Three-dimensional metrics for the analysis of spatiotemporal data in ecology

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Abstract

A suite of simple metrics that can be used to analyse three-dimensional data sets is presented. We show how these metrics can be applied to raster-based, ecological mosaics sampled over uniform time intervals, such as might be obtained from a series of photographs or from repeated spatial sampling in the field. In these analyses, the concept of a 2D landscape "patch" is replaced by a 3D space-time "blob". The structure of a dataset can be analysed via the characterisation of blobs, using a number of simple composition and configuration metrics. The use of different metrics, including modified versions of some common landscape metrics such as contagion, that describe the distribution of blobs in space and time, is demonstrated using both model and empirical data. With the increasing availability of spatiotemporal data sets in ecology, such three-dimensional metrics may be indispensable tools for the detection and characterization of landscape change in the context of human and naturally caused disturbances.

Keywords: spatiotemporal analysis, ecological dynamics, landscape metrics, complexity, heterogeneity, spatially-explicit models, landscape ecology, remote sensing, patch dynamics

Introduction

With the advent of increasingly sophisticated grid-based ecological monitoring techniques, combined with the growing use of spatiotemporal models, ecologists now have at their disposal considerable amounts of data describing the evolution of ecological variables in both space and time. In landscape ecology and earth systems science, for example, the availability of several decades of remote sensing images means that the study of landscape change over time is a common practice (Kienast et al., 2007). Similarly, spatially explicit ecosystem models generate reams of data describing the evolution of variables on simulated landscapes (see examples in Bascompte and Solé, 1998). At the ecosystem scale, modern sampling programs often involve the automated measurement of specific variables at several spatial locations at fixed intervals over a period of time (Baldocchi et al., 2001; Collins et al., 2006). The availability of such data, combined with appropriate quantitative methods, should make it possible to study the inherently spatiotemporal nature of ecological dynamics.

Here, we present some simple metrics that can be applied to the characterisation of the complex spatiotemporal dynamics of ecological mosaics (categorical maps). These metrics apply to 3-dimensional datasets (e.g., a time series of spatial images), allowing for the characterisation of volumetric entities (having 2 spatial dimensions and 1 temporal dimension) that we call “blobs”. The behaviour of these different metrics is demonstrated for both model and empirical data. We propose that blob analysis via 3D metrics permits an integrated method of characterising the spatiotemporal nature of ecological dynamics from the local to landscape scale.

Spatiotemporal analysis in ecology

Effective monitoring and characterisation of ecological dynamics necessitates a truly spatiotemporal approach. Current methods of analysis in ecology are still largely centred on spatial or temporal analysis, but few address both space and time concurrently (Fortin and Dale, 2005; Bolliger et al., 2007). For example, indices of spatial heterogeneity do not include temporal variation (Gustafson, 1998; Fortin and Dale, 2005) and methods of time series analysis typically do not include a spatial component. Even when both spatial and temporal information is available, via remote sensing images for example, the analysis is typically done in space, and then repeated for images taken at different moments in time, resulting in a time series showing the temporal evolution of a spatial indicator. This approach is often taken to assess land cover change over time via the analysis of a series of remote sensing images (see for example, Hayes et al., 2002, Dunn et al., 1991). Similarly, Tobin (2004) studied space-time correlation in population data by calculating spatial autocorrelation in the data and then studying how this spatial correlation varied in time. Other methods involve the analysis of the temporal variation of specific points in space, and then compare this variation for different study sites (Liebhold et al., 2004). For example, most time-series analyses of species abundances for a community are the result of a two-step process. An estimate of species abundances is first obtained across space (e.g., using central tendency estimators such as the arithmetic mean), and then the trajectory in time is characterized. It is well recognized in landscape ecology that such a spatial ‘averaging’ process may generate scale artefacts (Jelinski and Wu, 1996; Rahbek, 2005). For this reason, there is a need for truly spatiotemporal methods of analysis that do not ‘collapse’ spatial or temporal dimensions.

While some recent statistical methods do allow for the detection of space-time patterns and clustering, they typically apply to irregularly sampled point data (Gatrell et al., 1996; Rogerson, 2006) or involve the analysis of correlations between time series recorded at different spatial locations (Bjørnstad et al., 1999). This method allows for a study of spatial autocorrelation of variation through time. It has been used to detect spatial synchrony in population dynamics and can also characterise more complex dynamics such as spiral waves when time-lagged spatial correlation is used (Liebhold et al., 2004). A few truly spatiotemporal methods of data analysis exist. For example, the join count has been used to quantify pairs of observations in time and space for transect data (1 spatial dimension) (Fortin and Dale, 2005). Wilson and Keeling (2000) present a method of reducing spatiotemporal data from grid-based models to lower dimensional vectors that can be used to characterize the structure of patterns observed. Recent work in geo-visualisation addresses the problem of describing and characterising higher dimensional space-time data, and methods such as the three-dimensional Fourier transform have recently been applied to detect space-time periodicities (Dykes and Mountain, 2003; Edsall et al., 2000). The variogram and covariance matrix, typically used to measure roughness in spatial data, may also be applied in three dimensions (Isaaks and Srivastana, 1989; Porcua et al., 2007). Lastly, Griffith's space-time index (Griffith, 1981; Fortin and Dale, 2005) extends the notion of spatial autocorrelation to a temporal dimension using weights that include space and time in the calculation of distances between observations.

While the above methods are typically applied to continuous valued variables, many are flexible enough to incorporate both continuous and categorical variables, as well as regular or irregular grids. However, these methods are typically based on linear mathematical models, assuming stationarity in time. Such models may fail to capture the complex spatio-temporal dynamics of ecological data. Secondly, these methods generally provide information about the scale or frequency of ecological processes (e.g., space-time variograms and correlograms), but not on the 'complexity' or 'heterogeneity' of the process per se. They can be considered as complementary to the metrics presented here, and to the collection of metrics developed by landscape ecologists to characterize the patterns present in ecological mosaics.

An ecological mosaic is a raster-based grid of categorical values describing the distribution of a specific ecological variable in space. The idea of ecological mosaics was first presented by Pielou (1969), who proposed a number of effective ways of analysing spatially-structured categorical data. Spatial mosaics are at the basis of most analyses in landscape ecology, which typically apply to raster data from remote sensing (Forman, 1995). Landscape ecologists have developed an entire suite of landscape metrics, designed to describe the composition and configuration of "patches" on a landscape, where a patch is defined as a contiguous region of cells (or pixels) containing the same categorical value (Gustafson, 1998; Turner et al., 2001). Patches may form part of a mosaic of patch types, or else a single patch type on a background matrix may be studied. In landscape ecology, researchers describe and characterise landscape change via the analysis of how key landscape metrics change from one moment in time to another (e.g., via the analysis of a historical series of satellite images or aerial photographs). The study of ecological mosaics has recently come to the forefront in other areas of ecology as well, with Murphy and Lovett (2004) calling for the use of mosaics for sampling in ecology as a means of better understanding metapopulation dynamics.

Here we present a suite of simple metrics that can be used to characterize the spatiotemporal dynamics of n-phase spatial mosaics. The metrics explicitly consider a temporal dimension in the analysis of spatial data. They are all extensions of common landscape metrics and information-based measures such as diversity, contagion and fractal dimension. While our examples are limited to specific ecological situations, these metrics can easily be applied in any field where three-dimensional data exist (e.g., measurements of a system involving at least 3 variables).

Methods

Our analyses are applied to space-time cubes[1] of data, having two spatial dimensions (*x,y*) and a third time (*t*) dimension. Thus, a space-time cube is simply a stack of successive spatial "images" in raster format that capture the state of a landscape or other spatial environment, sampled at uniform time intervals. The variable measured will typically be semi-qualitative or quantitative, and be divided into categories. Each spatial image is a grid of cells (also called 'pixels'), each of which has an associated value, corresponding to a type or category (Figure 1a). When we add the temporal dimension, a spatial pixel becomes a 3-dimensional 'voxel' having two spatial dimensions and a temporal dimension, the depth of which is equal to the sampling interval in time (Figure1b).

In the space-time cube, persistent entities in the dataset take on 3-dimensional forms composed of voxels that are adjacent in space-time. We call these 3-dimensional forms "blobs" and all of our analyses treat the characteristics of blobs in the space-time cube (Figure 1c). For example, a spatial patch (defined as a contiguous area of pixels) whose area remains constant over time will form a blob in space-time that has a columnar shape, whereas a patch that changes shape over time will form a blob having a much more complex form in space-time. This manner of representing space-time is similar to that used by geographers working with spatiotemporal data in GIS software (Peuquet, 2001) although most inquiries in time geography deal with trajectories (lines) in a space-time cube and not volumes composed of voxels. Exceptions include Forer (1998) who coined the term 'taxel' to describe a 3-dimensional entity in space-time in the context of studying the evolution of human constructs in urban landscapes and Morris et al. (2000) who developed a 3D visualisation system for GIS in which 2-D spatial entities have a third temporal dimension.

<u>Blob analysis: 3D Composition metrics</u>

Space-time density, number of blobs, distribution frequency and blob shape complexity

As for patches on a landscape, we can specify categories corresponding to different blob types. In a space-time cube of dimensions N_x, N_y, N_t voxels, each voxel thus belongs to one of *b* blob types, and adjacent voxels of the same type form a single blob. We consider a distinct blob to be a contiguous volume of identical voxels, where adjacency can be defined according to a 26-cell "Moore" neighbourhood or a 6-voxel "vonNeuman" neighbourhood. In the former, two voxels sharing a face, an edge or a point are considered to be neighbours, in the latter, only voxels sharing faces are considered to be neighbours. The volume of a blob is the sum of the number of voxels it occupies. Its surface area is defined as the number of faces not shared by an adjacent voxels of the same blob type. Similarly, we can define the bounding box as being the smallest hexahedron that can contain the blob.

Traditional composition metrics for landscape patches (area, perimeter, deviation from the mean, etc.) may thus be calculated for blobs. Composition metrics provide information about the constitution of the space-time cube. For each blob, a number of characteristics such as its type, volume, surface area, bounding box, centre of mass, etc. can be calculated. Similarly, we can also calculate a number of statistics describing the collection of blobs in the space-time cube, including: average and standard deviations of blob sizes (volumes), the frequency distribution of blob sizes (volumes), the space-time density (number of voxels occupied by a blob type divided by the total volume of the space-time cube), total edge (surface), etc. Shannon diversity metrics for the *b* blob types (weighted by blob

[1] The word "cube" is used here for simplicity although the space-time cubes are, in fact, hexahedrons since the 6 faces are not necessarily square (i.e., $N_x \neq N_y \neq N_t$).

volumes) can also be used to describe the composition of a space-time cube. A dataset with more complicated spatiotemporal dynamics may have more blob types, a higher standard deviation of blob sizes, a higher ratio of surface area to volume (i.e., complex blob shapes) or an uneven frequency distribution of blob sizes, for example.

To describe the complexity of blob shapes we use the ratio of blob volume to bounding box volume (we call this ratio the 'shape complexity'). The value equals 1 for simple rectangular objects and tends to 0 for objects that have a volume much smaller than the volume of their bounding box. This ratio gives a rough measure of the form of a blob, with more complex shapes tending to have lower values. We note that the ratio is much too simplistic to be a satisfactory measure of blob shape complexity, since it is subject to many exceptions (e.g., a spatiotemporal line going diagonally from one corner of a rectangle to another will have a ratio close to zero). The ratio does, however, give a rough idea of the volume occupied by a blob and thus of it's respective form.

Fractal dimension

The fractal dimension is a measure commonly used to describe the degree to which an object occupies its topological volume. It is commonly used in landscape ecology to describe the complexity of landscape patterns (Milne, 1991) and has been used in soil science and other fields to describe the complexity of 3-dimensional objects such as soil pore structure (Perret, 2003). An object's fractal dimension approaches its topological dimension (e.g. 2 for a surface or 3 for a volume) for very smooth objects. Irregular objects tend to have fractional fractal dimensions, indicating that they have complex, possibly self-similar, shapes. There are many ways to estimate the fractal dimension of an object. Here, we use the box-counting algorithm (Peitgen et al., 1992), which is one of the most common methods. The algorithm counts the number (N) of 3 dimensional boxes of length (L) needed to cover the non-zero elements of the data cube. For a fractal object, N scales as a function of L^d, where d is the fractal dimension.

<u>Blob analysis: 3D Configuration metrics</u>

Similar to 2D landscape configuration metrics, 3D configuration metrics describe how the blobs are distributed in space-time, taking into consideration adjacencies between cells of different blob types. These metrics can be used to compare the observed spatiotemporal distributions to random patterns. As is done for spatial patterns, a frequency table of blob adjacencies can serve to describe the complexity of the space-time pattern. More complex metrics may build upon the adjacency table. Here, we present and test two configuration metrics: contagion and spatiotemporal complexity.

Contagion

Contagion (O'Neill et al., 1988; Li and Reynolds, 1993; Ritters et al., 1996) is a measure that was originally developed for the analysis of landscape patches and is typically used to measure the dispersion or "clumpiness" of different patch types. Contagion compares the expected frequency with which two patch types should be adjacent for a random case with the actual frequency observed on a landscape. Here, we extend Li and Reynolds's (Li and Reynolds, 1993) formulas for contagion to three dimensions in order to measure the space-time dispersion of blob types. The metric is based on a calculation of the probability of finding a voxel of blob type i next to a voxel of blob type j. Note that the calculation is based on voxel (not blob) adjacencies. The value of contagion ranges from 0 to 1. Space-time cubes full of large, contiguous blobs give rise to high values of contagion, whereas a completely random mix of cell types gives rise to 0 contagion. Thus, high contagion corresponds to a fairly contiguous landscape that does not change substantially in time. The calculation for *b* blob types is as follows:

$RC = 1 - EE / EE_{max}$

where:

RC = contagion, as proposed by Li and Reynolds (1993);

$EE_{max} = b \ln(b)$

$$EE = -\sum_{i=1}^{b}\sum_{j=1}^{b} p_{ij} \ln\left(p_{ij}\right)$$

$$p_{ij} = n_{ij} / n_i$$

n_{ij} = number of adjacencies between voxels of blob type *j* and voxels of blob type *i*

n_i = number of voxels of type *i*

Spatiotemporal complexity (STC)

Spatiotemporal complexity measures how one type of blob occupies the 3-dimensional space, i.e, how the spatiotemporal landscape is *structured*. This measure was developed specifically for the analysis of space-time data. It was first introduced and demonstrated using data from an individual-based model in Parrott (2005). The metric applies only to 2-phase mosaics (i.e., space-time cubes with 2 blob types, or one type in a background matrix). More varied data must, therefore, be binarized before analysis. This can be done by selecting the mean (or some other pertinent) value and setting all values below the mean to blob type *i* and all that are above to blob type *j*. Alternatively, the analysis can be done for one particular blob type, considering all others to be the background matrix.

Spatiotemporal complexity is calculated by looking at the contents of successively offset 3D windows (of dimension *n* x *n* x *n*, where *n* is an arbitrary length that is considerably smaller than the data cube dimensions) in the space-time cube. For each possible placement of the 3D window in the cube the number of voxels occupied by blob type *i* is counted. The measure is based on observed frequencies of the different possible occupation levels, $M_k \in \{0 \ldots n^3\}$:

$$STC = \frac{-\sum_{i=0}^{n^3} p_k \ln p_k}{\ln(n^3 + 1)} \qquad 0 < STC < 1$$

where:

STC = spatiotemporal complexity

P_k = relative frequency of M_k

Division by $\ln(n^3+1)$ serves to normalise the measure. The value of STC ranges from 0 for the completely ordered case (equivalent to a space-time cube of solid zeros or ones) to 1 for the most complex case (equivalent to observing all occupation levels with equal frequency; i.e., a space-time cube containing both sparse and clumpy regions).

Data sets

To explore the behaviour of the different 3D metrics, a series of analyses was performed on six model data sets and one empirical data set. For the purposes of this demonstration, we treat only 2-phase spatial mosaics (2 blob types; equivalent to one type in a background matrix), although for some of the studied data sets, we could have included more categories.

Each modelled data set consists of a time series of 1000 successive images of approximately 100 x 100 cells. The first two sets are simply cubes of uniformly distributed random numbers. In the first set (*Random*), we assign all values < 0.5 to blob type 1 and all values ≥ 0.5 to blob type 2. In the second set (*Random30*), values < 0.3 are set to blob type 1 and all other values are blob type 2. The third set (*Column*) contains a single square column composed of blob type 1 voxels in the centre of the data cube. The fourth set (*Spread*) contains an inverted pyramid in the data cube, imitating the successive spread of a square patch of blob type 1 voxels. The fifth set (*Lotka-Volterra*) was generated using Wilson's (2000) spatial reaction-diffusion model of Lotka-Volterra dynamics. Voxels containing prey are assigned blob type 1 and all other voxels are assigned blob type 2. Lastly, the final set (*Host-Parasite*) contains spatiotemporal data from Hassell's host-parasite model (Hassell et al., 1991), which is known to generate a form of spatiotemporal chaos characterised by spiralling waves under some parameter values (here we used $\mu_N = \mu_P = 0.8$). Voxels containing the host are set to blob type 1 and all other voxels are set to blob type 2. Figure 2 shows sample images (2D slices) for each of the model data sets. To provide the reader with an idea of what this quantity of data looks like in three dimensions, a visualisation of the entire space-time cube of the Lotka-Volterra data is provided in Figure 3.

The empirical data set consists of a series of 100 photographs that capture the understory light variability in a Quebec hardwood forest during the spring budburst. The photographs were taken at the exact same location at 30-minute intervals over a period of 5 days from 8h00 to 17h30. The photographs were taken with a digital camera and were subsequently processed to produce low resolution, greyscale images (Figure 4). The images were then binarised (white and black) using a cut-off of 0.4. All of our analyses were done on the black voxels. Further details of the dataset and photographic setup are given in Proulx and Parrott (2008).

Results

For each data set, we calculated blob metrics for blob type 1, including: blob volume and shape characteristics and frequency distributions, density, fractal dimension, contagion and spatiotemporal complexity. For the purposes of demonstration, we calculated only a limited number of composition metrics for our datasets, selecting those that are non-trivial for 2-phase mosaics. Results of the calculations for the selected composition and configuration metrics are given in Table 1. Distributions showing the frequency of blob volumes are given in Figure 5.

<u>Composition metrics</u>

Space-time density, number of blobs, distribution frequency and blob shape complexity

A study of the space-time density of each data set compared to the number of blobs present, gives important initial information about the composition of the data cube. Four data sets (*Random30*, *Column*, *Spread* and *Lotka-Volterra*) all have a density of 30, but have very different numbers of blobs, indicating very different spatiotemporal patterns. The two sets containing only 1 blob (*Column* and *Spread*) can be differentiated by studying their shape complexity measures, through which we learn that the *Column* data set contains a single rectangular object (shape complexity = 1). The spiralling waves in the host-parasite model give rise to large contiguous areas in the *Host-Parasite* data set, explaining the low number of blobs. From the low blob shape complexity, we see that these blobs must have a fairly sparse form. The *Random30* and *Lotka-Volterra* data sets both contain very large numbers of blobs and have similar frequency distributions of blob sizes (Figure 5), with the important exception that the *Lotka-Volterra* data set has a fat-tailed distribution (as evidenced by the presence of low frequency, high volume blob(s), the presence of which is highly improbable for random data). A study of the frequency distributions of blob volumes is important for distinguishing random and complex data sets: while all but the *Host-Parasite* data sets appear to have power law distributions of blob volumes, those that have more complex spatiotemporal distributions (*Lotka-Volterra* and *Forest*) gives rise to distributions with fat tails (Figure 5).

Fractal dimension

The fractal dimension of each data set was estimated using the box counting algorithm. A graph of ln(N) versus ln(L) was generated and *d* was estimated as the slope of the best fit line through the points. The *Forest* data set was the only data set that was truly fractal, for which $N \alpha L^d$ over all scales. The other data sets, several of which are clearly not fractal, showed scaling relationships over limited ranges of L and the value of d was estimated for this range. All of these sets have $d \approx 3$, indicating that their dimensions are close to the topological dimension of 3.

Configuration metrics

Contagion

The contagion measure was calculated for all of the data sets using both von Neumann and Moore neighbourhood (6- and 26-neighbourhood sizes respectively). Contagion responds in a predictable fashion, giving a value of zero for the *Random* data set and the highest value to *Spread*. It is thus useful for characterising the degree of dispersion in a data set. Contagion is, however, sensitive to the density of the data set (giving a non-zero value to *Random30*) and to the neighbourhood type. The measure is also not able to differentiate the *Lotka-Volterra* dynamics (contagion = 0.15) from random space-time dynamics having the same blob density (*Random30*, contagion = 0.12).

Spatiotemporal complexity

The spatiotemporal complexity was calculated for each data set using a moving window size of 3x3x3 cells. The choice of window size was arbitrary (although see discussion below). STC is much more effective than contagion at describing the complexity of the spatiotemporal pattern. It clearly differentiates between uniform blob shapes (*Column* and *Spread* both have low STC values), random patterns (both random data sets have STC values around 0.7) and complex patterns (the *Lotka-Volterra*, *Host-Parasite* and *Forest* data sets all have high values (>0.9) of STC). It is also capable of distinguishing between the 4 data sets that all have a density of about 0.3 but which have different spatiotemporal patterns. This measure is thus highly recommended for characterising the complexity of spatiotemporal data.

Discussion

None of the metrics presented here can completely characterize a dataset. Each captures different aspects of how the blobs are distributed in space-time. Appropriate use of these metrics requires knowledge of what each one represents, and a combination of metrics is required to describe the overall spatiotemporal dynamics. An informed analysis using a suite of 3D metrics to compare data sets will, therefore, distinguish between different types and distributions of data. In general, the most complex data sets (*Lotka-Volterra* and *Forest*) had fat-tail power law distributions of blob volumes (indicating a scale-free structure in space-time) and high values of STC. Simple data sets, consisting of a single solid object (*Column* or *Spread*) had high values of contagion and low STC. It is interesting to note that the natural dataset (*Forest*) is the only example that exhibits a scale-free structure both in the calculation of the fractal dimension via box-counting and in the distribution of blob volumes. It also has the highest value of spatiotemporal complexity (STC=0.96). All of these indicators suggest that the natural dataset probably has the highest degree of complexity.

We note also that the analyses presented here were limited to 2-phase mosaics for reasons of simplicity, however all of the metrics (except for STC) are applicable to n-phases. The study of n-phase data (where $n>2$) opens up much richer possibilities for the characterisation of spatiotemporal dynamics and may enable the comparison of the dynamics of different categories of blobs on the same landscape.

<u>Neighbourhood effects, extent and grain of the dataset</u>

Like 2D landscape metrics, the values of the 3D metrics presented here will also be affected by neighbourhood and edge effects as well as by the extent and grain (resolution or size of the smallest sampling unit) of the dataset. We note that although the choice of neighbourhood affected the number of blobs identified in our datasets, it did not have a large effect on the values of the other metrics. It is well known, however, that the size of the sampling unit as well as the extent of the data set will change a number of attributes of spatial data, including variance, autocorrelation, and mean patch size (Dungan et al., 2002). Clearly, the extent and resolution of a dataset affects the number of scales over which certain dynamics can be observed. It is also possible that for certain data, there are "critical" resolutions at which certain phenomena are observable, and that the data is most (or least) complex at these resolutions. A thorough study of all of these factors should be done in future work.

<u>Notes on the fractal dimension</u>

While well defined for perfect mathematical objects, when applied to real objects, the fractal dimension is a problematic measure, since it is only applicable over a limited range of scales. It also does not appear to be very sensitive to differences in spatiotemporal pattern, since it was unable to discern between the randomly distributed data versus solid objects in our data sets.

<u>Notes on the spatiotemporal complexity measure and choice of window size</u>

This measure is superior to many others for the characterisation of the overall spatiotemporal pattern in a data cube. However, like other measures such as contagion, STC must be interpreted with caution. Its value is also affected by the density of the data cube and by the size of the moving window used to sample the data (here we always used a window of 3x3x3). When calculating STC for a data set, the value obtained should always be compared to that for random data having the same density. Figure 6 shows the effect of varying density and window size on the calculation of STC for randomly distributed data.

Data cubes that have large variations in density over space or time may give overall STC values that poorly represent the type of dynamics present. For example, a cube with periodic spatiotemporal dynamics alternating between a completely occupied spatial configuration (STC=0) and a random spatial configuration (STC=0.7) would give an overall STC value somewhere between the 2 cases. For an overall STC value to be characteristic of the whole space-time cube, data density should be relatively stationary in space and time. In situations for which this is not the case, sub-sampling of the data cube would be more appropriate.

Lastly, it is not necessary that the moving window used for STC calculations be cubic (square on all sides). The moving window may take on any dimension, and it may make sense, for example, in a case where the spatial resolution is much finer than the temporal resolution, to use a window having a large spatial extent and a smaller temporal dimension (e.g., 3n x 3n x n). The choice of window size is also something to consider when using STC and the effect of different window sizes should be tested on a dataset. As shown in Figure 6, for random data, the value of STC converges towards a stable value with increasing the window size.

<u>Sub-sampling</u>

For sufficiently resolved data sets (e.g., high values of N_x, N_y and N_t) there are a number of interesting analyses that can be done via the sub-sampling of the data cube. Metrics such as contagion and STC can be calculated for specific volumes of the space-time cube in order to detect regions of high complexity (e.g., areas on a landscape that, via their dynamics, are more complex than others) or regions for which the spatiotemporal dynamics is essentially random (as indicated by a low contagion value and an intermediate value of STC). Such sub-sampling will allow for a finer analysis of the space-time dynamics, potentially enabling the differentiation of regions governed by different underlying ecological processes. Sub-sampling may be done along only one axis (e.g., by taking successive “slices” of the cube in time) as a means of studying how the metric varies along this axis. In Parrott (2005), an STC analysis of vegetation dynamics in a model ecosystem based on calculations of successive temporal slices of the data set, was used to show how the spatiotemporal complexity of vegetation patterns varied over time in response to disturbance. The analysis showed that STC decreased immediately after disturbance and then increased as the community recovered.

<u>Applications to ecological monitoring</u>

Effective monitoring and characterisation of ecological dynamics necessitates a truly spatiotemporal approach. Almost all ecological variables exhibit a heterogeneity that varies in space and time. Exogenous factors that affect ecological processes are also heterogeneous in space and time. Ecological processes are thus affected by multiple, interacting variables that have different spatiotemporal patterns and which all contribute to emergent, ecosystem level properties.

Characterisation of these spatiotemporal patterns is thus a key element necessary for the understanding of ecological dynamics, particularly in the face of disturbance and climate change that might alter the historical spatiotemporal distributions of certain variables. It is thus imperative to be able to characterise the spatiotemporal distributions, as a means of monitoring and detecting change. Metrics such as those presented here are a possible approach, amongst others. Such metrics can be calculated for known ecological regimes, and serve as baseline values against which other systems may be compared. Lastly, the use of such metrics, especially those that characterize the complexity of the spatiotemporal dynamics, can serve as a common reference scale for the comparison of completely different systems and/or variables.

Future work

A limitation of all of these metrics is that they are applicable only to univariate data. Further work should include the development of measures for multivariate data, allowing, for example, the comparison of how 2 or more variables evolve in space-time. In addition, all of these metrics apply to categorical data, thus continuous variables need to be classified before analysis. Such categorisation ultimately results in loss of information and may cause artefacts, depending on the choice of boundaries and the number of categories used. In cases where this is problematic, other methods (such as 3D variograms) designed for continuous variables are more appropriate. Some of the metrics presented here may be adapted to deal with particular cases, such as irregularly sampled data, that are common in ecological data. For example, the definition of "neighbourhood" could be redefined. Through the use of a weighted distance matrix, a neighbourhood may be considered to be simply a certain number of nearest neighbours. Alternatively, a neighbourhood could be defined as all points residing within a sphere of a given radius. In certain cases, irregularly sampled data or data with missing values may be interpolated to generate a grid-based data set. Many specialised interpolation routines exist, including methods for 3 and 4 dimensions (Li and Revesz (2004)). Lastly, in all of our examples, we have referred to spatiotemporal data. It should not be forgotten that all of the metrics presented here are equally applicable to any 3-dimensional dataset. With modified definitions of neighbourhood adjacencies, some of these metrics may also be applied in higher dimensions (e.g., x, y, z and t).

Conclusion

We have presented a number of 3D metrics that can be used to describe raster-based spatiotemporal data. These metrics are not a panacea, but are intended to contribute to the growing toolbox of methods available to ecologists to analyse spatiotemporal data. We have purposefully extended already existing concepts of "patch" and associated landscape metrics to 3-dimensions in order to remain within the existing conceptual framework used to analyse raster-based ecological mosaics. The problem of classification that exists for all raster data is, of course, present. Many environmental variables are continuous in both space and time and discretization is scale-dependent and error-prone. When working with such data, one should always be aware of these limitations. On the other hand, many of the available datasets and existing sampling methods in ecology are grid- or raster-based, and it is therefore essential to continue the development of methods that are adapted to this type of data.

The methods presented here were developed by the authors as a way of dealing with the vast amounts of spatiotemporal data being generated by our ecological models. Such data is increasingly abundant amongst ecological modellers. In addition, repeat photography by field ecologists, combined with over 30 years of satellite data means that spatiotemporal datasets are increasingly common. The time is ripe to develop novel methods capable of analysing such spatiotemporal data. We hope that the ideas presented here will be adopted and further developed by others searching to understand and characterise the inherently spatiotemporal dynamics of ecological systems.

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MATLAB source code used to calculate the measures described here can be obtained by contacting the corresponding author. The box counting algorithm of F. Moisy was used to estimate fractal dimensions.

References

Baldocchi, D.D., Falge, E., Gu, L., Olson, R., Hollinger, D., Running, S., Anthoni, P., Bernhofer, C., Davis, K., Evans, R., Fuentes, J., Goldstein, A., Katul, G., Law, B., Lee, X., Malhi, Y., Meyers, T., Munger, J.W., Oechel, W., Pilegaard, K., Schmid, H.P., Valentini, R., Verma, S., Vesala, T., Wilson, K., Wofsy, S., 2001. FLUXNET: A new tool to study the temporal and spatial variability of ecosystem-scale carbon dioxide, water vapor and energy flux densities. Bulletin of the American Meteorological Society 82, 2415-2434.

Bascompte, J. and Solé, R. 1998. Modeling spatiotemporal dynamics in ecology. Springer-Verlag, Berlin. 230 pp.

Bjornstad, O., Ims, R. and Lambin, X., 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. TREE 14(11), 427-432.

Bolliger, J., Wagner, H. and Turner, M. 2007. Identifying and quantifying landscape patterns in space and time. In: F. Kienast, O. Wildi and S. Ghosh (Editors) 2007. A changing world: Challenges for landscape research. Springer, Dordrecht, The Netherlands. pp. 177-194.

Collins, S.L., Bettencourt, L.M.A., Hagberg, A., Brown, R.F., Moore, D.I., Bonoto, G., Delin, K.A., Jackson, S.P., Johnson, D.W., Burleigh, S.C., Woodrow, R.R., McAuley, J.M., 2006. New opportunities in ecological sensing using wireless sensor networks. Frontiers in Ecology and the Environment 4, 402-407.

Dungan, J. L., Perry, J. N., Dale, M. R. T., Legendre, P., Citron-Pousty, S. Fortin, M.-J., Jakomulska, A., Miriti, M. and Rosenberg, M. S., 2002. A balanced view of scale in spatial statistical analysis. Ecography 25, 626-640.

Dunn, C., Sharpe, D., Guntenspergen, G., Stearns, F. and Yang, Z., 1991. Methods for analyzing temporal changes in landscape pattern. In: M. Turner and R. Gardner (Editors), Quantitative

Methods in Landscape Ecology. Springer, NY. pp. 173-198.

Dykes, J.A. and Mountain, D.M., 2003. Seeking structure in records of spatio-temporal behavior: visualization issues, efforts and applications. Computational Statistics and Data Analysis 43, 581-603.

Edsall, R., Harrower, M., and Mennis, J., 2000. Tools for visualizing properties of spatial and temporal periodicity in geographic data. Computers and Geosciences 26, 109-118.

Forer, P., 1998. Geometric approaches to the nexus of time, space, and microprocess: Implementing a practical model for mundane socio-spatial systems. In: M. Egenhofer and R. Golledge (Editors), Spatial and Temporal Reasoning in Geographic Information Systems. Oxford University Press, New York. pp.171-190.

Forman, R.T. 1995. Land Mosaics: The ecology of landscapes and regions. Cambridge University Press, Cambridge. 652 pp.

Fortin, M.-J. and Dale, M., 2005. Spatial analysis: A guide for ecologists. Cambridge University Press, Cambridge, UK. 365 pp.

Gatrell, A., Bailey, T., Diggle, P., and Rowlingson, B., 1996. Spatial point pattern analysis and its application in geographical epidemiology. Transactions of the Institute of British Geographers 21, 256-274.

Griffith, D.A., 1981. Interdependence in space and time: numerical and interpretative considerations. In: D.A. Griffith & R. D. MacKinnon (Editors), Dynamic Spatial Models. Sijhoff & Noordhoff, Netherlands. pp. 258-87.

Gustafson, E., 1998. Quantifying landscape spatial pattern: What is state of the art? Ecosystems 1, 143-156.

Hassell, M.P., Comins, H.N. and May, R.M., 1991. Spatial structure and chaos in insect population dynamics. Nature 353, 255-258.

Hayes, D., Sader, S. and Schwartz, N., 2002. Analyzing a forest conversion history database to explore the spatial and temporal characteristics of land cover change in Guatemala's Maya Biosphere Reserve. Landscape Ecology 17, 299–314.

Isaaks, E. H., and Srivastana, R. M., 1989. An Introduction to Applied Geostatistics. Oxford University Press, New York.

Jelinski, D.E., and Wu, J., 1996. The modifiable areal unit problem and implications for landscape ecology. Landscape Ecology 11, 129-140.

Kienast, F., Wildi, O. and Ghosh, S. (Editors), 2007. A changing world: Challenges for landscape research. Springer, Dordrecht, The Netherlands. 296 pp.

Li, H. and Reynolds, J.F., 1993. A new contagion index to quantify spatial patterns of landscapes. Landscape Ecology 8,155-162.

Liebhold, A., Koenig, W., and Bjørnstad, O., 2004. Spatial synchrony in population dynamics. Annual Review of Ecology, Evolution and Systematics 35, 467–90.

Li, L. and Revesz, P. 2004. Interpolation methods for spatio-temporal geographic data. Computers, Environment and Urban Systems 28, 201-227.

O'Neill, R., Krummel, J., Gardner, R., Sugihara, G., Jackson, B. DeAngelis, D., Milne, B., Turner, M., Zygmunt, B., Christensen, S., Dale, V. and Graham, R., 1988. Indices of landscape pattern. Landscape Ecology 1, 153-162.

Milne, B. 1991. Lessons from applying fractal models to landscape patterns. In: M. Turner and R. Gardner (Editors). Quantitative Methods in Landscape Ecology. Springer, New York. pp. 199-235.

Morris, K., Hill, D. and Moore, A., 2000. Mapping the environment through three-dimensional space and time. Computers, Environment and Urban Systems 24, 435-450.

Murphy, H.T., and Lovett-Doust, J., 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105(1), 3-14.

Parrott, L., 2005. Quantifying the complexity of simulated spatiotemporal population dynamics. Ecological Complexity 2(2),175-184.

Peitgen, H.O., Jürgens, H. and Saupe, D., 1992. Chaos and Fractals. Springler-Verlag, New York, pp. 202-219.

Perret, J., Prasher, S.O. and Kacimov, A.R., 2003. Mass fractal dimension of soil macropores using computed tomography: from the box-counting to the cube-counting algorithm. European Journal of Soil Science 54, 569-579.

Peuquet, D., 2001. Making space for time: Issues in space-time data representation. Geoinformatica 5(1), 11-32.

Pielou, E.C., 1969. An Introduction to Mathematical Ecology. Wiley-Interscience, New York, 286 pp.

Porcua, E., Mateua, J., Zinib, A., Pinib, R., 2007. Modelling spatio-temporal data: A new variogram and covariance structure proposal. Statistics and Probability Letters 77, 83–89.

Proulx, R. and Parrott, L., 2008. Measures of structural complexity in digital images for monitoring the ecological signature of an old-growth forest ecosystem. Ecological Indicators 8, 270-284.

Rahbek, C., 2005. The role of spatial scale and perception of large-scale species-richness patterns. Ecology Letters 8, 224-239.

Ritters, H., O'Neill, R., Wickham, J. and Jones, K.B., 1996. A note on contagion indices for landscape analysis. Landscape Ecology 11(4), 197-202.

Rogerson, P., 2006. Statistical Methods for Geography, 2nd Ed. Sage Publications, London. 304 pp.

Tobin, P. C., 2004. Estimation of the spatial autocorrelation function: consequences of sampling dynamic populations in space and time. Ecography 27, 767-775.

Turner, M.G., Gardner, R.H. and O'Niell, R.V., 2001. Landscape ecology in theory and practice: pattern and process. Springer-Verlag: NY. 404 pp.

Wilson, H. and Keeling, M. 2000. Spatial scales and low-dimensional deterministic dynamics. In: Dieckmann, U., Law, R., Metz, J.A.J., (Editors). The Geometry of Ecological Interactions. University Press, Cambridge. pp. 209-226.

Wilson, W., 2000. Simulating ecological and evolutionary systems in C. Cambridge University Press, Cambridge, UK. 301 pp.

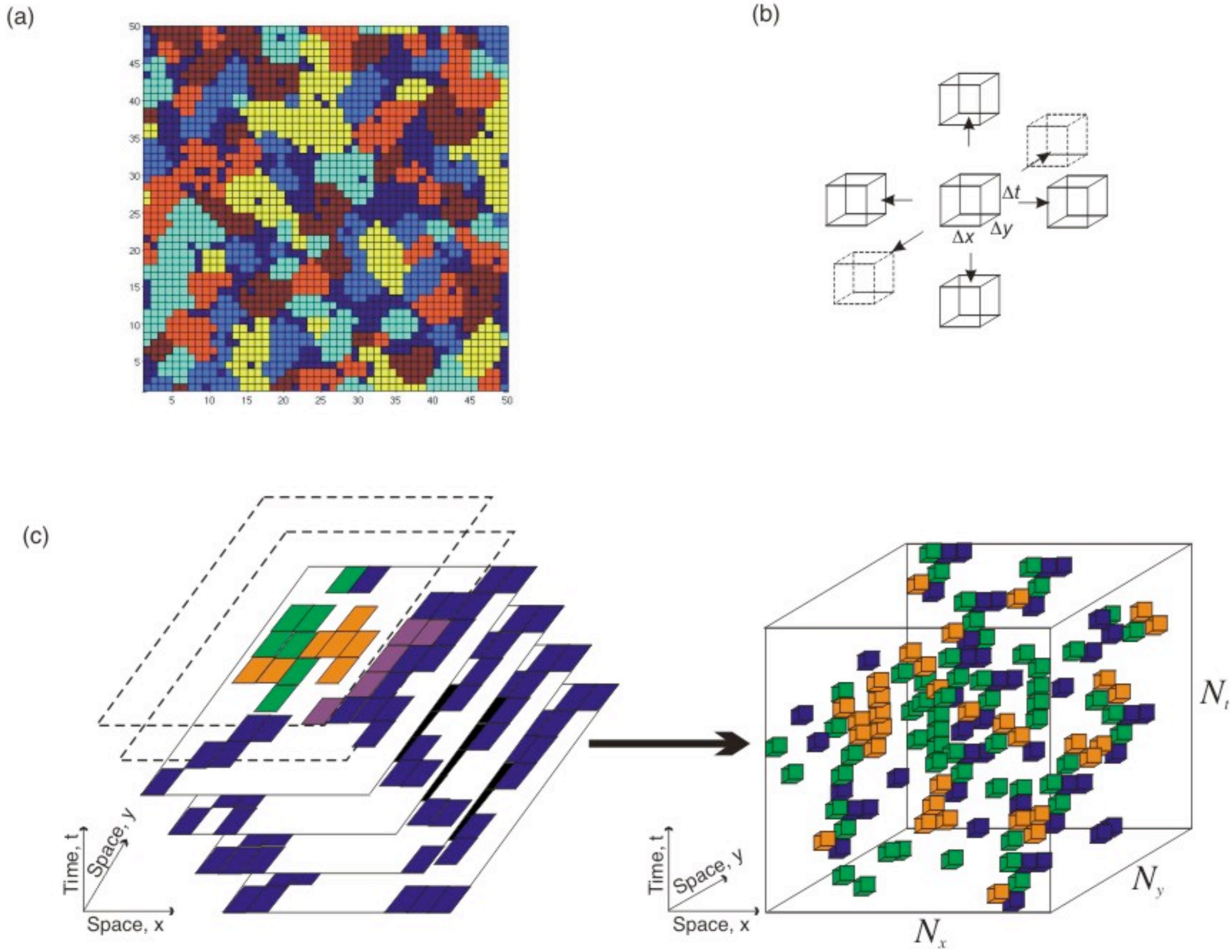

Figure 1: Format of spatiotemporal data used for the 3D metrics presented in this article: (a) An example ecological mosaic composed of categorical raster data; shades of gray correspond to different categories or patch types; (b) A pixel in raster data becomes a 3-D voxel in space-time having dimensions equal to the spatial (Δx, Δy) and temporal (Δt) sampling resolutions. Neighbouring voxels are used to calculate adjacencies for metrics such as contagion; the von Neumann neighbourhood is shown here; (c) A stack of spatial mosaics taken at successive points in time can be used to generate a 3-dimensional data matrix in which spatial patches take on an additional temporal dimension to become "blobs" composed of 3D voxels.

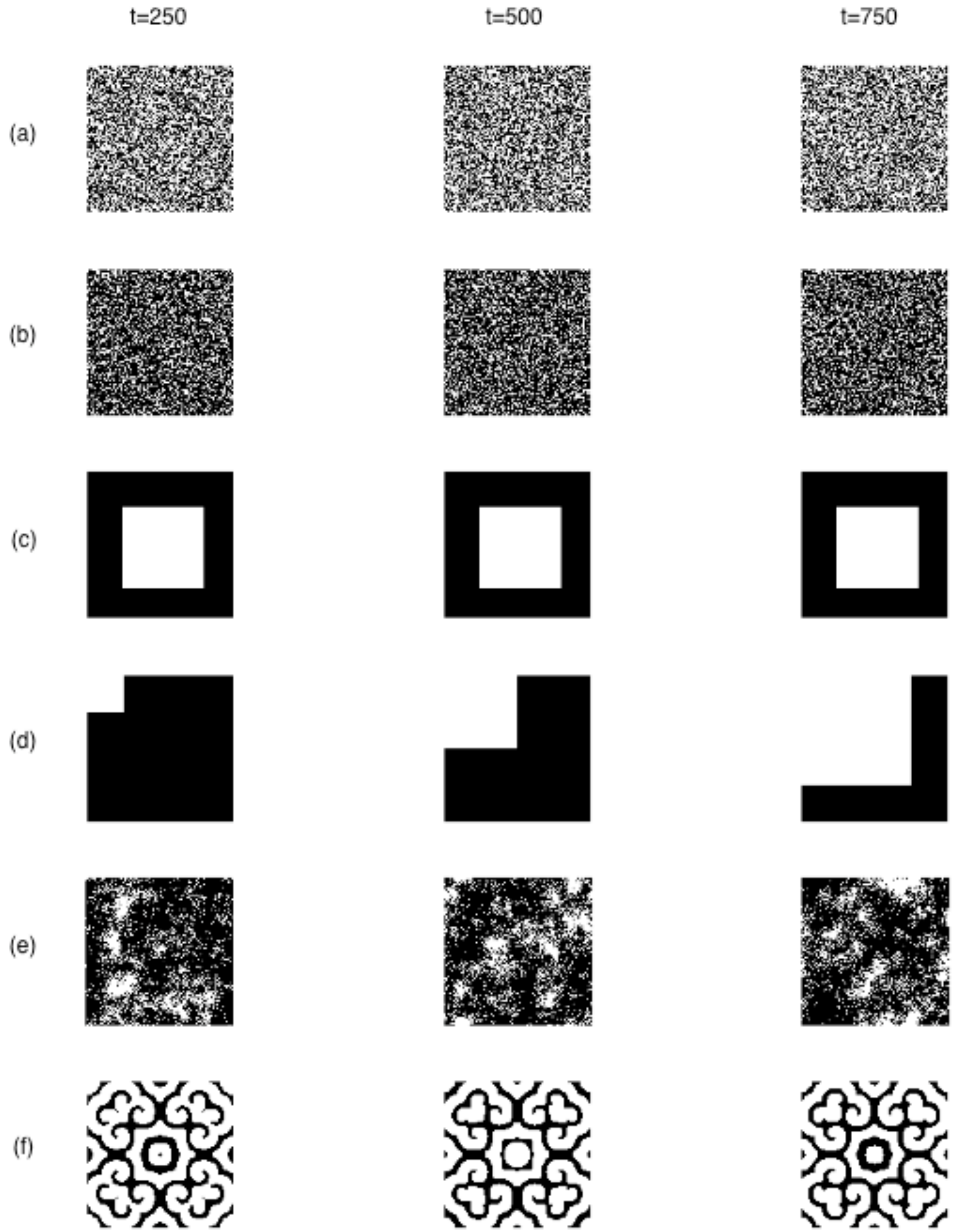

Figure 2: Examples of the different model data sets for selected moments in time. The analysed blob type is shown in white and the background matrix is black. (a) Random; (b) Random30; (c) Column; (d) Spread; (e) Lotka-Volterra; (f) Host-Parasite.

Figure 3: The space-time cube of Lotka-Volterra data (dimensions 100 x 100 x 1000 voxels) showing the stack of successive snapshots of the presence of the prey species on the landscape. Voxels containing prey are shown in grey; the background matrix is black.

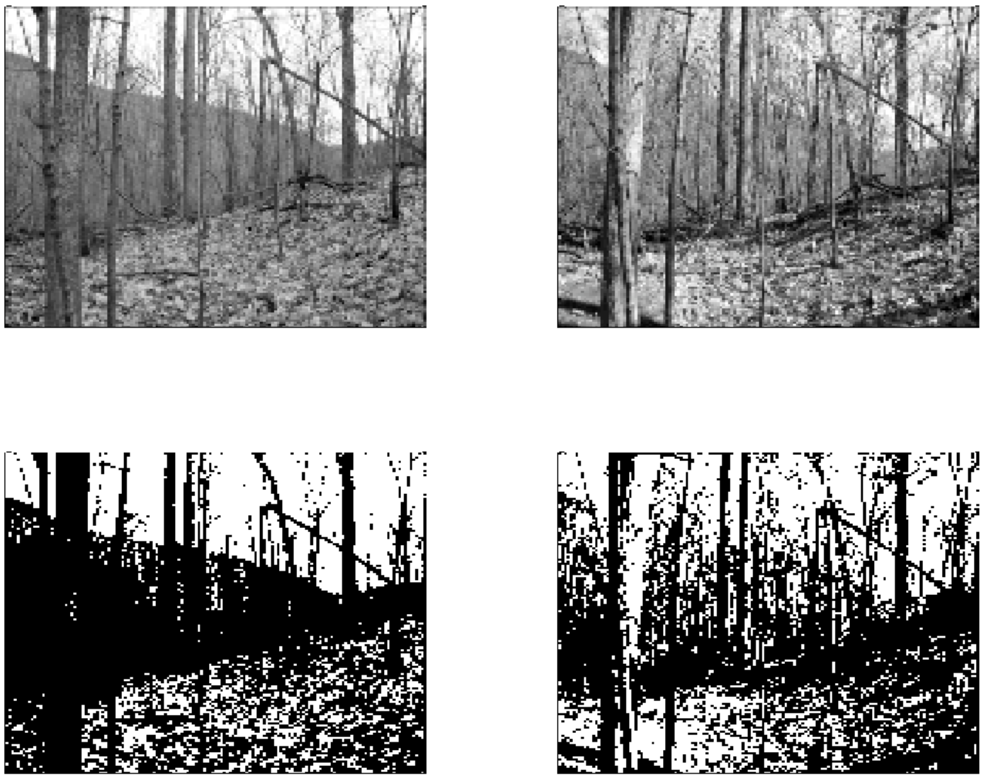

Figure 4: Two snapshots from the forest data set. Above: low resolution greyscale images; below: binary versions used for the blob analyses.

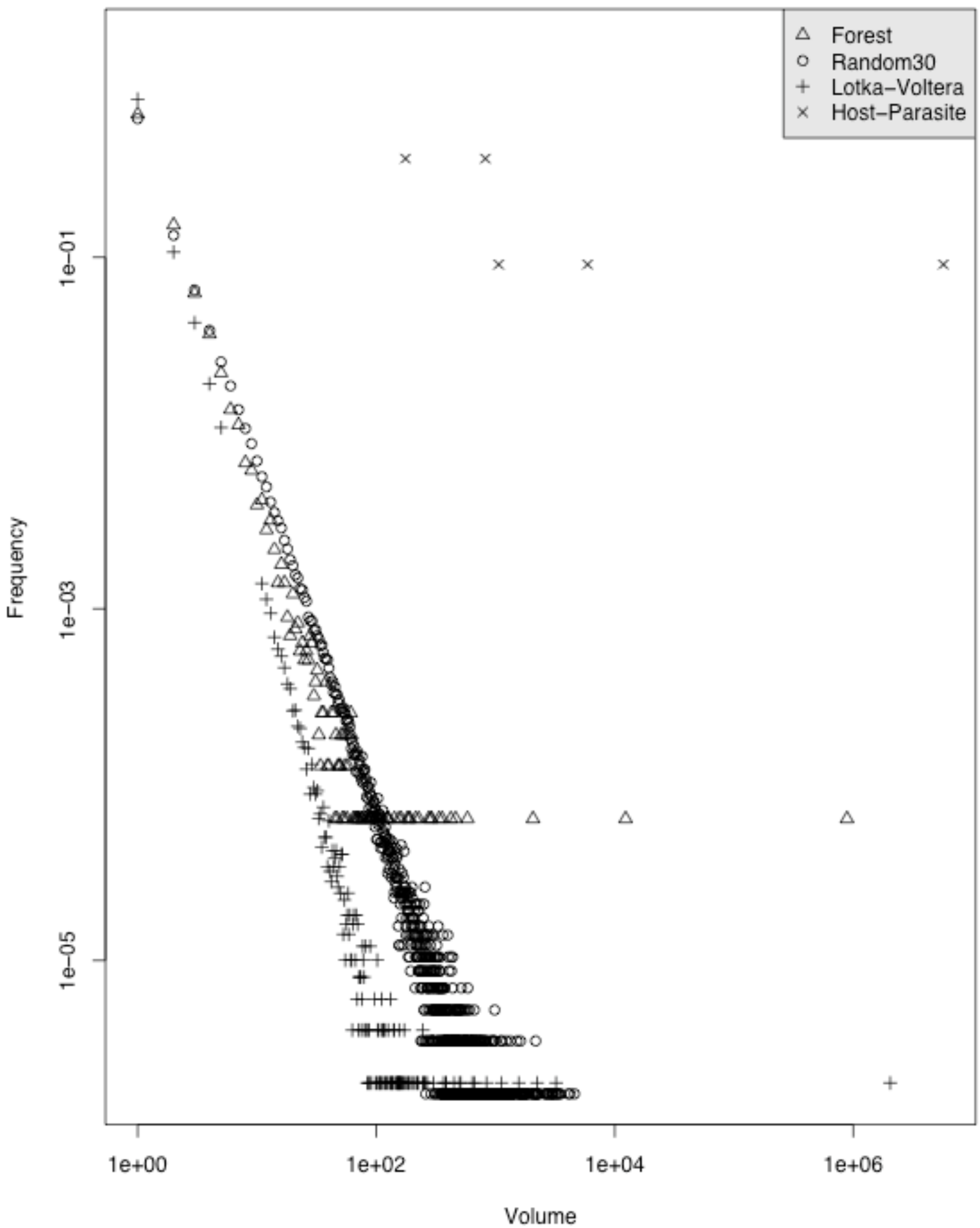

Figure 5: Probability density function of the volume of blobs present in selected data sets, using the von Neumann neighbourhood. Both axes are in the log scale.

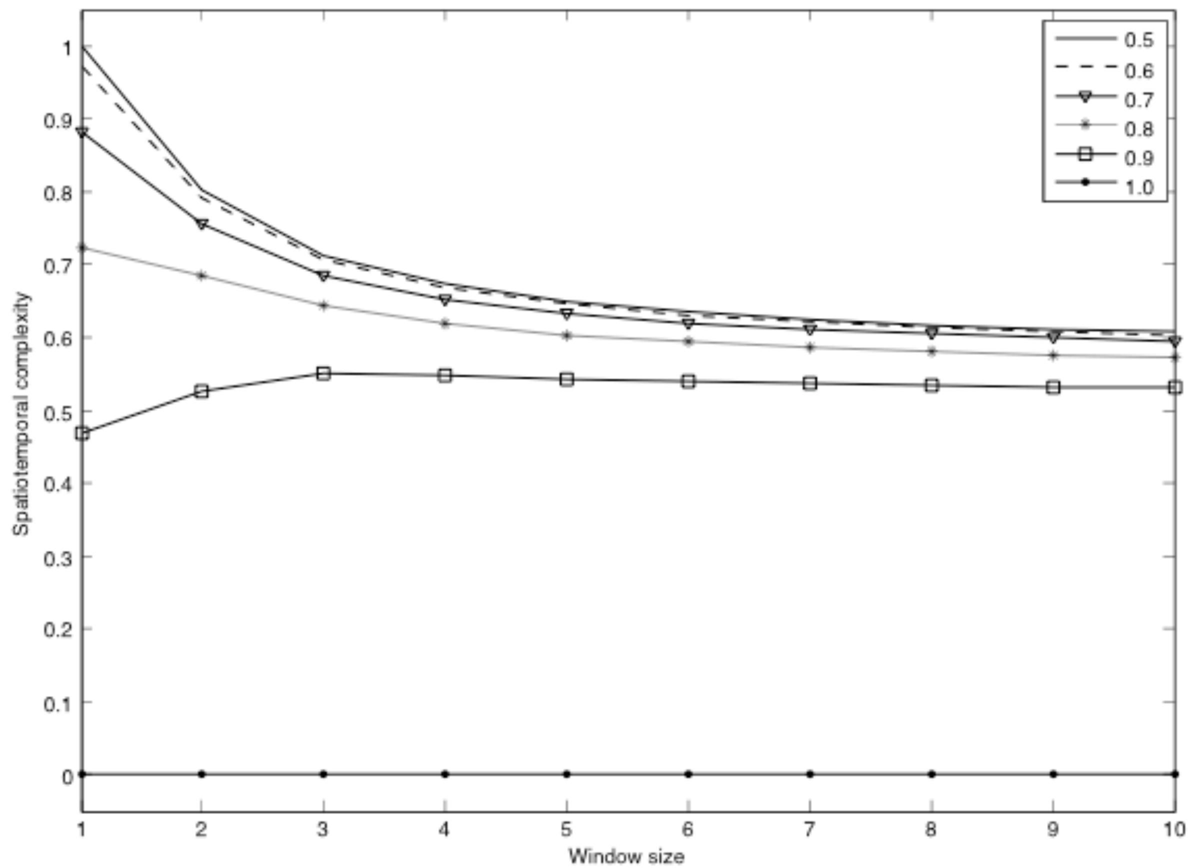

Figure 6: Effect of varying density and window size on the calculation of STC for uniformly distributed random data. Each line is for a cube having a different data density. Lines for equivalent densities (i.e., 0.4 & 0.6; 0.3 & 0.7; etc.) are overlapping. STC = 0 for densities of 0 and 1.0 regardless of window size.

Table 1

Values of composition and configuration metrics calculated for the model and empirical datasets. Shading indicates the four data sets having similar space-time densities. Confidence intervals for the STC values are 1 standard deviation and were calculated using 166 subsamples of the dataset.

Data set	Dimensions Nx x Ny x Nt	Composition metrics: Density	Number of blobs: Von Neuman	Number of blobs: Moore	Blob shape complexity: Von Neuman Mean	Blob shape complexity: Von Neuman Std	Blob shape complexity: Moore Mean	Blob shape complexity: Moore Std	Fractal dimension	Configuration metrics: Contagion Von Neuman	Contagion Moore	Spatiotemporal complexity (STC)
Random	99x99x1000	0.50	91744	5	0.99	0.08	0.90	0.22	2.9*	0.00	0.00	0.71±0.00
Random30	99x99x1000	0.30	574187	669	0.87	0.26	0.97	0.12	2.8*	0.12	0.12	0.69±0.00
Column	100x100x1000	0.30	1	1	1.00	0.00	1.00	0.00	2.9*	0.87	0.87	0.25±0.00
Spread	100x100x1000	0.3	1	1	0.34	0.00	0.34	0.00	2.8*	0.96	0.93	0.23±0.00
Lotka-Volterra	99x99x1000	0.29	498149	1390	0.96	0.13	0.76	0.31	2.8*	0.15	0.15	0.91±0.03
Host-Parasite	99x99x1000	0.67	11	11	0.37	0.12	0.37	0.12	2.9*	0.36	0.26	0.90±0.01
Forest	150x150x100	0.42	15641	3782	0.93	0.17	0.86	0.26	2.7	0.25	0.17	0.96±0.05

*value was estimated over a limited range of scales