

# Quantifying the complexity of simulated spatiotemporal population dynamics

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## Abstract

Spatially explicit models in ecology permit the investigation of population dynamics in both space and time. The resultant spatiotemporal dynamics is often irregular and patchy, giving rise to intricate spatial patterns that can be difficult to characterise. Here, the question of how to characterise the spatiotemporal dynamics of simulated populations is addressed and a method of quantifying the complexity of patchy vegetation dynamics is proposed. The method is inspired by information-based measures of complexity and entropy and can distinguish between ordered, disordered (random) and complex (patchy) spatiotemporal mosaics. The method is demonstrated using data generated by the individual-based, multi-species model WIST.

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## 1. Introduction

Spatially explicit models in ecology serve to study not only the temporal variations in population fluctuations, but also a population's variability in space, across different geographical locations. There are many examples where the introduction of a spatial dimension can radically change the predictions of standard, spatially-implicit models of population dynamics, such as the Lotka-Volterra equations and their derivatives, giving rise to co-existence not predicted by non-spatial equivalents and to intricate

spatial patterns of abundance (Solé and Bascompte, 1998; Lundberg et al., 2000). For example, Petrovskii et al. (2004) showed that spatial desynchronisation of population densities serves to decrease global extinction probabilities. Similarly, metapopulation and predator–prey models based on coupled map lattices (Solé and Goodwin, 2000) or coupled diffusion systems (Medvinsky et al., 2002) have generated a gamut of intriguing patterns including spatial chaos and spiral waves that correspond to the synchronous and asynchronous spatial oscillations that have been observed for certain natural populations. Other models, based on individual-based or cellular automata approaches, have also demonstrated the importance of local interactions in space on population

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dynamics (Durrett and Levin, 1994; Kawata and Toquenaga, 1994). In these models, the resulting spatiotemporal dynamics is usually irregular and patchy, corresponding well to many known patterns of vegetation dynamics. Such *patch dynamics* can be depicted by discontinuous mosaics of occupied and unoccupied regions over a landscape, the shapes and locations of which may change over time.

The study of complex spatiotemporal patterns has a long history, dating at least to Turing and his original studies of spatial structure in reaction–diffusion systems (Turing, 1952). In ecology, a large number of models combining a spatial diffusion process coupled to local interaction dynamics (predator–prey, host–parasitoid) have been used to reproduce Turing-like spatial structures (Solé and Bascompte, 1998; Wilson, 2000; Medvinsky et al., 2002). The study of these models has led to examinations of the conditions that give rise to spatiotemporal chaos in these systems, and the development of analytical tools that can be used to characterise the observed spatiotemporal dynamics (Medvinsky et al., 2002). Such tools include statistics-based spatial analyses (for a review, see Dale et al., 2002) as well as spatial versions of the common tests for chaos, such as Lyapunov exponents (Solé and Bascompte, 1995) and the correlation dimension (Petrovskii et al., 2003).

The question that is addressed here is how to quantify, or characterise, the dynamics of patchy spatiotemporal mosaics. Such mosaics may or may not show signatures of chaos. Unlike spatial point data that can be studied as a realization of a Poisson process, mosaics consist of patches that have recognizable shapes and surface areas. It is, therefore, the patch dynamics that becomes the phenomenon of interest and thus spatial statistics based on point processes that reduce data to dimensionless events in space are not applicable (Dale et al., 2002). Similarly, analytical measures such as spatial autocorrelation, Lyapunov exponents and correlation dimensions that treat continuous variables in space are also not applicable. Early ecologists developed methods of characterising spatial mosaics based on comparing the distribution of patch lengths along a transect to the expected distribution for a random mosaic (Pielou, 1969). More recently, the study of patch dynamics has been the object of many studies in landscape ecology, and various authors have used techniques such as

fractal analysis or landscape metrics (O'Neill et al., 1998; Ricotta, 2000; Moser et al., 2002) to describe the complex spatial patterns that occur on a landscape. In all of these cases, the indices describe characteristics of a spatial mosaic, but do not consider a temporal component. Studies of changing landscape patterns involve calculating the indices for images of a landscape taken at several different times in history and then observing how these indices vary over time.

Here, we propose a new measure for characterising patchy, spatiotemporal vegetation dynamics that takes into account the three-dimensional nature of space–time fluctuations. The measure, called spatiotemporal complexity (STC), applies to spatiotemporal data sets in which the state of a two-phase spatial mosaic (example, presence/absence data) has been recorded at regular intervals over time. Spatiotemporal complexity is similar to many information-based measures of complexity and Shannon entropy and can distinguish between ordered, disordered (random) and complex (patchy) spatiotemporal distributions. It also allows for the detection of certain spatiotemporal patterns such as space–time cycles. In this paper, the general characteristics of the measure are demonstrated, followed by an analysis of simulated vegetation dynamics generated by the individual-based, multi-species model WIST (Weather-driven, Individual-based, Spatiotemporal, Terrestrial ecosystem model). While the measure was developed specifically for the treatment of simulated data, it is equally applicable to real ecological systems, where appropriate data exists.

## 2. Measuring complexity

It seems natural to assume that, if an ecosystem is a complex system, any changes in its state (and correspondingly its “health” or “integrity”) will be reflected in established measures of the complexity of the system (where “complexity” is seen as a system attribute capturing one or more aspects of the system’s structure, function or dynamics). How to measure “complexity” however, is an ongoing subject of debate in the complex systems community. One common approach to characterizing complexity is to use information-based measures such as Shannon entropy and its relatives to classify a data set according to its degree of order or randomness (Grassberger,



Fig. 1. Which image is the most complex? Measures of complexity attempt to answer this question, generally differentiating between ordered (a), complex (b) and random (c) mosaics.

1986; Wackerbauer et al., 1994; Gell-Mann and Lloyd, 1996).

It is generally agreed that most complex systems exhibit a dynamics that falls in the intermediate zone between order (complete predictability equivalent to a limit cycle or stable point) and disorder (unpredictability equivalent to randomness or deterministic chaos) (Fig. 1). Any measure of complexity should, therefore, attribute the highest value to those systems whose dynamics falls within these two extremes (Grassberger, 1986; Wackerbauer et al., 1994). A measure such as Shannon entropy is thus most appropriately termed a measure of “regularity”, since it attributes the lowest value to ordered data and the highest value to random data. More recently proposed information-based measures such as effective complexity (Gell-Mann and Lloyd, 1996) or fluctuation complexity (Bates and Shepard, 1993) are better indicators of intermediate degrees of order. Such information-based measures of complexity can be used to analyse symbol sequences (for example, a string of binary bits) for regularities, permitting their classification along a scale from ordered to disordered, attributing the highest value to symbol sequences of intermediate order (those which have a combination of regular and random components) (Fig. 2).

Thus, there exist today two classes of information-based measures of complexity: (1) measures that attribute the highest value to disordered sequences and the lowest value to ordered sequences, and (2) measures that attribute the highest value to sequences of intermediate order. All of these measures apply to symbol strings, usually binary sequences of 1’s and 0’s (although, more generally, they can be applied to sequences of  $n$  symbols, we deal with binary sequences here for simplicity). Thus, in order to apply them to data from a real system, such as a time

series for example, the data must be translated into a binary symbol string of 1’s and 0’s. This is usually done by assigning a value of 0 to any point in the series falling below the median and a value of 1 to any point above the median.

All information-based measures are based on searching for repeated patterns, or “ $L$ -words”, in a symbol string using a moving window of size  $L$  symbols and then counting the relative frequency of occurrence of each  $L$ -word. For example, if  $L = 4$ , we might search for the  $L$ -words: 0000, 0110, 0001, 1011, 1001, etc. For a binary symbol string, the number of possible words ( $N$ ) of length  $L$  that can be made is  $2^L$ . The relative frequency of occurrence of each  $L$ -word in the symbol string is designated as ( $p_{L,i}$ ).

The Shannon entropy,  $H_s$ , of a binary sequence is thus computed as follows:

$$H_s(L) = - \sum_{i=1}^N p_{L,i} \log_2 p_{L,i} \quad (1)$$

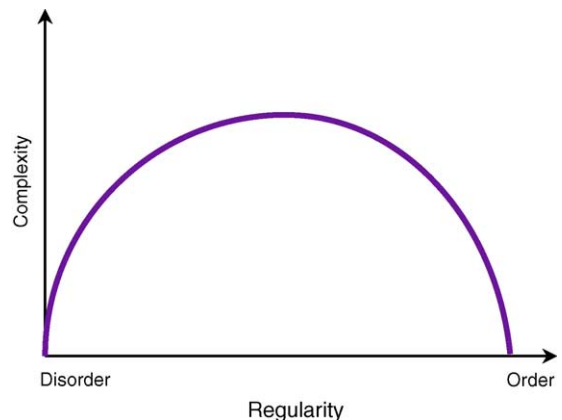


Fig. 2. Overall relationship between measures of complexity and regularity.

where  $p_{L,i} \log_2 p_{L,i} = 0$  for  $p_{L,i} = 0$ . For a random sequence, all words are equally probable (all  $p_{L,i}$  are equal), and the maximum value of  $H_s = \log N$  is obtained. The minimum value,  $H_s = 0$ , occurs when one  $p_{L,i} = 1$  and the others are all zero (maximally ordered string).

In ecology, the concept of Shannon information entropy was first appropriated by MacArthur (1955) to measure species diversity in ecological communities. In this case, rather than counting the frequency of  $L$ -words in a symbol sequence, one counts the relative frequency of individuals of  $N$  species in a community. This application of Shannon entropy to measure ecological diversity has been widely used and debated in the ecological literature (Magurran, 1998). While this measure provides a possible way of measuring the structural complexity of an ecological community, it provides no insight into the complexity of the system's dynamics.

### 3. STC: a measure of spatiotemporal complexity

The various information-based measures of complexity described above can all be applied to the analysis of time series, and in some cases, to spatial or other data (such as species diversity); none applies specifically to spatiotemporal data. Here, a new

measure called spatiotemporal complexity (STC) is proposed, that is inspired by Shannon entropy and other information-based measures, and that can be applied to spatiotemporal data.

To study the spatiotemporal evolution of a system, the proposed measure is applied to a cube of data, such as a stack of successive spatial “images” in raster format (Fig. 3). In other words, the state of a landscape (or some other spatial entity) is recorded at uniform time intervals, and then each spatial image is placed in a stack, such that the vertical axis is equivalent to time. The result is thus a cube of dimensions  $N_l \times N_w \times t$  cells, where  $N_l$  and  $N_w$  are the length and width of the landscape and  $t$  is the number of time slices. Each image must be in binary format (i.e., a matrix of 1's and 0's). For example, a 1 could be placed in each cell in which a particular landscape feature (e.g., a plant species) is present, and zeros placed in all other cells. Other alternative methods could also be used to categorize the data.

The measure is then calculated by studying the contents of successively offset, overlapping 3D windows (of dimension  $n \times n \times n$  cells, where  $n$  is an arbitrary length that is considerably smaller than the landscape dimensions,  $n \ll N_l, N_w$ ) in the data cube (Fig. 3). For each possible placement of the 3D window in the data cube the number of occupied (non-zero) cells ( $M$ ) is counted. For all of the different

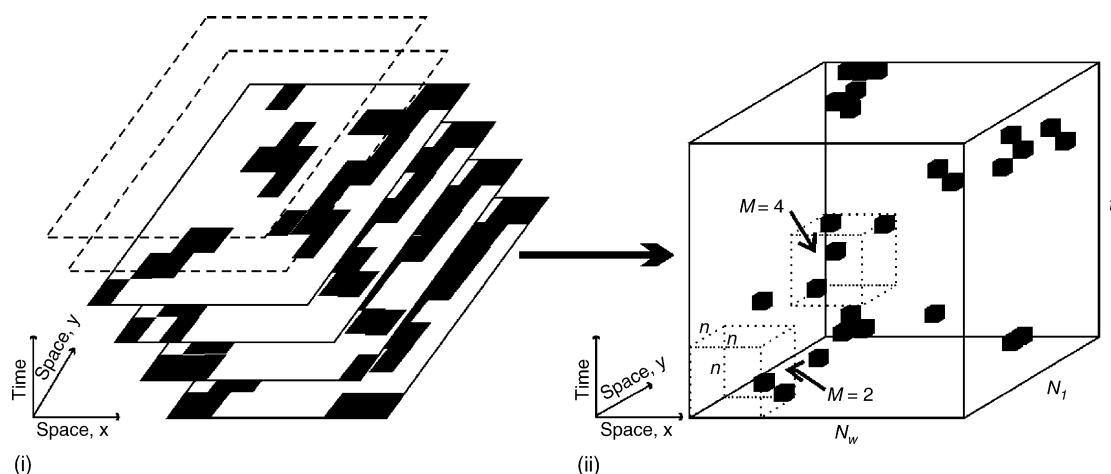


Fig. 3. Illustration of how spatiotemporal complexity is calculated. A series of raster-based spatial data (i) is compiled to create a single 3D data matrix (ii) that is subsequently sampled by an  $n \times n \times n$  moving window. See text for definitions of symbols.

possible occupation levels,  $M_i \in \{0, \dots, n^3\}$ , the relative frequency of occurrence is computed and the spatiotemporal complexity of the cube is calculated as follows:

$$\text{STC} = \frac{-\sum_{i=0}^{n^3} p_i \ln p_i}{\ln(n^3 + 1)}, \quad 0 < \text{STC} < 1 \quad (2)$$

where STC is the spatiotemporal complexity,  $p_i$  the relative frequency of  $M_i$ ,  $n$  the size of 3D window.

Division by  $\ln(n^3 + 1)$  serves to normalise the measure. The value of STC ranges from 0 for the completely ordered case where only one occupation level is observed (equivalent to a cube of solid zeros or ones) to 1 for the most complex case (equivalent to observing all occupation levels with equal frequency). Unlike the Shannon entropy for temporal series, the random case does not receive the highest value of STC, since, for a cube of randomly distributed 1's and 0's, the average occupation of a given 3D window is  $(n^3 + 1)/2$  and unoccupied or fully occupied 3D windows are very unlikely. Thus, for completely random spatiotemporal data, the distribution of

relative occupation frequencies is normal, giving rise to intermediate values of STC. At the other extreme, a very “clumpy” mosaic, with large-sized regularly shaped patches would have high frequencies of fully occupied or completely empty 3D windows and few intermediate cases. This type of distribution would tend to have lower values of STC, being closer to the completely ordered case. The highest values of STC correspond therefore to very “complex” spatiotemporal patterns that consist of irregular evolving patches of various sizes. For this type of spatiotemporal dynamics, all occupation levels of the 3D windows are likely and the frequency distribution is more uniform.

#### 4. Characterising the spatiotemporal complexity of simulated vegetation dynamics

To explore the potential of STC in characterising ecological dynamics, it was applied to simulated vegetation patterns generated with the model WIST

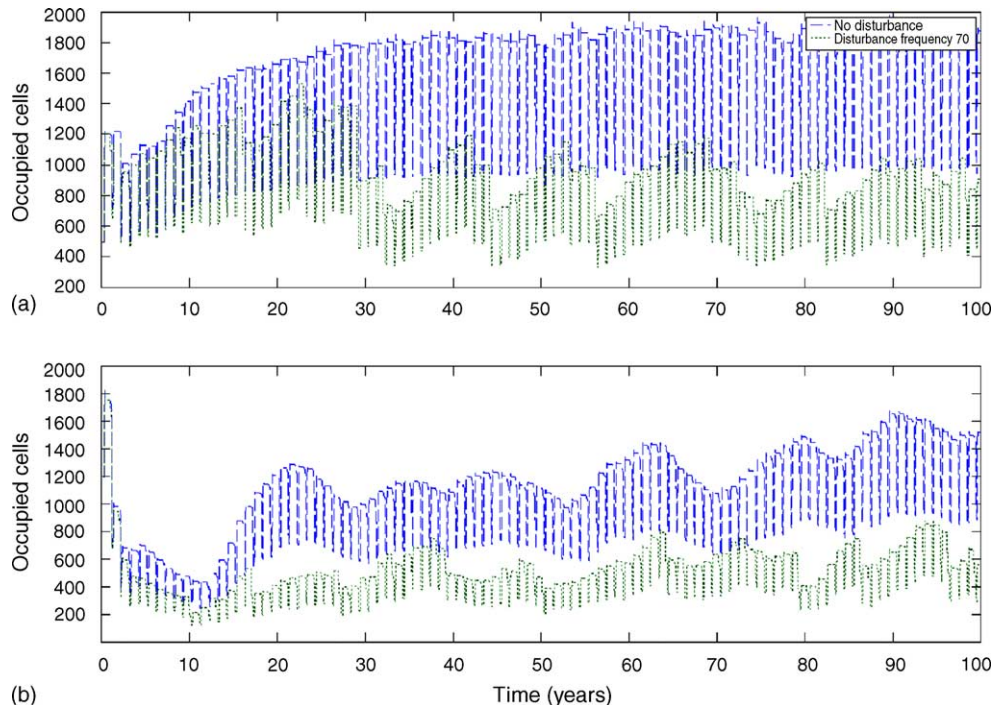


Fig. 4. Temporal population dynamics, measured as number of occupied terrain cells vs. time, of the studied grass species for the prairie (a) and herbivore (b) scenarios, with 0 and 70% disturbance frequency.



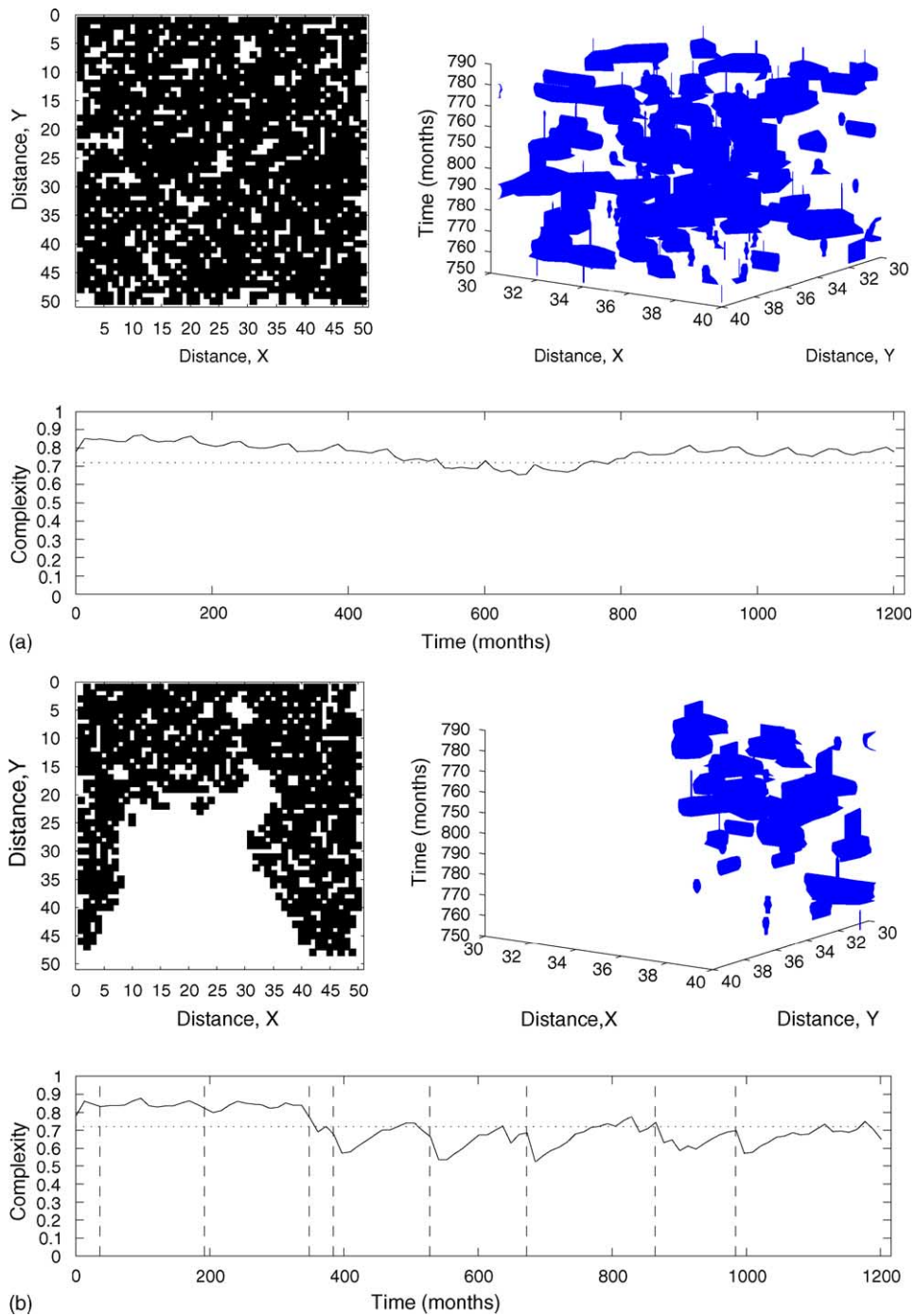


Fig. 5. Spatiotemporal dynamics of the studied grass species in the prairie scenario: (a) zero disturbance and (b) 70% disturbance. Top left panels: sample spatial mosaic for  $t = 800$ ; grass is present in the coloured cells. Top right panels: subset of the 3D data set for one part of the terrain between months 750 and 800. Dark “blobs” are patches of grass occupying both space and time. Bottom panels: STC ( $n = 3$ ) calculated over a 12-month moving window for the entire data set. Dotted horizontal line marks the value of STC for an equivalent stack of random images. Vertical lines mark significant disturbance events.

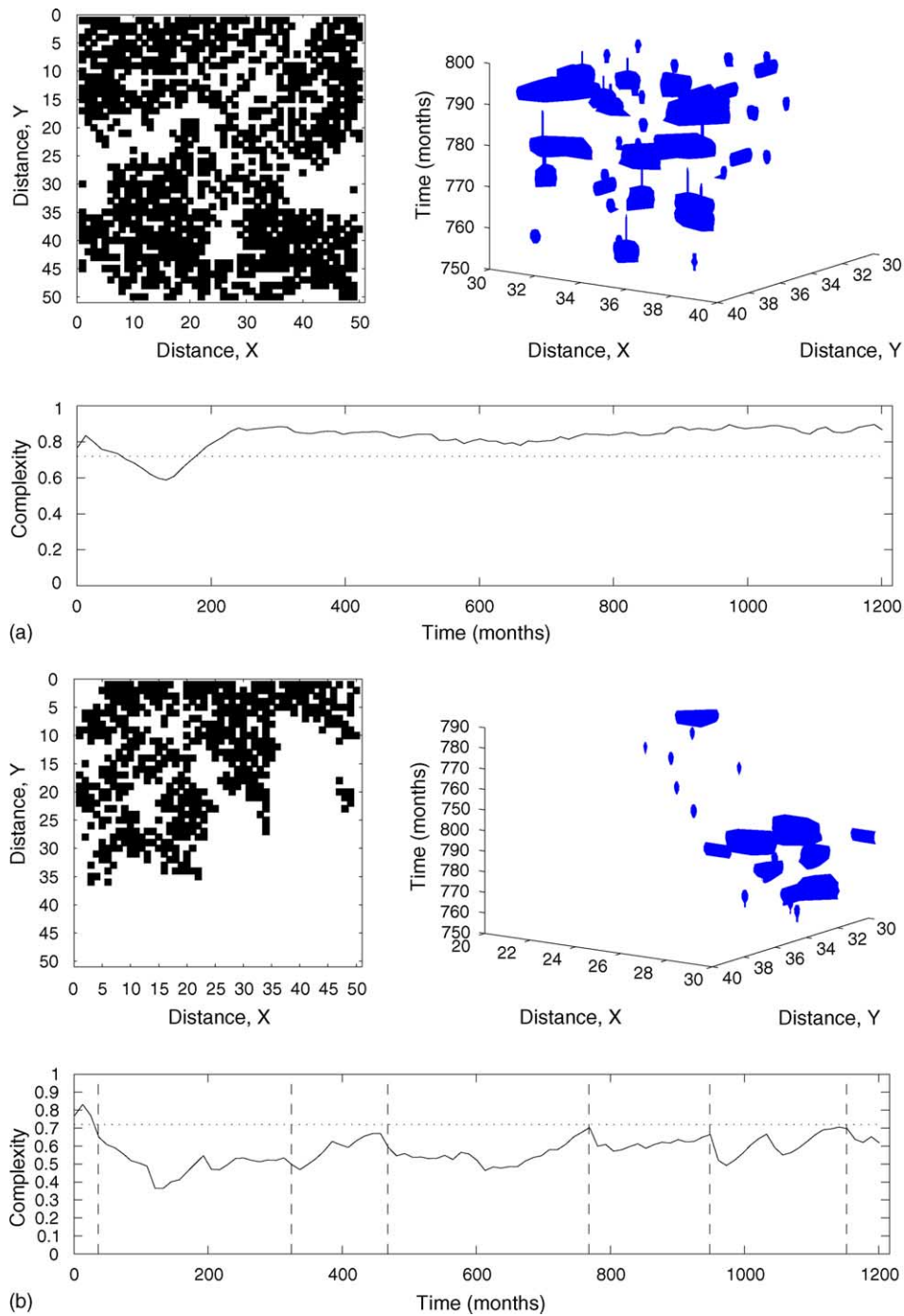


Fig. 6. Spatiotemporal dynamics of the studied grass species in the herbivore scenario: (a) zero disturbance and (b) 70% disturbance. Top left panels: sample spatial mosaic for  $t = 800$ ; grass is present in the coloured cells. Top right panels: subset of the 3D data set for one part of the terrain between months 750 and 800. Dark “blobs” are patches of grass occupying both space and time. Bottom panels: STC ( $n = 3$ ) calculated over a 12-month moving window for the entire data set. Dotted horizontal line marks the value of STC for an equivalent stack of random images. Vertical lines mark significant disturbance events.

(Parrott and Kok, 2001, 2002). WIST is a generally configurable, individual-based ecosystem model that includes both plant and animal species. Here, we explore the spatiotemporal dynamics of one specific herbaceous species in two different model scenarios subject to different degrees of perturbation. The overall dynamics of the simulations studied here, as well as more detailed descriptions of the scenarios, are given in Parrott (2004).

The species studied is a perennial grass. We explore its pattern of presence/absence recorded at monthly intervals for a period of 100 years on a grid of  $50 \times 50$  cells that represent a simulated terrain. This is done for two different scenarios: the first is a “prairie” ecosystem, in which the grass competes with several other grasses and forbs for light, water and nutrients and the second is a “herbivore” ecosystem, which is identical to the prairie scenario except that three small herbivorous species that eat the studied grass are present. In both scenarios, there is a possibility of introduced disturbances, which consist of randomly occurring “mowing” events in which all of the vegetation on selected areas of the terrain is removed.

The temporal population dynamics of the grass species for the two scenarios, subject to 0 and 70% disturbance frequencies are shown in Fig. 4. A 70% disturbance frequency means that, on average, there should be 70 disturbance events in 100 years. The temporal dynamics show clear yearly cycles, population crashes and then re-growth due to disturbances, and, for the herbivore scenario, longer-term cycles due to an emergent predator–prey dynamics (Parrott, 2004). Analysis of the spatiotemporal dynamics of these same scenarios, represented by stacks of 1200 spatial images containing presence/absence data, is shown in Figs. 5 and 6. In both scenarios, the spatiotemporal dynamics of the grass is irregular, characterized by patches of various sizes that form, expand and disappear over time. In the data cubes, such patches form irregular 3D clumps (see top right panels in Figs. 5 and 6). Evidently, the more disturbed systems have a lower density of grass in both space and time.

The STC for the prairie scenario is 0.80 and 0.74 for 0 and 70% disturbance, respectively. The STC for the herbivore scenario is 0.85 and 0.59 for 0 and 70% disturbance, respectively. In both cases, STC was calculated for cubes of dimension  $50 \times 50 \times 1200$

using  $n = 3$ . The corresponding value of STC for a randomly filled cube of 1's and 0's having the same dimensions is 0.71. The calculated values for the two grass scenarios show, therefore, that its spatiotemporal dynamics is typically more complex than the random case. The herbivore scenario with 70% disturbance is an exception, with  $STC = 0.59$ . This lower value reflects the significant fragmentation of the grass when subject to pressure by both grazing and external perturbation. In the non-disturbed cases, the herbivore scenario has a slightly higher value of STC than the prairie scenario, which is not unexpected, since grazing introduces a more pronounced spatial heterogeneity than just competition alone.

Also shown for each scenario in Figs. 5 and 6 is the STC history, calculated using a moving window of 12 months, which allows for a study of how the value varies over time as the landscape evolves. It is this time history that is the most informative. Firstly, it enables the detection of spatiotemporal cycles, such as that which appears for the undisturbed prairie scenario (Fig. 5(a)). Here, the STC history clearly shows the presence of a 5–6-year cycle in the spatiotemporal vegetation dynamics. This cycle is not readily evident in the population time series (Fig. 4(a), dashed line), meaning that the spatial displacement of the grass is cycling while total population numbers remain relatively constant. This cycle, which seems to represent a natural part of the grass's dynamics, is not present in the disturbed systems, nor in the herbivore scenario where the grass is subject to pressure by grazing. Secondly, for both scenarios, STC decreases significantly with disturbance events and then increases as the system recovers. This shows STC to be a clear and sensitive indicator of landscape fragmentation, one of the most common forms of ecological disturbance.

## 5. Discussion and conclusion

The significant quantity of data arising from large ecosystem models and from remote sensing studies necessitates the development of new analytical methods that allow for rapid filtering and treatment of information. While at a different magnitude, this is exactly the challenge that was faced by early theoreticians who developed the first information-



based measures of complexity in search of pattern detectors for decoding incoming binary messages. The measure presented here, inspired by this early work, applies an information-based complexity measure to the analysis of spatiotemporal data on vegetation change.

In ecology, and especially landscape ecology, the problem of quantifying the complex patterns that we observe in space and time is intricately linked to an improved understanding of relations between pattern, process and disturbance. The measure of spatiotemporal complexity presented here helps to quantify a certain aspect of spatiotemporal patterns, serving as a kind of indicator of the complexity of patch dynamics, whether on a landscape or a smaller scale. Applied to three-dimensional data, the measure also contributes a new dimension to the analysis of spatial mosaics: While there exist a myriad of different landscape metrics that can be used to describe patchiness or geometrical complexity, such metrics do not apply directly to spatiotemporal data. This measure is thus a contribution to the growing toolbox of methods for the detection of space–time patterns and clustering, which typically apply to point data (Gatrell et al., 1996; Rogerson, 2001) or involve the analysis of correlations between time series recorded at different spatial locations (Bjørnstad et al., 1999).

STC was developed specifically to deal with the characterization problem related to spatiotemporal vegetation data. It can, however, be calculated for any cube of binary data and its application is thus not restricted to this limited example. In addition, while simulated data has been used here, the method may be readily applied to real data such as time series of satellite images. Since it is based in the context of information-based measures of complexity, STC has the limitation that it applies only to binary, presence/absence data. More subtle information regarding changes in vegetation density or abundance is thus not reflected in the measure. STC is thus a good indicator of overall patch dynamics, but not of more continuous spatial processes.

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