

# Structural complexity in digital images as an ecological indicator for monitoring forest dynamics across scale, space and time

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## ARTICLE INFO

### Article history:

Received 12 February 2008

Received in revised form 29 January 2009

Accepted 26 March 2009

### Keywords:

Ecological complexity

Close-range image

Mean information gain

Recurrence plot

Spatiotemporal analysis

Repeat photography

## ABSTRACT

The development of ecological indicators for actively monitoring an ecosystem at a high resolution in scale, space and time is a challenge of primary interest. In this context, measures of structural complexity derived from close-range repeat photography may form a part of the solution. Moreover, recent mathematical tools, such as recurrence plots and recurrence quantification analysis (RP-RQA), are becoming accessible for characterizing the multivariate dynamics of natural systems given short, stochastic and non-stationary series. In this study, a total of 9360 grey-level digital images were recorded on a weekly basis across 72 sites in an old-growth forest ecosystem and analyzed for structural complexity. Structural complexity was assessed using an information theoretic measure (mean information gain). The effect of the scene scale on the observed dynamics was verified across a gradient of forest descriptors and light habitats. Multiscale dynamics responded nonlinearly to changes in scene scale, whereas seasonal trends in structural complexity showed a range of deterministic and stochastic behaviours. The determinism of multiscale time-series was related to sapling density, tree cover, and tree species richness. The sensitivity and flexibility of the RP-RQA approach applied to proxy measures of structural complexity in digital images forms an efficient methodology which might be used for actively monitoring forest ecosystems. This field study is one of the first to demonstrate that old-growth forest ecosystems behave like complex systems exhibiting nonlinear vegetation structure and dynamics across scales.

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## 1. Introduction

Sorting the patterns and processes we observe in nature is an issue at least as old as systemic ecology itself [e.g., climax and seral units, Clements, 1936; efficiency and trophic dynamics, Lindeman, 1942]. The idea of classifying ecosystem functions has since motivated the development of various individual-, community- and landscape-based indicators, among which the notion of complexity (see Polis and Strong, 1996; Maurer, 1999; Brown et al., 2002; Storch and Gaston, 2004; Green et al., 2005) is gradually complementing the one of diversity. In ecology, the word *complexity* is often used in a soft sense to relate to natural patterns that arise through multiscale processes driven by nonlinear dynamics in space and time. The recognition that ecosystems behave as complex systems, as opposed to being stochastic or

dynamically stable systems, is furthermore challenging our ability to derive general principles of their functioning (Levin, 1998; Milne, 1998; Storch and Gaston, 2004).

In an influential paper, Milne (1992) reported that: “*The existing theories of diversity, community composition, succession, and species interactions may be confounded somewhat by the limited ability of theory and empirical work to accommodate the recently discovered consequences of scale*”. More than a decade later, Milne’s statement still applies. Alternatively, complex systems theory is often viewed as an interdisciplinary corpus to the study of ecosystem dynamics (Milne, 1998; Proctor and Larson, 2005; Solé and Bascompte, 2006). However, the question of how to characterize complexity in ecological systems remains entirely open. For instance to link complex system phenomena (e.g., critical thresholds, self-organization, or transiency) to empirical ecosystem patterns/processes, one must be able to define hard measures of complexity in the field (Anand and Orlóci, 1996; Ricotta, 2000). Because any definition of something like ecological complexity in the real world is context dependent, a hard measure of complexity should be mathematically framed, have bounded extensive limits, as well as being a realistic indicator of the system’s state across scales.

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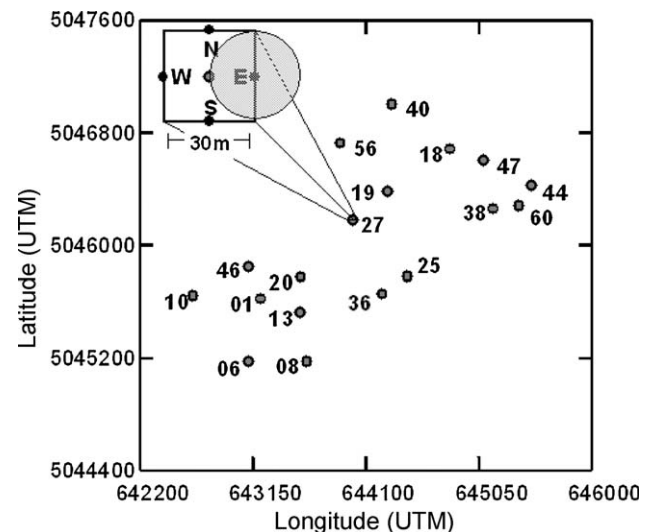
The present study builds on previous research work for monitoring the spatiotemporal dynamics of a forest ecosystem at multiple scales (e.g., Proulx and Parrott, 2008). The methodology consists of repeatedly taking close-range (side-view) photographs of the forest while varying the scene scale; i.e., the mean distance between the observer and the elements that compose the scene (Torralba and Oliva, 2003). The mean information gain (MIG) measure was used by Proulx and Parrott (2008) as an ecological indicator for quantifying structural complexity in natural images, where the maximum of structural complexity was shown to occur at intermediate MIG values. This state of high structural complexity was shown to be associated to plant species richness and forest phenology (Proulx and Parrott, 2008).

Rapid assessment of structural complexity in digital images can be used to generate spatiotemporal series of the ecosystem's state at multiple scales of observation. But even a detailed description of the ecosystem's state provides little information on its dynamics. For example, the average structural complexity of a forest ecosystem may be high, while local trajectories of the indicator could lack any determinism. One way of studying the presence of temporal determinism in ecosystem dynamics is through the concept of recurrence states (Proulx et al., 2008). Using coupled temporal series captured at regular time intervals, Romano et al. (2004) recently introduced multivariate recurrence plots as a mean of characterizing dynamical complexity. The recurrence plot (RP) is most simply defined as a threshold distance matrix of ones on a background of zeros, where black points (ones) illustrate the times at which the system's state is revisited (Marwan et al., 2007).

The objective of this paper is to present a methodological framework for monitoring the spatiotemporal dynamics of an ecosystem's state at multiple scales and demonstrate its applicability using data from an old-growth forest ecosystem. For this purpose, we considered MIG in digital images to be an indicator of the structural complexity state of the ecosystem, while used the RP approach to provide determinism estimates of the observed dynamics in structural complexity across scales. MIG and RP-based approaches are also compared with more standard measures of an ecosystem's structure and dynamics.

## 2. Methodology

The experiment was designed for monitoring spatiotemporal fluctuations in structural complexity of over- and under-storey vegetation at the Gault Nature Reserve (Mont St-Hilaire, Québec, Canada). Eighteen forest sites were sampled on a weekly basis for a total of 27 weeks, from May 10 to November 10, 2005. All sites were visited in the same sequence each week and sampled within a 48 h period from Tuesday to Thursday. At the centre of each site a steel rod was planted in a vertical position and at a fixed height above the ground. These rods served as markers for positioning the camera's tripod when revisiting sites. Sampling always occurred within the 9:30–15:30 h daylight interval to control for large periodic variations in illumination, both in direction and luminance. Digital images were taken with the camera (EOS Rebel 6.3 MP, Canon Inc., Tokyo, Japan) held at the centre of the site and pointing outwards in four directions: North, East, South, and West (Fig. 1). For each direction, images were recorded at five different scene scales by varying the focal length as follows: 18, 24, 35, 44, and 55 mm (Fig. 2); which is equivalent to a 30–90 mm lens under 35 mm standards. In addition to the use of steel rods for positioning the tripod, multiple markers and reference points on the tripod were used to ensure that the same scene was photographed over time. The whole setup included 72 different scenes (i.e., 18 sites multiplied by four directions) repeatedly photographed at five scene scales over 26 weeks, for a grand total of 9360 images. Each image was converted before processing to



**Fig. 1.** Experimental setup with UTM coordinates (zone 18T) of the 18 sites sampled on a weekly basis on Mont St-Hilaire. Box sides approximately delineate the size of Mont St-Hilaire's Reserve. The whole setup included 72 different scenes, 18 sites multiplied by 4 directions (North, East, South, West), repeatedly photographed at five scene scales. The grey circle illustrates the circular plot used to quantify forest descriptors in each scene.

grey-level (intensity) values. Images were 1000 × 1500 pixels in size and recorded under a low compression JPEG format. Additional details about the sampling protocol and photographic settings can be found in Proulx and Parrott (2008).

### 2.1. Measures of vegetation structure

In each of the 72 scenes we established a 15 m radius circular plot, centred in each direction 15 m away from the site's focal steel rod (Fig. 1), and scored 11 forest descriptors during week 11, from July 19 to 21. For each circular plot, or each shooting direction (N, E, S, W) at a given forest site, an exhaustive survey of the following descriptors was realized: sapling density (number of trees <10 cm and >2 cm diameter breast height); tree density (number of trees >10 cm diameter breast height); tree species richness; shrub species richness; total species richness (including shrubs, saplings, seedlings, and trees); sapling cover; tree cover; shrub cover; herb cover; fern cover; total cover (sum of all covers). Percent cover was attributed from the consensus between two observers using 10% increments. Note that the total cover does not have to sum to 100%. A snapshot sample of this forest system was expected to reflect understorey and overstorey dynamics in structural complexity through both density and cover descriptors.

### 2.2. Structural complexity in the image

Mean information gain (MIG) may be depicted as a hard measure of complexity, the legitimacy of which has been demonstrated in the context of: food webs (Aoki and Mizushima, 2001; Ulanowicz, 2004), hydrological processes (Lange, 1999; Mogheir et al., 2004), and landscape ecology (Loehle and Wein, 1994; Johnson et al., 1999). MIG in an image determines the amount of spatial heterogeneity that excludes the fraction devoted to aspatial heterogeneity and is defined as

$$\text{MIG} = \frac{\left[ -\sum_{i=1}^{M^k} p(\chi_i) \log p(\chi_i) \right] - \left[ -\sum_{i=1}^M p(\gamma_i) \log p(\gamma_i) \right]}{\log(M^k/M)} \quad (1)$$

$p(\gamma_i)$  is the probability of observing a pixel's grey-level value  $\gamma_i$  independently of its location in the image (i.e., aspatial hetero-



**Fig. 2.** Spatiotemporal snapshots of site 13, North scene, during (a) early spring, (b) mid summer, and (c) late fall at Mont Saint-Hilaire. Left panels are photographs taken at a focal length of 18 mm (large scale), whereas right panels are the same scenes at a focal length of 55 mm (small scale).

geneity) and  $M$  is the number of frequency bins of pixel values.  $p(\chi_i)$  denotes the probability of finding a specific grey-level combination  $\chi_i$  made of  $k$  neighbouring pixels in the image (i.e., spatial heterogeneity) and  $M^k$  represents the maximum number of such possible combinations. Expressions within brackets represent the joint Shannon entropy and the marginal Shannon entropy calculated from the frequency distributions of the  $k$ -dimensional co-occurrence grey-level matrix. The fixed quantity  $\log(M^k/M)$  returns the maximum obtained for equiprobable distributions and it serves to normalize MIG between zero and one. MIG is zero for uniform spatial patterns and is maximal ( $MIG \rightarrow 1$ ) for random ones. We defined here a  $2 \times 2$  square configuration of four ( $k = 4$ ) neighbouring pixels and  $M = 12$ . An example of how MIG is calculated from a raster image is presented in Fig. 3 for  $k = 2$ .

One aspect of our methodology demands that MIG in natural images represents a realistic indicator of the developmental state of the ecosystem. A comparable task has previously been undertaken for the fractal dimension ( $D_f$ ) of natural landscapes (e.g., O'Neill et al., 1988; Milne, 1992). Although tools exist for calculating the fractal dimension of natural images,  $D_f$  is computationally prone to estimation errors, especially considering that most natural objects are known to be statistically self-similar over a limited range of scales only (Schepers et al., 1992; Loehle and Li, 1996).

For the purpose of bridging here fractal theory to structural complexity patterns in natural images, we examined how MIG is related to the fractal dimension ( $D_f$ ) of two-dimensional surfaces

through a simulation experiment. Providing that a grey-level surface can be modelled as a fractional Brownian function,  $D_f$  can be calculated as  $D_f = (7 - \beta)/2$  (e.g., Pentland, 1984), where  $\beta$  quantifies the spectral signature of a digital image. The coefficient  $\beta$  can be estimated from the linear slope of the log-log Fourier transform spectrum:

$$P(\omega) = B\omega^{-\beta}. \quad (2)$$

$P(\omega)$  is the two-dimensional power (squared amplitude) spectrum averaged over all orientations at radial frequencies  $\omega$ , and  $B$  is a constant which is a function of the overall image contrast. The slope coefficient  $\beta$  is mathematically related to  $D_f$  through Hurst's exponent  $H$  as follows (Keitt, 2000):  $\beta = 1 + 2H$ . We thus simulated 101 images ( $1000 \times 1000$ ) having a predetermined  $D_f$  in the interval 2.0–3.0 and calculated their MIG values from Eq. (1). To generate the images we adapted Peter Kovess's Matlab function 'noiseonf' which uses the inverse Fourier transform of a predetermined two-dimensional power spectrum (Kovess, 2000).

### 2.3. Measures of temporal determinism

Scene dynamics across multiple scales, expressed here as the temporal change in structural complexity (MIG), were characterized using the techniques of recurrence plot and recurrence quantification analysis (RP-RQA). The embedding theorem provides a way to



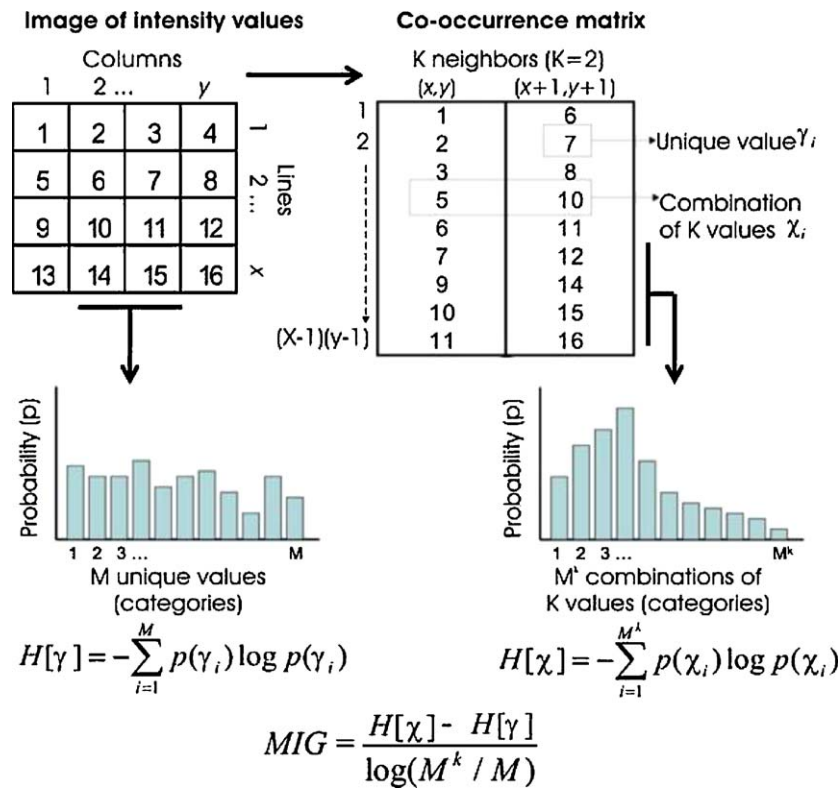


Fig. 3. Schematic representation of the calculation steps of the structural complexity measure mean information gain (MIG) in raster images (see text).

reconstruct the system dynamics in state space using the method of time delay coordinates. Given a one-dimensional time-series of length  $n$ :  $\mu = \{\mu_1, \mu_2, \mu_3, \dots, \mu_n\}$  the reconstructed attractor is defined from a series of vectors such that:

$$v_i = \langle \mu_i, \mu_{i+\tau}, \dots, \mu_{i+(m-1)\tau} \rangle \quad \forall i = 1, \dots, n - (m-1)\tau, \quad (3)$$

where  $\tau$  is the reconstruction delay,  $m$  is the embedding dimension, and  $N = n - (m-1)\tau$ . The recurrence plot (RP) is visualisation of the  $N \times N$  binary matrix denoted  $r_e^\mu(i, j)$ , which is filled according to the following rule:

$$r_e^\mu(i, j) = \begin{cases} 1 & \text{if } \|v_i - v_j\| < \varepsilon \\ 0 & \text{elsewhere.} \end{cases} \quad (4)$$

The parameter  $\varepsilon$  corresponds to the threshold distance for which two states are considered to be on neighbouring trajectories (recurrent) in the state space, where  $\|v_i - v_j\|$  is the distance norm. Visually, a black point in the RP signifies that one state observed at time  $t$  is revisited at time  $t + i$  (i.e., if  $r_e^\mu(i, j) < \varepsilon$ ; Eq. (4)). A more complete overview of the RP-RQA approach can be found in Marwan et al. (2007), which also discuss the most recent mathematical developments and review examples borrowed from different scientific applications.

For multivariate systems one wishes to include additional variables in the description of the time behaviour (e.g., Romano et al., 2004). From Eqs. (3) and (4) it is possible to construct  $J(i, j)$  the multivariate RP as follows:

$$J(i, j) = \Phi r_e^\mu(i, j), \quad (5)$$

where  $\Phi$  denotes the dot (Hadamard) product operator. This operation consists of joint multiplying all RPs  $r_e^\mu(i, j)$  constructed for each variable  $\mu$  independently. For our present purposes, the multivariate time-scale matrix of a given forest scene was formed of the MIG estimates measured through time across five different

scene scales. Our version of the multivariate RP considers the joint probability that recurrences in structural complexity occur simultaneously across all scene scales. The system is therefore expected to recur if the multiscale state in structural complexity at one time is encountered at another time.

A first characterization of the temporal dynamics is given by the recurrence rate (RR), which is obtained by counting the number of observed recurrences (or black points) divided by the theoretical maximum  $N(N-1)$ . A closer estimation of temporal determinism (DET) is to divide by  $N(N-1)$  the number of recurrences which are not solitary points but are parts of diagonal segments (Marwan et al., 2007). The presence of several long diagonal segments in the RP is considered the hallmark of deterministic signals. At the limits DET can vary between approximately 0.05 for white noise dynamics and 0.20 for perfectly deterministic dynamics, according here to our choice of parameters:  $m = 2$ ;  $\tau = 1$ ;  $RR = 0.2$ . DET estimates of multiscale dynamics provide us with a basis for the relative comparison of determinism in our 72 forest scenes.

Perhaps the most common way of characterizing ecological dynamics is to quantify temporal dispersion using the coefficient of variation (CV). Since it gives a measure of the relative variability of the system, the CV can be seen as a measure of determinism under the assumption that more highly variable dynamics are more sensitive to external perturbations, thus less deterministic. We calculated the multivariate version of the CV after summing and standardizing variances and covariances across all possible pairs of structural complexity (MIG) vectors in each time-scale matrix as follows (Lehman and Tilman, 2000):  $[\sum \text{Variances} + \sum \text{Covariances}] / \sum \text{Means}$ . All measures and analyses were performed with Matlab Version 7.0.1, MathWorks, Natick, USA.

#### 2.4. Data analyses

The simulated relationship between structural measures of complexity MIG and  $D_f$ , as well as the observed relationship

between dynamical measures of determinism DET and CV were plotted to evaluate their degree of interdependence.

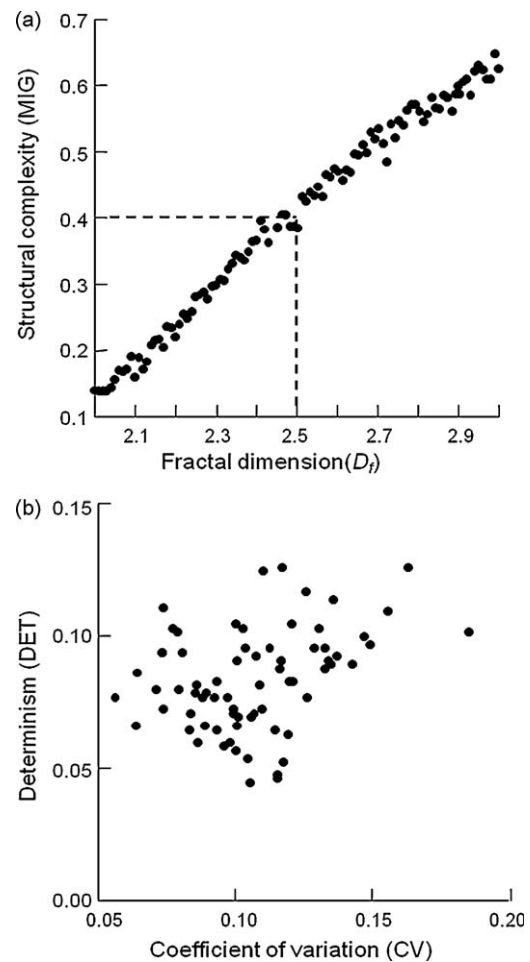
For each site we inspected the response curve of time-averaged MIG estimates across the five scene scales, and did so for each of the four directions independently. Error bars ( $\pm 1$ S.D.) were used to display the temporal variation around MIG for each site-direction-scale interaction. If structural complexity in digital images is scale invariant one should observe a flat response curve, whereas a nonlinear response curve is to be expected if discontinuous patterns are present across scales. Similarly, if the temporal variability in structural complexity shows scale invariance, one should observe error bars of comparable size at all scene scales.

To examine trends among scenes, a principal component analysis of the correlation matrix was performed on the 11 forest descriptors and a multiple linear regression analysis was performed on the results. The components explaining independently more than 10% of the overall scene variation in forest descriptors were used to detect the presence of a multivariate relationship between vegetation structure and multiscale temporal complexity. The matrix to analyze therefore consisted of 72 scenes; one dependent variable (DET) and three orthogonal components representing the vegetation structure. The same analyses were performed using CV as the dependent variable for quantifying temporal determinism in structural complexity.

Due to the presence of a nested design in our sampling (i.e., four directions within each of 18 sites; Fig. 1), we performed a multiple linear regression test with restricted randomization (Manly, 2007). The idea of a randomization test for nested design is based on the concept of exchangeable units. Exchangeable units are groups of observations that are equally likely to have occurred in any order when the effect being tested does not exist (Manly, 2007). Steps of the permutation test were as follows: (1) calculate the pivotal test statistic  $t_{\text{obs}}$  for the multiple linear regression between the principal components as predictors and DET as the response variable, (2) randomly permute DET values of the four scenes (observations) within each site, (3) randomly permute groups of DET values between sites (i.e., permute blocs of four observations), (4) calculate  $t_{\text{perm}}$  for the multiple linear regression between the principal components and the permuted DET values, (5) repeat steps (2) to (4) 9999 times, and (6) for a two-tailed test, calculate the number of times  $t_{\text{perm}}$  obtained under randomization falls outside the limit interval  $[-t_{\text{obs}}; t_{\text{obs}}]$ . The probability  $p$  of accepting the null hypothesis is the number of times  $t_{\text{perm}}$  fell outside this interval divided by 10 000. This randomization test controls for spatial dependence in this nested design and is also less sensitive to multinormal assumptions of the linear regression.

### 3. Results

Fig. 4a reports  $D_f$  and MIG values for the 101 simulated images. The dashed line on the y-axis indicates the fractal dimension ( $D_f = 2.5$ ) at which the ruggedness of a grey-level surface yields scale invariance (i.e., Brownian random walk) across all scales (Schepers et al., 1992; Keitt, 2000). The dashed line on the x-axis indicates the critical intermediate state of structural complexity (MIG  $\approx 0.4$ ) previously reported in forest images of the same ecosystem (Proulx and Parrott, 2008). Beyond the fact that MIG and  $D_f$  are strongly correlated within this interval, the point that MIG  $\approx 0.4$  when  $D_f \approx 2.5$  will be further discussed. Fig. 4b illustrates the relationship between DET and CV measures of temporal determinism in structural complexity across multiple scales. The correlation between the two measures is positive but scattered (Pearson's  $r = 0.32$ ), indicating that each measure captures a different facet of temporal determinism. Using these same two measures, Proulx et al. (2008) achieved a similar

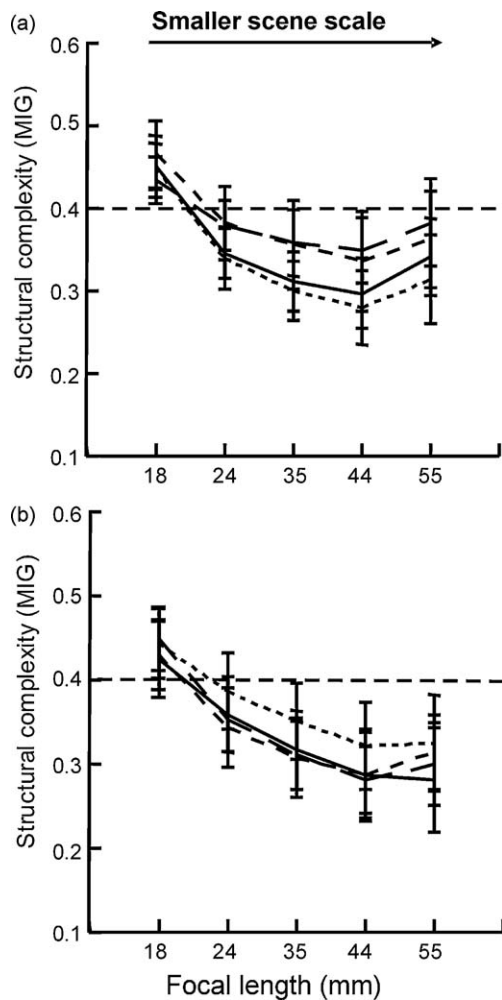


**Fig. 4.** Correlation between (a) the fractal dimension  $D_f$  and structural complexity MIG for 101 simulated images ( $1000 \times 1000$  pixels) and (b) between the multivariate coefficient of variation CV and DET as multiscale measures of temporal determinism ( $n = 72$  forest scenes).

conclusion following a re-evaluation of the diversity–stability relationship in a theoretical plant competition model.

As determined by the focal length gradient 18, 24, 35, 44, and 55 mm, scene scales corresponded respectively to scene extents of 18, 14, 10, 8, and 6 m wide at the focus distance. The shape of the MIG response curve across scene scales was a concave function in 60 out of the 72 scenes and was linearly decreasing with decreasing scene scale in the remaining 12 others. Fig. 5 shows these typical response curves for two sites and each of the four directions. The dashed line specifies the maximum state of structural complexity (MIG  $\approx 0.4$ ; see Section 4). This critical state is reached in a majority of images at either small or large scene scales, but generally not at the intermediate scales. Scenes captured in different directions within a given site tended to be more similar in structural complexity at a focal length of 18 mm, whereas they appeared to differ in average structural complexity at smaller scales (Fig. 5). In addition, temporal variability increased as the scene scale became smaller. Although more subtle, this time–scale interaction is supported in Fig. 5 by the presence of larger error bars at smaller scales.

Among our 11 forest descriptors we found three principal components of the vegetation structure (Fig. 6), explaining respectively 28, 22 and 17% of the overall variation among scenes, for a total of 67%. The first component depicted a gradient of forest scenes ranging from an open overstorey vegetation layer (negative values on PCA 1) to a closed overstorey layer (positive values). The

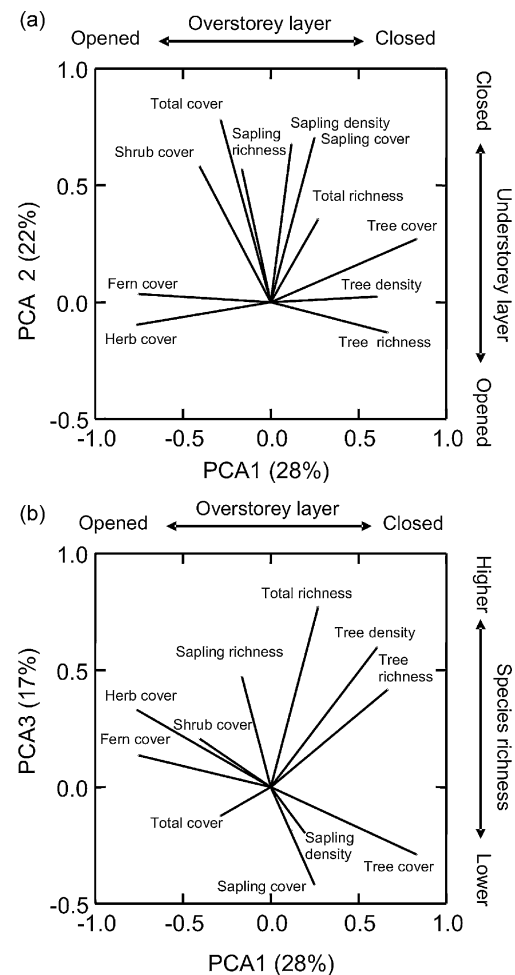


**Fig. 5.** Response curves of time-averaged MIG estimates across five focal lengths (scene scales). Each line is a different direction within (a) site 36 and (b) site 26. Directions from top to bottom in panel (a) North, East, West, and South. Error bars ( $\pm 1$  S.D.) represent the time variation for each direction–scale combination. The dashed horizontal line indicates the state of maximum structural complexity.

second component distinguished scenes having an open understorey vegetation layer (negative values on PCA 2) from those having a closed understorey (positive values; Fig. 6a). Finally, PCA 3 showed a gradient of tree species richness, with scenes having higher species counts on the positive side and those having lower counts on the negative side (Fig. 6b).

Table 1 reports the standardized slope coefficients of the principal components, for their multivariate relationship to DET and CV independently. The randomization test indicates a significant effect of the vegetation structure ( $p < 0.01$ ) on DET and a percentage of explained variation of 19% ( $R^2 = 0.19$ ). A higher determinism (DET) was observed in sites negatively associated to the first two principal components (i.e., less dense overstorey and understorey vegetation layers), and positively to the third one (i.e., higher tree species richness; Table 1). Although the positive relationship between tree species richness (PCA 3) and DET turned out to be marginally significant in the model ( $p = 0.065$ ), the fact that PCA 3 still explains a considerable fraction of the residual variance may suggest the existence of a non-trivial effect. When using CV as a measure of temporal determinism, only the first principal component showed a significant relationship to CV for an overall  $R^2 = 0.12$  (Table 1).

To facilitate interpretation of the multiple regression, we show graphically two variables that revealed apparent trends against



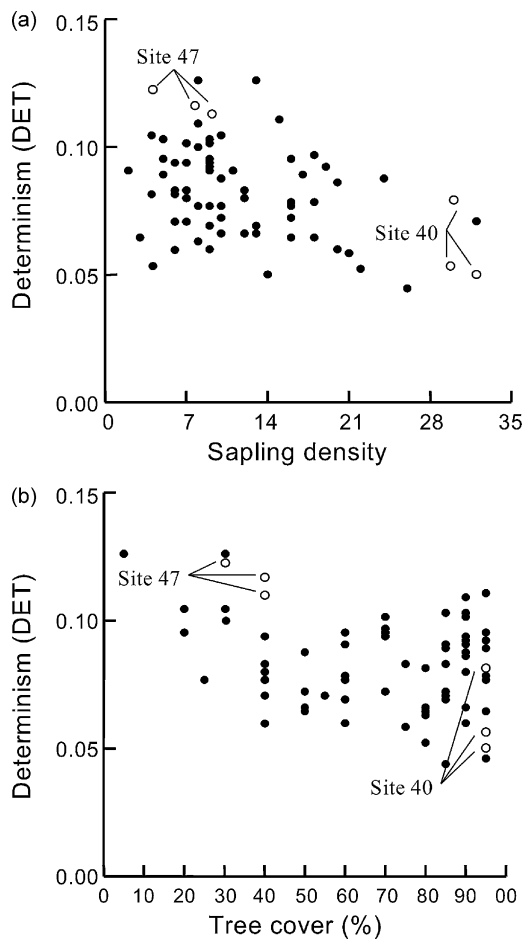
**Fig. 6.** Principal component loadings (eigenvectors standardized to the square root of their respective eigenvalues) of the 11 forest descriptors, for (a) PCA 1 and PCA 2, and (b) PCA 1 and PCA 3. The principal components 1–3 explained respectively 28, 22 and 17% of the overall variation in the vegetation as captured by the 11 forest descriptors.

DET. Deterministic temporal dynamics were absent when the sapling density was high ( $>14$  individuals; Fig. 7a). On the other hand, a large range of DET estimates was present at low sapling densities (Fig. 7a). Tree percent cover was the other forest descriptor which showed a univariate relationship with DET (Fig. 7b). Stochastic dynamics were largely absent when the tree cover was low ( $<40\%$ ), whereas a broader range of DET estimates

**Table 1**

Results of two randomization tests for the multiple regression between the forest vegetation predictors (PCA 1–3) and each response variable: determinism (DET) and coefficient of variation (CV). Partial  $R^2$ ,  $t$ -, and  $p$ -values were obtained by including the model terms stepwise.

Effect	Std. coefficient	$t$ -Value	$p$ -Value	$R^2$
DET				
PCA 1	−0.2604	2.33	0.0365	0.07
PCA 2	−0.2696	2.34	0.0467	0.07
PCA 3	0.2153	1.97	0.0651	0.05
Model		3.95	0.0037	0.19
CV				
PCA 1	−0.3131	2.75	0.0182	0.10
PCA 2	−0.1322	1.16	0.2453	0.02
PCA 3	0.0356	0.31	0.6491	0.00
Model		3.95	0.0037	0.12



**Fig. 7.** General trends for (a) sapling density and (b) tree cover forest descriptors in relationship to DET. The sample size in each graph is  $n = 72$ . Field sites 40 and 47 represent respectively forest shade and woodland shade habitats (see text).

was observed in scenes having a dense tree cover ( $>80\%$ ; Fig. 7b). Marked deterministic and stochastic dynamics were observed respectively in sites 47 and 40, for at least three of the four scenes (Fig. 7). Site 47 was an open floodplain habitat characterized by a dense herb cover and a sparse tree cover. Site 40 was a maple dominated habitat including sapling regeneration within a fully developed canopy. A scene with pure deterministic dynamics in structural complexity would obtain a DET value close to 0.2 ( $DET \approx RR$ ).

#### 4. Discussion

Our results support the presence of scaling nonlinearities in structural complexity and a gradient of temporal determinism in an old-growth forest ecosystem. Stochasticity of structural complexity dynamics at multiple scales increased in scenes characterized by a more developed understorey and overstorey canopy, but decreased for scenes with higher tree species richness. To make forest dynamics in structural complexity yet more challenging, different scene directions revealed contrasting behaviours in their time-scale interactions. A majority of our 18 sites yielded dissimilar multiscale dynamics among their four directions as concluded from the RP-RQA analysis, even if time-averaged MIG estimates were often found to be similar at larger scene scales. These results together suggest that different viewpoints (or observation scales) within a forest ecosystem, embedded in different scenes, themselves embedded in different forest habitats, can attain a maximum of structural complexity at

different times. Such time-scale interactions are evocative of how the addition of spatial and temporal degrees of freedom can make the understanding of ecosystem dynamics increasingly complex (Solé and Bascompte, 2006).

One central message of this work is that structural complexity in an old-growth forest ecosystem is a multifaceted function of time, space, and observation scale. If we acknowledge that structural complexity in natural images represents a valid ecological indicator of the developmental state of an ecosystem, hence both the local instantaneous states in space and their interrelated dynamics could help characterizing ecosystem development. An increasing body of literature is supporting the principle that a more developed (or mature) ecosystem tends towards higher levels of structural complexity (i.e., its structural state is intermediate between perfect uniformity and randomness). Nevertheless, a developed ecosystem also possesses enough dynamical suppleness in structural complexity to oppose the disturbance gradients without falling into unstable regimes (i.e., its dynamical behaviour is intermediate between perfect determinism and stochasticity). This balanced behaviour of ecosystems is typically expressed using different labels such as: 'edge of chaos', 'intermediate disturbance hypothesis', 'diversity-stability hypothesis', or 'self-organization'. Mechanisms involved in the maintenance of intermediate structural and functional heterogeneity in nature remain obscure and may lie deep at the heart of complex system studies. Nevertheless, this field study is one of the first to demonstrate that old-growth forest ecosystems behave like complex systems exhibiting nonlinear vegetation structure and dynamics across scales.

##### 4.1. Mean information gain as a measure of structural complexity

Previous results from the same system revealed that, at a small scene scale (1.25 m focus distance), the MIG of grey-level variations in natural images is positively related to plant species richness. At a larger scene scale (15 m focus distance) the understorey and overstorey vegetation patterns showed phenological signatures in MIG which reached their maximum of structural complexity in mid-summer and their minimum in spring and fall (Proulx and Parrott, 2008). The present study builds on this work by revealing a multivariate relationship between the forest vegetation structure and temporal determinism across five observation scales. These results together support the premise that structural complexity (MIG) in natural images is a realistic indicator of ecosystem development.

We reported the positive linear correlation between MIG and  $D_f$  over the range ( $0 < \text{Hurst's exponent } H < 1$ ) for which dimension estimates of fractional surfaces are known to apply. This correlation is useful to investigate at this stage since fractals have previously attracted more attention than information theoretic measures to characterize the complexity of 2D patterns. For example, using a spatially and dynamically explicit community model, With and King (2004) reported that species assemblages evolving on landscapes with an intermediate degree of order ( $D_f = 2.5$ ) were able to attain higher levels of species richness. The correlation between MIG and  $D_f$  is strong because we did not have to estimate the fractal dimension from an algorithm, thus our simulated images could be considered as perfect fractals in terms of their Fourier spectrum. In practice a much noisier positive correlation occurs when computing the two measures on natural images.

Another aspect of the correlation between  $D_f$  and MIG merits our attention: the maximum of complexity is attained when  $D_f \approx 2.5$  and  $MIG \approx 0.4$ . For theoretical reasons, a 2D fractional Brownian function should yield a maximum of complexity for MIG when the process is a random walk ( $H \approx 0.5$ ), thus when  $D_f \approx 2.5$  or alternatively  $\beta \approx 2$ . Interestingly, this state appears to be a



universal property of natural images and has recently been put forward to explain the co-evolution of visual systems along with spectral characteristics of the environment (Torrallba and Oliva, 2003). A fractal dimension of  $D_f = 2.5$  implies a natural surface that forms as a result of the summation of weakly interacting local processes at multiple scales (i.e., there are no key or dominant drivers). Using a different formalism, Proulx and Parrott (2008) suggested that  $MIG \approx 0.4$  represents a maximum state of complexity in close-range forest images. Although speculative, this specific state has been termed 'critical' because of its analogy with the behaviour of self-organized systems.

#### 4.2. Recurrence quantification analysis as a measure of temporal determinism

Recurrence analysis of the multiscale dynamics in structural complexity revealed two extremes on a continuum of behaviour: a stochastic type associated with more developed canopies, including denser sapling density and high tree cover, and a deterministic type associated with open canopies, including low sapling and tree cover. In the field these two behaviours were exemplified by sites 40 and 47, which respectively correspond to forest shade and woodland shade sites following Endler's nomenclature (Endler, 1993). The light spectrum of forest shade sites is mostly ambient light made of sunflecks or light transmitted through leaves, whereas light gaps shape the spectrum of woodland shade sites by penetrating the forest understorey deeper (Endler, 1993). Alternatively, the natural phenology of deciduous forests would recreate these light habitats along a spring-fall temporal gradient as follows: large gap  $\rightarrow$  woodland shade  $\rightarrow$  forest shade  $\rightarrow$  woodland shade  $\rightarrow$  large gap. Since forest shade sites must undergo a larger seasonal gradient of light habitats than woodland shade sites, the dynamics of mature sites (forest shade) over the growing season could appear more stochastic. However, this line of reasoning was not supported here by the relationship observed between PCA 1 and CV, which rather suggests a decreased seasonal variance in the overstorey vegetation layer of forest shade sites.

Species abundance (or biomass) has been the most common currency proposed so far to study temporal dynamics in ecological systems. Our results based on the multiscale dynamics of structural complexity measures, instead of customary species abundance estimates, support the hypothesis of a positive relationship between tree species diversity and determinism in forest habitats. The relationship between diversity and determinism was detected independently of (and after adjusting for) the effects of the overstorey and understorey vegetation structure. One could therefore argue that any deterministic system is likely to remain in the same state for a longer period of time, and thus to have more stable local trajectories. This definition of dynamical stability contrasts with the CV definition (Lehman and Tilman, 2000; Ives and Hughes, 2002), which averages the overall variation in multivariate time-series and obscures any information about the local trajectories in time. CV and DET capture different aspects of the stability behaviour. While the CV is concerned with the amplitude of the temporal change in structural complexity and how this change synchronizes across scales, DET tells us about how smooth and regular (i.e., recurrent) is the change in structural complexity (Proulx et al., 2008). Our results advocate that DET is potentially a superior measure of ecosystem stability than CV, but the question needs to be directly addressed through a systematic comparison of the two measures in empirical tests of the diversity–stability hypothesis.

## 5. Conclusion

The present study innovates on two aspects: (1) structural complexity (MIG) in close-range digital images was used as a local

ecological indicator of ecosystem development in place of community-wise estimates that are logistically more difficult to sample; (2) the multivariate RP-RQA approach permits a robust yet flexible characterization of the temporal dynamics embedded in field data. The efficiency of the photographic approach to detect structural complexity could allow field monitoring of an ecosystem, and not just populations or communities, at a high resolution in scale, space and time. To quantify temporal signals decoupled on a scene-by-scene basis has the advantage to precisely point out where and when a significant change of dynamics has occurred. Assuming that ecological indicators in structural complexity and temporal determinism can be identified, regions of the landscape which are drifting away from their target indicator state could be detected and, if necessary, local management practices initiated. For instance, it would be interesting to track, year after year, the relative position of the forest scenes in Fig. 7. Finally, the complete methodology described here may be seen as a quantitative extension to rephotography, a method which typically consists of forming an historical series of one site by the act of repeat photography from the same viewpoint (Kull, 2005).

Future research directions would include: (1) testing the methodology on different ecosystems and making predictions about their relative level of development; (2) correlating other field descriptors with complexity measures to help understand ecological mechanisms; (3) promoting theoretical and empirical advances in the study of self-organization; (4) constructing extended multiscale time-series across space and time at high resolution; (5) inspecting the effect of scene scales across a wider gradient of photographic viewpoints; (6) achieving a complete standardization of the photographic settings to facilitate the comparison between studies; (7) integrating the method in the growing number of wireless sensor networks.

## Acknowledgements

We thank Véronique Tremblay, Yan Levasseur, Gabriel Valois and André Doyon for their assistance in taking photographs. We are also indebted to Dr. Martin Lechowicz and everyone at the McGill's Research Station on Mont Saint-Hilaire. Professors Madhur Anand, Jeffrey Cardille, André Roy and two anonymous reviewers also provided helpful comments on the manuscript. This research was supported by a NSERC (Natural Sciences and Engineering Research Council) grant to L. Parrott and a FQRNT (Fond Québécois de Recherche sur la Nature et les Technologies) scholarship to R. Proulx.

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