the wave-edge. Because balsam fir forests vigorously regenerate, strips of dead trees are rapidly replaced by seedlings and young firs soon appear. The wave-edge marches forwards as the wind disturbance affects a newly exposed layer of mature firs. A spatial wave pattern thus emerges, with strips of dead trees found at regular distances, and with the wave slowly moving through the forest in the direction of the wind. Note that the time-sequence in growth is evident in the spatial-distribution (see Fig. 6), just as predicted by Watt’s theory.

Although Watt’s ideas largely went forgotten, in recent years there has been a revival of interest in the patch-mosaic ecosystem concept he put forward (Remmert 1991). Mathematical and computer models have been found to be particularly useful for examining patch dynamics in ecosystems for which species and resources interact locally according to a set of very simple rules (Rand & Wilson 1995; Hendry & McGlade 1995). The resulting and changing structures often look haphazard and random, and seem to lack any organizational qualities whatsoever to the naked eye. However, subject to mathematical analysis, these model ecosystems show surprising internal structure and organization because the simple rules they are derived from may sometimes yield spatiotemporal chaos, i.e. a form of chaos that carries over into both space and time. The new techniques available for examining spatiotemporal chaos (Rand 1994; Rand & Wilson 1995) are extremely exciting for they provide a way of probing for deterministic pattern and structure in spatially sampled ecosystems; patterns that would most likely go undetected with more usual statistical approaches. Such methods have great potential in ecosystem analyses, especially given the new shift towards remote sensing surveys by satellite and other means.

Spatial modelling has also led to the development of the concept of metapopulation dynamics. A metapopulation consists of a set of local subpopulations located over a large spatial terrain that are linked by dispersal. In his book *The Diversity of Life*, Wilson (1992) provides a very eloquent description of metapopulation dynamics:

‘Watched across long stretches of time, the species as metapopulation can be thought of as a sea of lights winking on and off across a dark terrain. Each light is a living population. Its location represents a habitat capable of supporting the species. When the species is present in that location the light is on, and when it is absent the light is out. As we scan the terrain over many generations, lights go out as local extinction occurs, then come on again as colonists from lighted spots reinvade the same localities. The life and death of species can then be viewed in a way that invites analysis and measurement. If a species manages to turn on as many lights as go out from generation to generation, it can persist indefinitely. When the lights wink out faster than they are turned on, the species sink to oblivion.

The metapopulation concept of species existence is cause for both optimism and despair. Even when species are locally extirpated, they often come back quickly, provided the vacated habitats are left intact. But if the available habitats are reduced in sufficient number, the [species can disappear for all time]. A few jealously guarded reserves may not be enough. When the number of populations capable of populating empty sites becomes too small, they cannot achieve colonization elsewhere before they themselves go extinct. The system spirals downward out of control, and the entire sea of lights turns dark.’

Currently theoretical ecologists are attempting to understand the species extinction process using modelling approaches to identify processes which cause systems to spiral out of control (Tilman et al. 1994; Stone 1995). Wilson’s conceptual picture of habitat destruction is in some ways counter-intuitive and might be considered to be at odds with notions of linear systems theory. In a ‘linear world’ it seems reasonable to conjecture that species populations might drop proportionally as habitat destruction increases, but with extinctions never occurring unless the habitat is completely destroyed. As the Tilman et al. (1994) model of forest ecosystems makes evident, the dynamics of species extinctions are far more complicated. In a nonlinear world, when species are dispersing across a landscape and competing for patches on which to thrive, the spatiotemporal picture is extremely complex and as recent theoretical work is suggesting, sometimes chaotic in structure.

**Discussion**

The possibility that population dynamics might be chaotic has radically shifted the emphasis in ecology away from its founding core principles. Ideas of ecosystems that sit at some possibly mythical stable equilibrium, or expressions of faith in tenuous linear (or linearizations of) ecosystem models, usually lead only to conclusions that are based in science fiction. Similarly, it would be unrealistic to believe unwaveringly that chaos is some sort of generic ecosystem behaviour; for the time being it is still impossible to point to one single study in which population dynamics are unambiguously chaotic.

Nevertheless, the examples we have discussed make clear the changing vision in ecology. Not only has there been an increased interest in exploring the many ways in which populations change over time, but there
has been a concerted effort to also understand their changes in spatial organization.

Our review has attempted to synthesize the case for nonlinear dynamics in the most enthusiastic way possible. In our view, nonlinearity is an ubiquitous feature in natural systems making it not unreasonable to expect associated signals of oscillating and chaotic dynamics, especially in ecosystems governed by strong deterministic growth processes. However, it would be wrong to ignore the straightforward possibility that much of nature's variability arises from random (possibly nonlinear) stochastic processes, or in other words, is simply an expression of unpredictable chance events. To what extent the latter possibility predominates over the former is still very much an open question.

We find it interesting that a number of the major themes discussed in this review, were promoted decades ago by early pioneering ecologists, but have not been developed much further since then. Thus Watt's (1947) research on the 'dynamic concept' and the 'mosaic cycle' in plant ecology, largely went forgotten. Perhaps this only reflects the absence of adequate modelling and statistical tools required to examine the ideas in the depth they deserve. The theory of nonlinear dynamics and chaos should help fill this gap, since it provides a novel and exciting framework with which to explore the variability and change in plant communities from both a theoretical and applied perspective. Success in many ways depends on the willingness of ecologists to accept the challenge and welcome with an open mind these useful mathematical tools.

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