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MATHEMATICAL MODELLING OF SPATIAL-ECOLOGICAL COMPLEX SYSTEMS: AN EVALUATION

ABSTRACT

Assessing the complexity of landscapes is one of the top research priorities for Physical Geography and Ecology.

This paper aims at a methodological evaluation of the discrete and analytical mathematical models hitherto available for quantitative assessments of spatial ecological complex systems.

These models are derived from cellular automata and nonlinear dynamics. They describe complex features and processes in landscapes, such as spatial ecological nonlinear interactions, unpredictability and chaos, self-organization and pattern formation.

Beginning with a distinction between two basic types of spatial ecological complexity (structural, functional), and after reviewing the quantitative methods so far available to assess it, the areas where the major challenges (and hence, difficulties) for future research arise are identified. These are: a) to develop measures of structural spatial-ecological complexity, b) to find Lyapunov functions for dynamical systems describing spatial interactions on the landscape (and related attractors), and c) to combine discrete

time and continuous spatial data and models.

Key-words: Geographical Modelling, Nonlinear Dynamical Systems, Complex Geo-Systems, Lyapunov functions, Cellular Automata

INTRODUCTION

Various research efforts undertaken over the last years aimed to evaluate how complex a landscape may be. If successful, such methods would have been useful for the theory of landscape ecological analysis, as well as for the practice of landscape management. Geomorphology does not appear to have any widely accepted tool or method to evaluate landscape complexity, while Landscape Ecology presents studies in which assessments of landscape complexity are made by using various (and, to a certain extent, subjective) combinations of already known landscape-ecological indices.

To date, neither of these disciplines possesses a set of general methods to measure landscape complexity. Consequently, a number of questions rise: Why is this so difficult? What are the main analytical models for calculating how complex a landscape is? How far have we advanced in modelling

landscape complexity by using analytical methods? These questions are tackled theoretically in this paper.

Landscape complexity is a key research priority in Landscape Ecology according to Wu & Hobbs [2002] and several studies have appeared over the last years in the literature, related to quantitative assessments of landscape complexity [e.g. Gabriel et al, 2005; Kolasa, 2005; Herzon & O'Hara, 2006]. Research has produced evidence of non-linear interactions in the landscape [Pahl-Wostl, 1995] and findings related to complexity observed from within landscape dynamics [Turchin & Taylor, 1992].

In Geomorphology also, there is evidence of complexity in landforms [Werner, 1999] and landform formation processes [Fonstad, 2006] and it was also suggested that landscape complexity should be one of the highest research priorities in Geomorphology [Murray & Fonstad, 2007].

The objectives of the paper are: a) to present a state-of-the-art account of the discrete and analytical mathematical methods used to model landscape complexity (particularly functional landscape complexity, which seems more difficult to decipher) and b) to present an effort to shed light on the fields in which ambiguities or difficulties arise, related to modelling and computation of landscape complexity with such methods.

TWO TYPES OF LANDSCAPE COMPLEXITY

Despite the recognition of the importance of the subject, there are however difficulties in the classification of types of landscape complexity. For instance, Loehle [2004] suggested, that there are five types of "ecological complexity", aside of spatial ecological complexity: temporal (population dynamics etc), structural (referring to relationships within the ecosystem), process (i.e. steps and compounds), behavioural (i.e. adaptation) and geometric. The latter

might be considered as yet another form of spatial complexity, with emphasis on the third dimension and the particular shapes of ecological objects. Yet, this is one classification only, available from the domain of Ecology. There is no widely accepted typology of ecological complexity however, nor any classification from the domain of Landscape Ecology. In line with previous publications, in this paper it is suggested that landscape complexity may be of two basic types: structural and functional, which can both change with time and hence can be "dynamic" (in the sense of [May & Oster, 1976]). The words "structure" and "function" have precise meanings in Landscape Ecology and the reader is referred to any classic text of landscape ecology [Forman & Godron, 1986] for their explanation.

The *structural* landscape complexity can be computed in various ways, i.e. through the study of a landscape's map or a landscape's satellite image or aerial photograph. In this case, the computation of landscape complexity is equivalent to the calculation of spatial complexity from the landscape's land use, land cover, soil and vegetation maps. Hence, a landscape's structural complexity is higher than another's, if it has higher diversity of land cover types and longer boundary length of its patches. The main problem here is that we do not have a general algorithm providing us with these characteristics in a unifying way.

The computation of *functional* landscape complexity is more elaborate than that of structural landscape complexity, due to the non-spatial characteristics of landscape functions. Such functional characteristics (i.e. species interactions, water flows, soil movements, trophic chains) render the calculation of landscape complexity particularly difficult, because quantitative assessments of the relationships among the landscapes' constituents (plant and animal species, soil and non-biota) are much more complex than the landscapes' structural components are.

What mathematical tools do we need to model structural and functional landscape complexity?

Ecological modelling entails a diverse array of mathematical methods. But, two main categories of mathematical methods prevail: discrete and analytical. Given that ecosystems are usually described as populations, we often use analytical mathematical methods (i.e. differential equations models). These equations are modelling the change of a population species X with time: dX/dt . They are typically nonlinear and therefore describe how different populations (i.e. prey X and predator Y) interact. These interactions are shown by “nonlinear” terms in these equations (terms such as X^2 and XY).

Yet, when we need to explore the spatial components of ecological changes, the analytical mathematical models are very difficult to handle, because solving differential equations in space and time per grid cell is a painstaking undertaking, due to the many mathematical difficulties arising (boundary conditions etc). It is for this reason that researchers have turned their attention to non-analytic models also, such as cellular automata. With cellular automata, we have the possibility to explore changes over a geographical space with relatively simple rules, without solving any complicated equations, as we do with differential equations models.

COMPLEX SYSTEMS AND SELF-ORGANIZATION

“Complex Systems Theory” entails a very wide spectrum of applications, in many disciplines, such as economics, physics, physiology, astronomy, materials science etc. We most often use this term to signify precisely what is understood by the layman as “complex” and to explore how some system becomes complex, why, by what processes, and, once it becomes, how does it evolve in time.

Complex Systems Theory usually focuses on processes and behaviours that lead to

“complex behaviour”. As such, we often mean behaviours difficult to decipher, difficult to predict, difficult to quantify. Such behaviours can thus be unpredictable or chaotic. A major discovery of Complex Systems Theory is that unpredictability and chaos may also emerge from purely deterministic systems. In fact, as will be seen in the next chapters, it may emerge from even simple differential equations systems.

As there is a variety of features of complexity aside of pattern formation in an observed system (i.e. connectivity of elements, stabilization and resilience, emergence of new properties), the mathematical methods, that can be used to model complexity in any system vary immensely and they can range from methods of discrete mathematics to calculus. But it is the mathematical analysis of nonlinear systems that occupies the foremost and central tool we possess to tackle issues of complexity in any system. In fact, the major part of Complex Systems Theory uses analytical methods for tackling complexity. And landscapes are no exception to this. Furthermore, analysing the role of time in the spatial evolution of ecosystems constitutes a central theme in landscape ecological analysis. It is precisely in this respect, that cases of “self-organisation” (or “pattern formation”), observed on a landscape are hallmarks of complexity and complex behaviour. It is also at this point that models using analytic approaches (differential equations) are most valuable and preferred at the expense of any other mathematical approaches.

Self-organization in ecosystems may be spatial and non-spatial. For instance, when spatial units interact and, after some time, result in a “permanent” spatial allocation, we may call this process a self-organization. Also, when populations interact and, after some time stabilize, this is also a (*sensu lato*) self-organization process. Examples of purely spatial self-organization can be seen from cellular automata, and examples of “functional” self-organization occur in the case of species interactions, such as

those described by Lotka-Volterra models (with certain values of their parameters only).

WHY IS LANDSCAPE COMPLEXITY DIFFERENT THAN LANDSCAPE HETEROGENEITY

Clearly, the “complexity” of a landscape is different than its “heterogeneity” and the latter concept is simply a sub-concept of the former. A highly heterogeneous landscape is also highly complex. But a highly complex landscape may not be such because of the complexity of its heterogeneity only. It can also be complex due to the complexity of its functions. So high heterogeneity may imply high complexity, but the reverse does not always hold. Further, a less heterogeneous landscape and with lower functional complexity, may develop a more complex dynamic behaviour than another more heterogeneous landscape, and this complex behaviour may lead to the creation of patterns or self-organisation, which, as stated earlier, constitute a key difference between complexity and its components, such as heterogeneity. In fact, considering the context of the word “complexity” (as understood in the domain of Complex Systems Theory) is enough to reveal its difference with “heterogeneity”: in Complex Systems Theory, complexity is perceived as a condition *in between order and randomness*,

where self-organization appears and spatial patterns emerge (fig. 1).

Following these methodological concerns, the computation of each one of the two types of landscape complexity previously referred to presents distinct challenges. We therefore have both discrete and continuous approaches to it. Discrete (algorithmic) methods are mainly used to assess structural landscape complexity, while continuous (analytical) approaches are more suitable for problems of functional landscape complexity, without precluding the possibility of using analytic methods for both types. Also, both methods are used for describing temporal changes in landscape complexity (either structural or functional).

MODELLING STRUCTURAL LANDSCAPE COMPLEXITY

Discrete models for structural landscape complexity are mainly based on cellular automata. These are automatic evolutionary processes depending on a set of “states” S_1, S_2, \dots, S_n and a set of “transition rules” T_1, T_2, \dots, T_m , acting on these states. Each cell is found in one state only and its state is determined by the rules and the states of the surrounding cells. Consequently, at each time $t + 1$, the state of each cell, S_{t+1} , is determined from the transition rule T_i acting on the state of the cell at time t .



Fig. 1. According to Complex Systems Theory, complexity is a condition in between order and chaos, so neither landscape A (ordered) nor landscape C are “complex”, because A is completely ordered and C is completely random. But landscape B is complex, because it is in between the two states of order and randomness and displays distinct patterns (such as the dark area in the middle) (Fivos Papadimitriou, 2009).

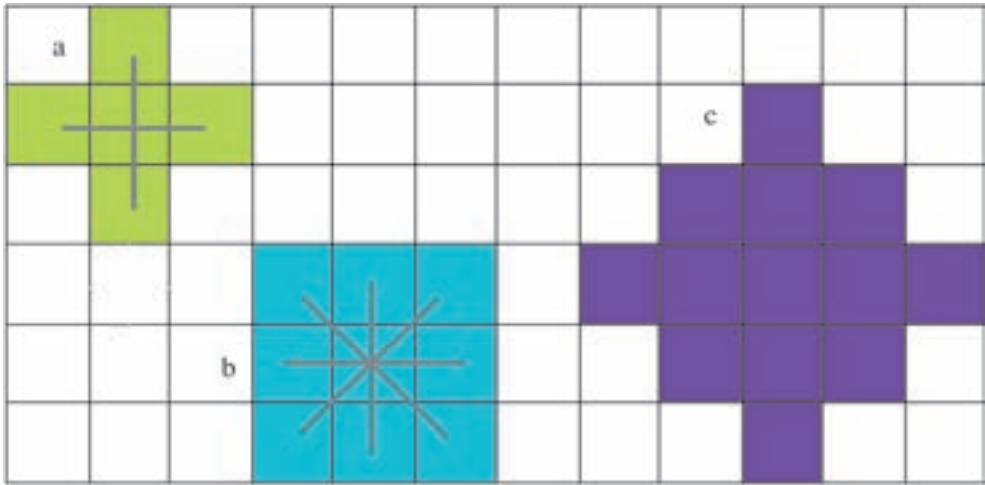


Fig. 2. Elementary cellular automata: in “rook’s case” (a), the central cell interacts only with four surrounding cells, while in “king’s case” (b) it interacts with all nine surrounding cells. In a 5-cell von Neumann neighbourhood (c), the central cell interacts with 12 cells around it (Fivos Papadimitriou. 2009)

$$S_t \xrightarrow{T_i} S_{t+1}$$

The “rules” are simple algorithms acting on landscape cells in two dimensions (fig. 2), that can interact with their neighbouring cells, either in the “rook” sense or in the “king” sense (as the rook’s or the king’s movements in chess) in cases “a” or “b” respectively. The former is also called a “3X3 von Neumann neighbourhood”, while the latter is also called a “9-cell Moore neighbourhood”.

There are other possibilities for constructing cellular automata with longer interactions than in the 9 cells surrounding the immediate neighbourhood of the central cell. One such is the “5X5 Von Neumann neighbourhood” (case c).

The simulation usually needs object-oriented languages, such as Java, C++ and Delphi.

Cellular automata have been applied to explain complexity in a number of cases in Landscape research, ranging from the possibility to establish general algorithmic ecological laws, to the exploration of ecological processes such as niches, industrial ecologies, interspecies competition, latitudinal gradients and species diversity [Rohde, 2005; Baynes, 2009].

Also, they have been applied in Geography to model the expansion of urbanization in the course of time [Barredo et al, 2003; Guermond et al, 2004], geomorphological processes (i.e. run-off and soil erosion) in basins [Guermond, et al, 2004; D’Ambrosio et al, 2001], and overall landscape evolution [Matsuba & Namatame, 2003; Sprott et al, 2002].

With cellular automata, we can simulate the ways by which landscapes change with the spatial propagation of fire [Green et al, 1990; Duarte, 1997], we can even explore the complexity of spatial synchronization processes [Satulovsky, 1997], as well as phenomena of self-organization in landscapes [Manrubia & Sole, 1996; Malamud & Turcotte, 1999].

It must be noticed however, that cellular automata are useful to *simulate* the spatial mechanisms of complexity of some geographical processes, but they do not help us measure landscape complexity. This is because with cellular automata we simulate landscape changes over time and observe pattern formation and self-organization, which are signs of complexity (fig. 3), but they are not particularly enlightening as computational measures of spatial

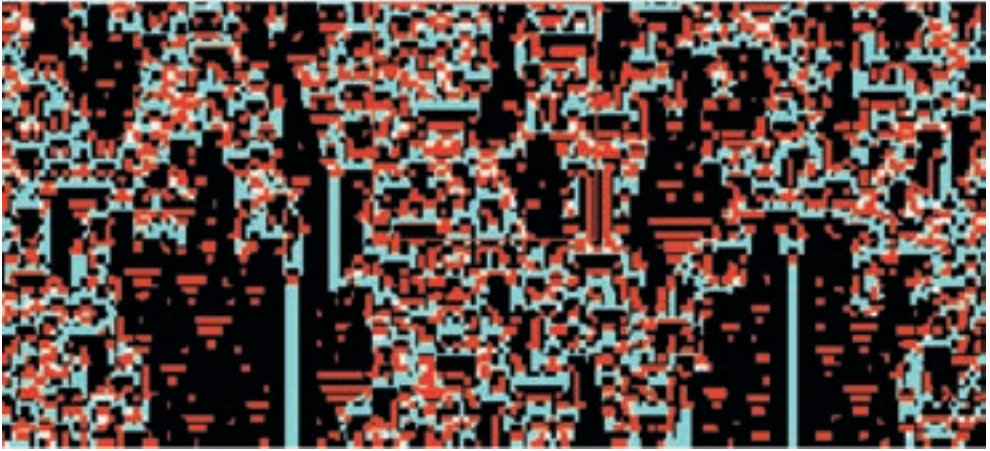


Fig. 3 An example landscape covered by a cellular automaton with 4 interacting “land cover” types, which has evolved after 100 time steps and begun from a random initial spatial distribution of its four land cover. After this number of time steps, it now shows areas of “self-organization” (areas of homogeneity, i.e. down-left and down-right), even some linear features (the vertical lines in the lower half of the landscape) (Fivos Papadimitriou. 2009)

complexity (*describing* a complex process as it evolves with time is different than actually *measuring* it).

Furthermore, in cellular automata the transitions between landscape states are given by rules and not by equations, so we cannot apply analytic mathematical methods for studying the evolutionary processes they describe. In a way, with cellular automata we trade realism with ignorance. In other words, the more realistic our representations are, the more ignorant we are about the analytic details behind the processes we model.

MODELLING FUNCTIONAL LANDSCAPE COMPLEXITY

SINGLE SPECIES MODELS

One of the major discoveries in Complex Systems Theory was that complex phenomena, such as bifurcations and chaos may appear from even simple nonlinear dynamical systems. A typical such case is the logistic differential equation:

$$\frac{dX}{dt} = aX(1 - X)$$

which displays periodicity for $a = 3.2$, whilst for other values such as $a = 3.75$ for which it

is plotted here, it displays stable and chaotic orbits (fig 4).

In its discrete and recurrent form

$$X_{n+1} = aX_n(1 - X_n)$$

it holds for $a \leq 4$ (otherwise $X \rightarrow -\infty$) and it displays another interesting complex behavior, which is bifurcations (fig 5), for iterative values of X_n (plotted for $X_0 = 0.5$ here).

Interestingly, when $a > a_{critical} = 3.569945$, the solutions become very complex and fluctuate wildly. Thus, even simple ecological models can display very complex dynamic behavior and this discovery has been one of the cornerstones of Complex Systems Theory, as it reveals that even simple deterministic systems are difficult to predict, because they are “infinitely sensitive” to initial conditions.

Another single-species model which has attracted much attention is the *Levins* model [Levins, 1969], because it aims at exploring analytically the spatial inhomogeneities of a population.

Defining with X the fraction of patches occupied at a given time, the model considers that each occupied patch may

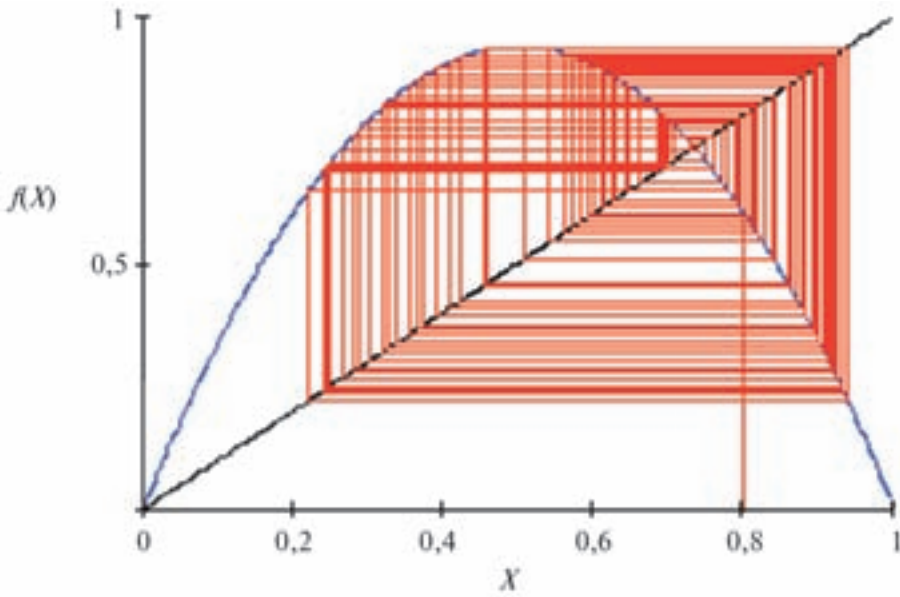


Fig. 4 “Chaotic orbits” generated in the logistic function for values of $a = 3.75$ (Fivos Papadimitriou. 2009)

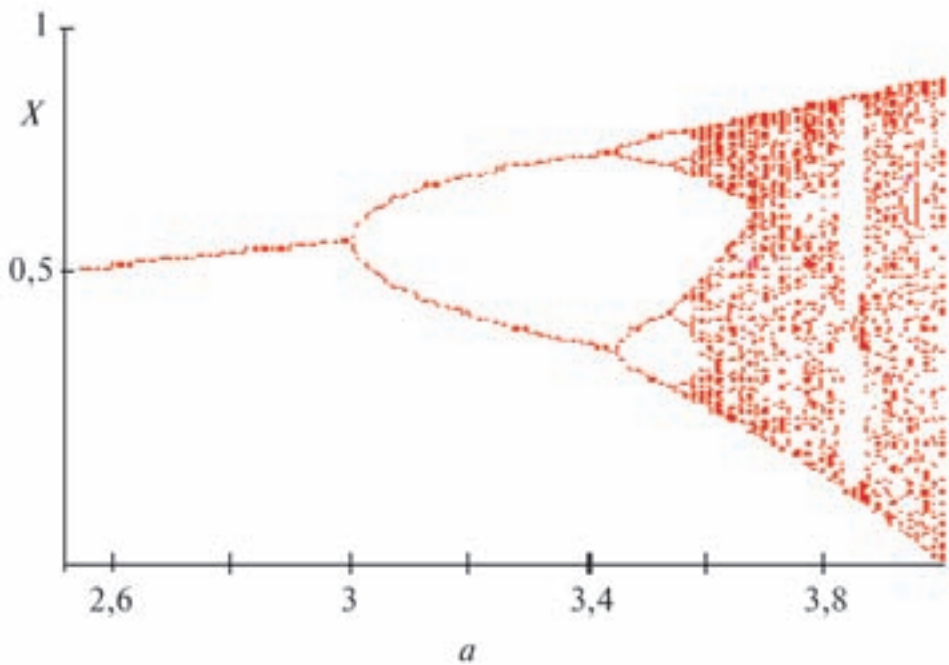


Fig. 5 Bifurcations generated in the logistic function for values of $X=0.5$ (Fivos Papadimitriou. 2009)

become unoccupied after some time t , with probability m . Hence, $1 - X$ is the proportion of unoccupied patches (which nevertheless remaining subject to colonization). Letting c be a constant rate of propagule generation for each of the

X occupied patches, the probability for each unoccupied patch to be colonized is cX . Consequently, the change in the proportion of occupied patches, dX/dt , is:

$$\frac{dX}{dt} = cX(1 - X) - mX$$

Setting dX/dt equal to zero, gives either $X = 0$ or

$$X = 1 - \frac{m}{c}$$

The latter relationship implies that $X \leq 1$, so some fraction of a species habitat will always remain unoccupied.

Also, this model predicts that increasing colonization rate leads to increasing numbers of occupied patches, but does not consider the effects of local dispersion (fig. 6).

A variance of the Levins model is the Nee-May model:

$$\frac{dX}{dt} = cX(1 - D - X) - mX$$

where D is the proportion of permanently destroyed habitat areas.

With this spatial model, Nee & May [1992] showed that habitat destruction increases the population of the inferior competitor when two species compete in a non-homogeneously fragmented landscape. This unexpected finding is interpreted as an outcome of the process, whereby the superior competitor suffers greater losses, because of the habitat construction (e.g. due to its lower colonization rate).

TWO-SPECIES MODELS

Yet, we seldom use single species models to model geographically complex situations. Our mathematical models in spatial analysis typically use dynamical systems approaches, based on differential equations models describing systems of species interactions, such as the *Lotka-Volterra*. These systems constitute the “standard” for the analysis of complex nonlinear dynamics. Aside of ecological complexity analysis, Lotka-Volterra systems have been useful in analysing geomorphological landscape evolution (erosion, regeneration and tectonic uplift), by developing models of nonlinear dynamics [Phillips, 1995], from which may emerge new landscape structures through changes of the overall stability regime, described by these differential equations. Phillips [1993] for instance, showed that the landscapes of drylands are inherently unstable, because perturbations tend to grow in these areas.

The basic Lotka-Volterra model of nonlinear ecosystemic dynamics (where $X = \text{prey}$ and $Y = \text{predator}$) is:

$$\begin{aligned} \frac{dX}{dt} &= aX - bXY \\ \frac{dY}{dt} &= -cY + gXY \end{aligned}$$

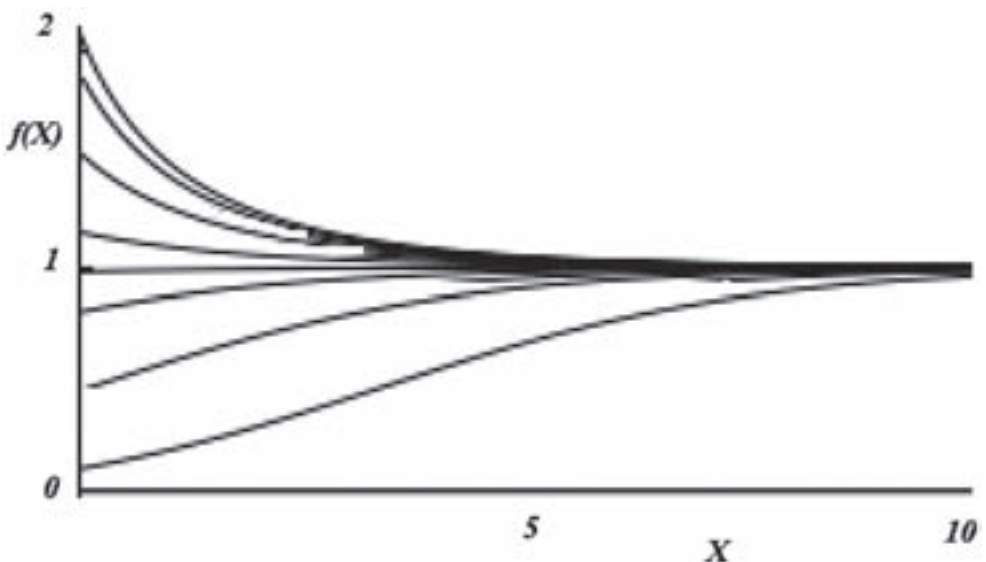


Fig. 6. Graph showing curves of solutions of the Levins model (Fivos Papadimitriou, 2009)

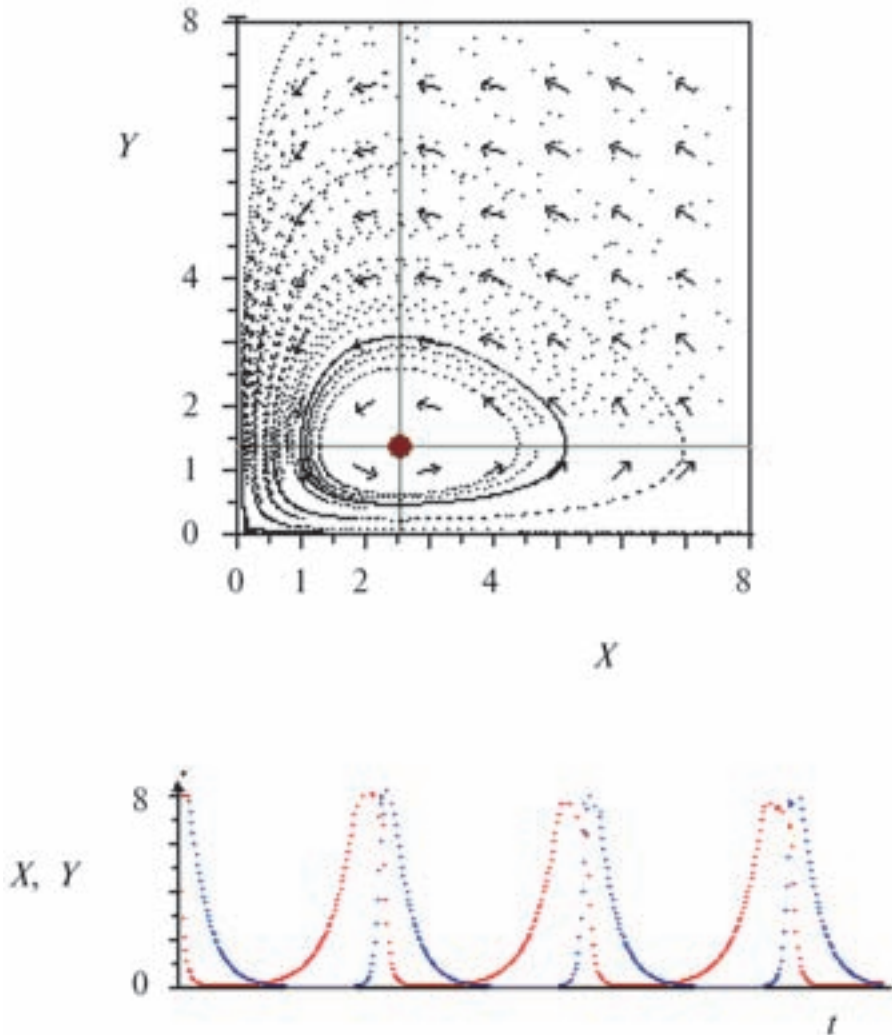


Fig.7. The solutions of a non-linear dynamical Lotka-Volterra system of two species ($X = \text{prey}$, $Y = \text{predator}$). The attracting region, or “attractor” is shown in the lower left area of the upper diagram (a quasi-ellipsoid area). In the lower diagram, appear the oscillating species populations X and Y plotted against time. The calculation here is with parameters $a = c = 0.95$, $b = g = 0,7$ and initial values $X_0 = Y_0 = 8$ (Fivos Papadimitriou. 2009)

The prey X has a growth rate a and depletes according to a predation rate b .

The predator Y has a mortality rate c and grows according to the food conversion rate d .

An example calculation of this system with $a = c = 0.95$, $b = g = 0,7$ and $X_0 = Y_0 = 8$, is shown in fig. 7, from which a possible long-term evolution of the system’s behaviour becomes obvious: the system tends to concentrate to the ellipsoid attractor in the lower left part of the graph, over a

range of possible orbits (depicted with arrows).

Lotka-Volterra systems display easily spectacular nonlinear behavior, because the nonzero equilibrium point $(X, Y) = (a/b, c/g)$ is unstable. In ecological analysis at the landscape level, it is remarkable, that spatial heterogeneity can lead to behaviors different than those expected from non-spatial species interaction models, so allowing for the survival of populations at the landscape level, which otherwise would not happen.

THREE-SPECIES MODELS

For three species (X , Y , Z), a well known variant of the Lotka-Volterra model is the *May-Leonard* model [May & Leonard, 1975]:

$$\frac{dX}{dt} = X\{1 - X - aY - bZ\}$$

$$\frac{dY}{dt} = Y(1 - bX - Y - aZ)$$

$$\frac{dZ}{dt} = Z(1 - aX - bY - Z)$$

This model displays a noticeable behavior from the point of view of Complex Systems Theory, because the system's trajectories show pairs of species approaching extinction with closeness to extinction growing with time.

With three species also, the *Hastings-Powell* model is equally suitable for complexity analyses: t represents the functional relationships in a three-species ecosystem, where species X is the resource species, lying at the bottom of the food chain, Y is a species feeding on X and Z is a predator feeding on Y , with a_i , b_i parameters:

$$\frac{dX}{dt} = X(1 - X) - a_1 b_1 \frac{XY}{X_1 + X_0}$$

$$\frac{dY}{dt} = a_1 Y \left[\frac{b_1 X}{X_1 + X_0} - 1 \right] - a_2 b_2 \frac{YZ}{Y + Y_0}$$

$$\frac{dZ}{dt} = a_2 Z \left[\frac{b_2 Y}{Y + Y_0} - 1 \right]$$

The complexity of interactions among the three species becomes evident when, for certain parameters a_i and b_i , the model displays a chaotic behaviour [Klebanoff & Hastings, 1994].

N-SPECIES MODELS, LYAPUNOV STABILITY AND CHAOS

Both instability and stability are linked with complex systems. A system may be stabilising with time and, by doing so, it may lead to pattern formation and self-organisation. When it destabilises, it may give rise to chaotic and unpredictable behaviors.

A prominent measure of system stability are the Lyapunov exponents. When the Lyapunov exponents are positive, then the system displays diverging orbits with time in its phase space, instability and, possible, chaotic behavior. When the Lyapunov exponents are zero, then a constant distance between orbits is maintained and, when they are negative, the orbits converge to a region of the phase space (or to a point) and the system is stable. Consequently, they are useful in the study of long-term behaviors of complex systems.

Besides Lyapunov exponents, there are "Lyapunov functions", usually symbolized as $V(X(t))$, which characterize the stability of a dynamical system of population species X . These functions must be positive or zero if and only if $X = 0$ and their derivative $\dot{V}(X(t))$ must be negative.

The usefulness of Lyapunov functions is that they can be employed to explore a system's stability without having to calculate its real energy potential (which can be frustratingly difficult in many domains of the natural sciences).

More generally, for n -interacting species, the Lotka-Volterra model is:

$$\frac{dX_i}{dt} = r_i X_i \left(1 - \sum_{j=1}^n a_{ij} X_j \right)$$

where r_i is the inherent growth rate for X_i and a_{ij} is the interaction matrix.

In other words, the change in the population

$\frac{dX_i}{dt}$ of the species X_i is equal to the growth

$r_i X_i$ of this species modified by the interactions

a_{ij} of this species with all other species present in the same ecosystem: $\sum_{j=1}^n a_{ij} X_j$

So for a changing landscape whose dynamics is described by a matrix of nonlinear differential equations, such as:

$$\frac{d\vec{X}}{dt} = \begin{bmatrix} f_1(X_1, X_2, \dots, X_n) \\ f_2(X_1, X_2, \dots, X_n) \\ \dots \\ f_m(X_1, X_2, \dots, X_n) \end{bmatrix}$$

the system's divergence or convergence of orbits (repellers or attractors) is given by its Lyapunov exponents (λ). They are as many as the dimensions of the system's states and each one of them gives the rate of convergence or divergence of nearby orbits to the orbits of the system's dynamics. Hence, Lyapunov exponents constitute the prominent measure of stability. Typically, they are defined as:

$$\lambda = \lim_{\substack{t \rightarrow \infty \\ \Delta X_{0_i} \rightarrow 0}} \frac{1}{t} \ln \left| \frac{\Delta X_i(X_{0_i}, t)}{\Delta X_{0_i}} \right|,$$

where X_i is a variable of the landscape (e.g. species population),

or, alternatively,

$$\lambda = \lim_{N_t \rightarrow \infty} \frac{1}{N} \sum_{n=1}^N \ln \left| \frac{\partial f(X_n)}{\partial X_n} \right|$$

Thus, the Lyapunov exponents are defined from the iterations $n = 1, 2, \dots, N$ and the

derivative $\left| \frac{\partial f(X_n)}{\partial X_n} \right|$ measures the speed of

divergence of nearby orbits of population changes of species X with time.

When the Lyapunov exponents are positive ($\lambda > 0$), the system is unstable and/or chaotic.

It is precisely at this point that certain interesting challenges to these deterministic nonlinear models of landscape complexity begin to surface.

As is known from Complex Systems Theory, the complexity of such landscape-ecological systems could be described by analytic methods, based on "Lyapunov functions". These functions give descriptions of the overall stability regime of a dynamical system

and relate to the "Lyapunov exponents" of the system previously referred to. Consequently, the challenge for landscape analysis is to find attractors in the phase space of the dynamical system (which adequately represents the landscape dynamics) with a (fractal) dimension that would be lower than that of the system considered.

Identifying a low-dimensional attractor from within a deterministic model (such as in the case of the nonlinear differential equations models presented previously) predicts the model's long-term dynamic behavior. This procedure is tantamount to the "shrinking" of the initially hard problem to an easier problem, of lower dimension, and with some easier to describe long-term behavior.

In this respect, it is interesting to notice, that by studying the ecosystem's (and, more generally, the landscape's) dynamics by means of a Lyapunov function, it is possible to derive its long-term (qualitative) dynamics *without* solving numerically the set of equations of the dynamical system [Pykh, 2002]. Although this is theoretically possible, identifying a Lyapunov function for any dynamical system can be a painstaking undertaking, often unsuccessful without some good luck, so we can always attempt to discover Lyapunov functions in order to derive assessments of a landscape's dynamics, but we can not be assured that we will always be able to find them.

CONCLUSIONS

We need to model landscape complexity for both theoretical and practical purposes. Theoretically, we need to be able to model landscape complexity and practically, we need to know whether a landscape is more complex than another and so consider its higher complexity as a potentially additional reason to protect it.

We know that striving to model landscape complexity analytically over the last years has been a particularly difficult undertaking. This study elucidates the causes behind these

difficulties, while, at the same time, pointing to possible directions where future research in landscape complexity might focus on.

From the evaluation of these mathematical models, we notice that we do not know whether there exists a numerical algorithm which could compute *both* structural and functional landscape complexity simultaneously. Hence, the difficulties in modelling the two types of landscape complexity pose limitations to modelling “landscape complexity” in its entirety.

To summarize, by evaluating the methods of landscape complexity modelling, we deduce the following:

a) A universally accepted “library” of computer programs for geographical automata is yet to be created. Ideally, this should be a component of a G.I.S. (geographical information system).

b) Cellular automata describe processes of complex behavior in landscapes, but do not constitute measures of landscape complexity themselves. For this reason, we have to explore other computational approaches in order to measure structural landscape complexity.

c) The development of differential equations models of landscape complexity is an uncomplicated procedure, but it is not always possible to find Lyapunov functions for dynamical systems describing spatial interactions on the landscape.

d) Further, it is not always possible to find an attractor from time series of observations of functional landscape changes (even in the case that we may have temporally dense measurements of landscape and/or species population changes, we may encounter difficulties in finding attractors in our data).

e) A central challenge for future research lies in the achievement of combination of discrete-time and continuous-space data and models.

Until the practical and theoretical aspects of landscape complexity are linked together within an overall theoretical framework of quantitative landscape analysis, we need to refine our models of landscape complexity (structural, functional etc), in ways that will gradually provide us the missing links between the hitherto disjoint disciplines of Landscape Ecology and Complex Systems Theory. ■

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