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Identifying scales of pattern in ecological data: a comparison of lacunarity, spectral and wavelet analyses

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Abstract

Identifying scales of pattern in ecological systems and coupling patterns to processes that create them are ongoing challenges. We examined the utility of three techniques (lacunarity, spectral, and wavelet analysis) for detecting scales of pattern of ecological data. We compared the information obtained using these methods for four datasets, including: surface temperature across space (linear transect), surface temperature across time, understory plant diversity across space (linear transect), and a simulated series of known structure. For temperature and plant diversity across the transect, we expected to find dominant scales of pattern of approximately 220 m and, for plant diversity scales of pattern of >450 m, corresponding to management activities on the study landscapes. For temperature across time, we predicted a dominant scale of 24 h. The simulated data included a sine wave with a known period of 9.9 units, an edge at approximately 30 units, and a random component. The different analyses provided unique but complementary information. Lacunarity and spectral analyses were most consistent with each other across datasets, both indicating a dominant scale of pattern at 400–500 m (coarser than expected) for the transect temperature series, a lack of dominant scale in the pattern of understory diversity, and scales of pattern at 1.8–5.1 and 8.5–11.1 units (≈wavelength) for the simulated data series. Spectral analysis best approximated an expected, 24 h period in the temporal temperature series. Wavelet variance detected finer scales of pattern (240 m) in transect temperature and suggested patterns in plant diversity at scales of 460 and 1100 m. By retaining locational information, only the wavelet transform and associated position variance detected the abrupt edge in the simulated data series. Wavelet analysis also emphasized variability, even within cyclic phenomena, not identified by spectral or lacunarity analyses, and suggested hierarchical structure in the pattern of understory plant diversity. The appropriate technique for assessing scales of pattern depends on the type of data available, the question being asked, and the detail of information desired. This comparison highlighted the importance of: (1) using multiple techniques to examine scales of pattern in ecological data; (2) interpreting analysis results in concert with examination and ecological

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knowledge of the original data; and (3) utilizing results to direct subsequent descriptive and experimental examination of features or processes inducing scales of pattern.

Keywords: Lacunarity; Spectral analysis; Wavelet analysis; Landscape structure; Scale; Spatial heterogeneity

1. Introduction

Ecological systems are characterized by spatial and temporal heterogeneity. Much research in landscape ecology is based on the assumption that processes at specific scales of space and time drive this complexity in landscape structure (Delcourt and Delcourt, 1988; Holling, 1992). Therefore, a meaningful approach for assessing scales of pattern is essential to augment the theoretical understanding of these relationships. Further, consistent methodology for coupling patterns and processes at appropriate scales would increase confidence in the predictions of landscape dynamics used in management and planning (Bradshaw and Fortin, 2000; Wu and Qi, 2000).

A number of quantitative methods have been proposed to describe the spatial heterogeneity of landscapes and help provide information about the relationships between processes (e.g., landscape management or natural disturbance) and spatial patterns (e.g., Turner, 1989; Li and Reynolds, 1995; McGarigal and Marks, 1995; Wu et al., 2000; Lundquist and Sommerfeld, 2002). This quantitative underpinning is vital when researchers across geographic areas and disciplines are comparing spatial patterns of data. Indices of landscape structure provide a standard language with which both managers and researchers can describe structural features, compare information about different systems, and monitor spatial dynamics over time and space. However, it is often difficult to choose the most appropriate measures of pattern for the ecological question being investigated, and to interpret correctly the information that is conveyed (Gustafson, 1998).

Identifying and quantifying structure across scales can add to the complexity of examining pattern–process relationships. The components of scale, both grain and extent, play a role in changing the appearance and description of a landscape (e.g., Turner et al., 1989; Hargis et al., 1997; Bradshaw and Fortin, 2000; Lundquist and Sommerfeld, 2002). To be characterized adequately, pattern–process relationships must be assessed at the multiple scales (Levin, 1992) relevant to the inherent structure (or rate) of the system (or process) being studied (Holling, 1992), or the scale of perception of the organism of interest (Wiens, 1989). Prior to conducting any patch-based characterization or analysis of a landscape, it is essential to identify the scales of pattern or the distance between centers of adjacent gaps and patches (Dale, 2000) relevant to the ecological system being studied (Gustafson, 1998). The scales at which structure exists within a dataset can also relate to specific, physical features on a landscape, and suggest the processes that determine or modify data patterns. Techniques are needed to elucidate scales of heterogeneity in a landscape. The influences of different quantification techniques and data types on the assessment of scales of pattern must also be considered (Dale et al., 2002; Perry et al., 2002)

We examined three different quantitative techniques (spectral, wavelet, and lacunarity analyses) used to extract information on scales of pattern for continuous or evenly spaced data. These techniques have been used to evaluate the inherent structure in data and to infer characteristics of the processes that imposed those patterns. However, there are differences in the forms of data used, the expectations regarding the patterns that can be detected, and in the information that can be produced about data structure (Table 1). Our goal in this analysis was to aid researchers in choosing methods for multiscale pattern analysis. We undertook to: (1) compare the utility of these techniques for describing data structure and the scales at which patterns in empirical and simulated data are detected; (2) assess the ability of the techniques to suggest causal mechanisms for the patterns and, thus, subsequent avenues of study; and (3) determine how the information obtained from these techniques differed among variables of interest.

Table 1
Comparison of characteristics of lacunarity, spectral and wavelet analysis for examining scales of pattern in ecological data

Characteristic	Lacunarity	Spectral	Wavelet
Scale or type of pattern best detected	Inconsistent (imprecise estimates?[a])	Repeating, cyclical, fine scale	Specific to analyzing wavelet
Type of data	Binary or continuous	Continuous	Continuous
Data dimensions	1 or 2 (also 3[f])	1 or 2	1 or 2
Missing data OK	Yes	No	No
Robust to nonstationarity	Yes	No	Yes
Sensitive to edges	No	Yes	Yes
Robust to nonnormality	Yes	No (may not be a concern)	Yes
Global summary	Yes	Yes	Yes (variance)
Retention of locational info	No	No	Yes (transform, position variance)
Detection of multiple scales	Yes?	Yes	Yes
Detection of hierarchical structure	Yes?	No	Yes
Hypothesis testing possible	Yes[b]	Yes (use of traditional inference methods, e.g., ANOVA[c]; comparison to hypothesized distributions[d])	Yes (use of bootstrapping, Monte Carlo techniques[e])

[a] Dale (2000).
[b] McIntyre and Wiens (2000).
[c] Keitt (2000).
[d] Turner et al. (1991).
[e] Keitt (2000), e.g., Torrence and Compo (1998).
[f] Exploration of three-dimensional pattern detection by Chen et al. (2004).

2. Analysis techniques

2.1. Lacunarity

Lacunarity is a "scale-dependent measure of heterogeneity or texture" (Plotnick et al., 1993). It describes the distribution of gaps in the data across scales, with higher lacunarity indicating a greater distribution (or heterogeneous arrangement) of gap sizes (Plotnick et al., 1993). The lacunarity index can also suggest scales of analysis at which the data appear random, and hierarchical structure within data (Table 1; Plotnick et al., 1996; but see Dale, 2000). Lacunarity has been used to measure scale-dependent changes in patterns of habitat distribution (Plotnick et al., 1993; Henebry and Kux, 1995; Krug and Henebry, 1995 using Landsat TM; Henebry and Kux, 1997 using Synthetic Aperture Radar over multiple seasons), seedling distribution (Plotnick et al., 1996; Larsen and Bliss, 1998), sediment transport rates (Plotnick et al., 1996), and soil pore structure (Zeng et al., 1996). McIntyre and Wiens (2000) used lacunarity to quantify both landscape heterogeneity and patterns of landscape use by beetles, thus linking structure and function through a common metric.

Fractal lacunarity provides an alternative to fractal dimension (D) for characterizing the deviation of objects and patterns from translational invariance, i.e., the similarity, at a specific scale, of different portions of the data (Gefen et al., 1983; Plotnick et al., 1993). Lacunarity can provide a unique descriptor (and thus more information) in some cases where objects have a common value of D (Zeng et al., 1996). However, Dale (2000) noted different lacunarity results for complementary patterns and questioned the precision of the technique for determining the distributions of patch sizes.

Lacunarity was originally developed to examine binary data but was later extended for use on continuous datasets (see Plotnick et al., 1996). The value of the index, $\Lambda(w)$, is determined by the ratio of the variance of sites occupied by a habitat or feature of interest to the square of the mean number of occupied sites, determined within a gliding box of size w (Plotnick et al., 1993):

$$\Lambda(w) = \frac{1 + \text{variance}(w)}{(\text{mean}(w))^2}$$

The relationship between lacunarity and box size can discriminate among random, clustered, or regular organization, and indicate ranges of scales over which a data pattern is self-similar (Plotnick et al., 1996). The use of the gliding box ensures complete sampling of the transect or map, and the technique has the advantage of being insensitive to map (or transect) edges (Plotnick et al., 1993; Dougherty and Henebry, 2002).

2.2. Spectral analysis

Spectral (Fourier) analysis is used to assess the periodicity (i.e., scale over which a pattern repeats itself) in a temporal or spatial series (Turner et al., 1991). In ecology, the technique has also been used to assess the periodicity of population dynamics over time (e.g., Bigger, 1973; Steven and Glombitza, 1972), to assess scales of spatial pattern in marine plankton populations (Platt and Denman, 1975) and terrestrial vegetation (e.g., Usher, 1975; Ripley, 1978; Greig-Smith, 1983; Renshaw and Ford, 1983; Cullinan and Thomas, 1992), and to examine predator–prey associations over space and time (e.g., Logerwell et al., 1998). The periodogram is sensitive to repeating, cyclic patterns in data and to small-scale patterns (O'Neill et al., 1991; Turner et al., 1991), and the technique is appropriate for use in both exploratory analysis and hypothesis testing (Platt and Denman, 1975). However, spectral analysis is most robust when data are stationary (i.e., have constant mean and variance over space or time). The analysis can be relatively insensitive to large-scale patterns and other (e.g., noncyclic) types of spatial patterns (Legendre and Fortin, 1989; Gardner, 1998).

Spectral techniques decompose a data series, x_i, with n observations, into a sum of sine and cosine waves with different amplitudes and Fourier frequencies, ω:

$$x_i = \bar{x} + \sum_{k=1}^{m} (a_k \cos(\omega_k i) + b_k \sin(\omega_k i))$$

where a_k and b_k are the cosine and sine coefficients respectively, $\omega_k = 2\pi k/n$, and $m = n/2$ if n is even or $m = (n - 1)/2$ if n is odd.

The periodogram, a form of graphical output, represents the simultaneous least squares fit of this linear combination of sine and cosine functions of different frequencies. The periodogram thus describes the distribution of variance in the data series among frequencies (Renshaw and Ford, 1983), and an estimate of the relative importance of the fitted waves of period k. The choice of values of the Fourier frequencies ensures orthogonality of the periodogram ordinates (Percival, 1993). Periodograms can show high fluctuations; spectral density, a periodogram smoothed using a weighted moving average, is often used to reduce the variance and allow for easier interpretation of patterns (Priestley, 1981; Dale, 1999). Peaks in the periodogram or spectral density can indicate the scale(s) at which the data pattern changes, or identify the dominant (explaining large portions of variation in the data) frequencies (scales) in the data. For example, Turner et al. (1991) used spectral analysis to identify scales of patchiness in the distribution of two species. The similarity in the scales at which peaks occurred in the periodograms suggested that the same underlying process might be responsible for the spatial pattern of both species.

Although spectral analysis may suggest average scales of pattern and multiple scales of heterogeneity (Cullinan and Thomas, 1992), this information may not always be apparent from a periodogram, and hierarchical structure is difficult to identify. The interpretation of plots can be difficult due to spurious peaks (Cullinan and Thomas, 1992; Dale, 1999). For example, the determination of scales of pattern in the data based on the frequency at which spectral density is maximal can be particularly confounded when spectral density tends to zero or infinity at the origin (Beran and Ghosh, 2000). The latter can occur if the series has not been detrended sufficiently and is nonstationary, or can imply a long memory process, i.e., a stationary process in which the correlations between observations that are far apart decay to zero more slowly than expected from independent data (Beran, 1994); long memory may be reasonably hypothesized to exist for an ecological process across time or space. Trend removal to achieve stationarity may also affect the bias of the spectral density estimate at specific frequencies; for small sample sizes this bias is worth approximately correcting (e.g., see Priestley, 1981).

2.3. Wavelet analysis

Wavelet analysis is a relatively new technique in ecological research, first introduced by Bradshaw and Spies (1992) to examine canopy structure. The technique has since been used to explore multiscale, patterns in microclimate along transects (Saunders et al., 1998; Redding et al., 2003), soil variability (Lark and Webster, 1999), solar activity (Rigozo et al., 2002), understory plant diversity (Brosofske et al., 1999; Chen et al., 1999; Perry et al., 2002), plant productivity (Csillag and Kabos, 2002), and land cover (Dale and Mah, 1998), and to examine properties of neutral landscapes (Keitt, 2000). Temporal scales of pattern in atmospheric flow (Gao and Li, 1993), relationships between precipitation and hydrologic discharge (Bradshaw and McIntosh, 1994), concentrations of chlorophyll at the ocean surface (Nezlin and Li, 2003), and the El Niño Southern Oscillation (Torrence and Compo, 1998) have also been studied.

Wavelet analysis mathematically approximates a data series by a linear combination of functions (wavelets) with specific scales (resolutions) and locations (positions along the data series). In discrete form, the transform is expressed as:

$$W(a, b_i) = \frac{1}{\sqrt{|a|}} \sum_{i=1}^{n} f(x) \cdot g\left(\frac{x - b_i}{a}\right)$$

where the shape (i.e., dimension of the analysis window) of the analyzing wavelet, $g(x)$, changes with scale, a, and the analyzing wavelet moves along the series of data, $f(x)$, centered at each point, b_i, along the data series (Bruce and Gao, 1994; Li and Loehle, 1995). The size of the coefficient by which a wavelet is multiplied to produce the final data representation indicates the importance of that wavelet function for reproducing the data signal (Bruce and Gao, 1994).

One advantage of wavelet analysis over other signal approximation methods, such as spectral analysis, is the ability to choose the type of function (i.e., wavelet) with which to analyze the data (Bradshaw, 1991). Smoothness, width, and symmetry vary among classes of wavelets (e.g., see Graps, 1995; Torrence and Compo, 1998). For example, one could choose a step function, such as the square Haar wavelet (e.g., Dale and Mah, 1998), to approximate data that are characterized by a series of abrupt, discrete changes. Alternatively, a relatively smooth wavelet from the Daublet, Symmlet, or Coiflet families (see Bruce and Gao, 1994) would be appropriate for producing a pattern of continuous gradients, as is common for many environmental variables, such as soil moisture and nutrients. The appropriate wavelet can be chosen based on the type of data and the hypothesized pattern. One can also relate a strong wavelet coefficient to its position in space or time along the data series, suggesting specific features that may influence the observed pattern. More importantly, wavelet analysis does not is robust to nonstationarity in data. The technique allows interpretation of signals that change over time or space (Nezlin and Li, 2003). This confers a distinct advantage over the Fourier transform, given that most data collected over broad spatial scales reflect environmental gradients and are nonstationary.

The wavelet (scale) variance (Dale and Mah, 1998):

$$V(a) = \frac{\sum_{i=1}^{n} W^2(a, b_i)}{n}$$

which is the average contribution of wavelet coefficients from all positions along the transect for a given scale, can be used to examine overall, "global" structure (i.e., scales of pattern) within the data (Bradshaw and Spies, 1992). The scale corresponding to a peak in wavelet variance is an estimate of the scale of dominant structure within the data (Gao and Li, 1993; Li and Loehle, 1995). Position variance,

$$P(b) = \frac{\sum_{i=1}^{m} W^2(a_i, b)}{m}$$

the average of the squares of the wavelet coefficients across scales (a) from 1 to m, at any one position (b) in time or space, can suggest features that produce high variance in the data (e.g., see Dale and Mah, 1998).

The type and detail of information about data structure provided by the wavelet variance can be compared to that produced by lacunarity or spectral analysis. The wavelet transform can clarify the structure of highly variable patterns concurrently across multiple scales, while retaining locational information in space or time. Thus, the wavelet transform provides "local" information which is supplementary to the global results produced with wavelet variance, or spectral or lacunarity analysis. Position variance complements the information provided by the wavelet transform, by indicating locations within the data that contribute to variance averaged across all (not just a single) scale. These results of wavelet analyses are relatively insensitive to random variation in a series, conferring an advantage over techniques such as spectral analysis. Though the heights of peaks in variance may vary, the scales (wavelet variance) or locations (position variance) of peaks are retained for relatively high levels of random error in a regular pattern (e.g., Dale and Mah, 1998).

3. Data collection and development

3.1. Field site

We analyzed the scale of pattern of three variables measured on a field transect, and of a simulated dataset of equal length. We collected field data along an east-west transect through the Chequamegon National Forest, northern Wisconsin, USA. The study area is managed by the US Forest Service as a mosaic of small harvest units of approximately 16 ha, to mimic the historical, natural disturbance regime. The topography in the area is flat to rolling and soils are uniform, loamy, glacial outwash sands (Chequamegon National Forest, 1993). Dominant overstory species include planted red pine (*Pinus resinosa* Ait.) and naturally occurring jack pine (*P. banksiana* Lamb.), with patches of hardwoods resulting from successional dynamics and silviculture.

3.2. Datasets

The first data series, TSPACE (hereafter also called transect temperature), is the average morning temperature (°C) recorded every 5 m along a 3820 m transect, resulting in 765 observations (Fig. 1A). We used copper–constantan thermocouples, secured at the ground surface, and Campbell Scientific CR10 dataloggers to measure temperature at each point every 20 s, and average these data every 15 min. We calculated the morning (05:00–11:00 h) average for each point. Any single point was monitored for 10 days to 2 weeks over the study period (Julian Days 163 through 237, 1995) as only 760 m (152 points) could be measured simultaneously due to equipment limitations. We thus standardized the temperature averages based on surface temperature measured concurrently at a reference climate station in the same landscape (see Saunders et al. (1998), for computational details).

The second data series, SHANND, is understory plant diversity (Shannon–Wiener index), calculated

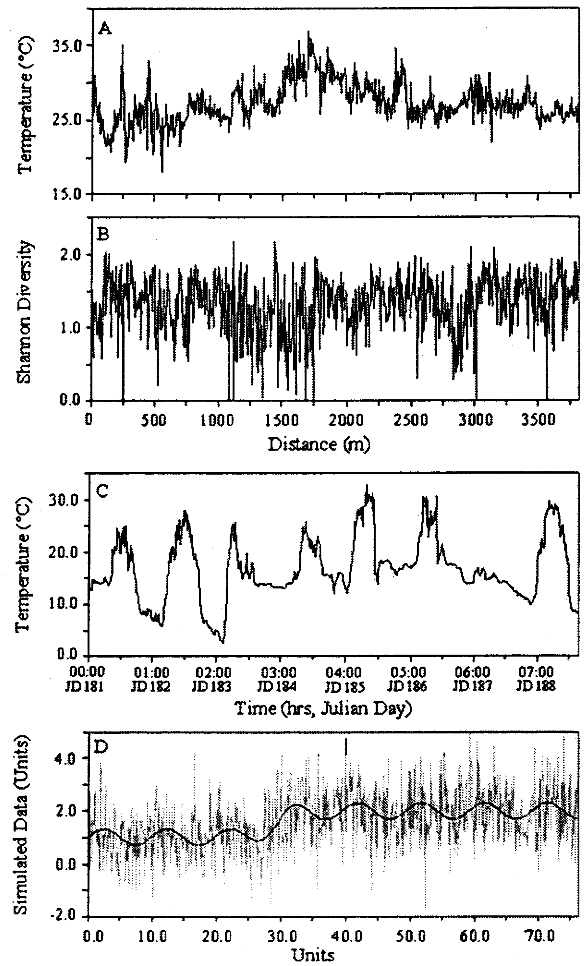

Fig. 1. Datasets used in the comparison of lacunarity, spectral, and wavelet analysis to detect scales of pattern. $n = 765$ evenly spaced points for all series: (A) TSPACE, average morning (05:00–11:00 h) surface temperature (°C) along a transect; (B) SHANND, understory plant diversity (Shannon–Wiener index) from percent cover in 1 m^2 quadrats along a transect; (C) TTIME, surface temperature (°C) across time at a single point; and (D) SIM (gray), a simulated dataset consisting of a random series imposed on a regular sine wave (black).

from percent cover in 1 m^2 quadrats centered on the same points at which surface temperature, TSPACE, was monitored (Fig. 1B, see Brosofske et al., 1999). Plant data were also collected in 1995. Dominant (occurred in >30% of all quadrats) understory plants in the study area included *Amelanchier* spp., *Diervilla lonicera*, *Gaultheria procumbens*, *Rubus alleghaniensis* (shrubs), *Carex* spp. (graminoids), and *Aster macrophyllus*, *Maianthemum canadense*, *Pteridium* *aquilinum*, and *Trientalis borealis* (herbs). We recorded a total of 68 understory shrubs, graminoids and herbaceous species along the transect.

The third data series, TTIME (Fig. 1C), is surface temperature measured as for TSPACE, and recorded 15 min at a single point along the transect (1300 m) that had constant, reliable coverage over the study period. TTIME was restricted to values from Julian Day 181, 0:00 h to Julian Day 188, 23:00 h, to give a series of the same length as TSPACE and SHANND (i.e., $n = 765$).

We used a fourth, simulated data series, SIM (Fig. 1D), to examine the ability of the techniques to detect scales of pattern and features, such as abrupt changes, that are known to occur in the data. First, we produced a sine function:

$$y = \sin\left(x\frac{2}{\pi}\right) \times 0.3 + a + 1$$

where

$$a = 1 - e^{-(x/30)^{15}}$$

and $x = 0, 0.1, 0.2, 0.3, \ldots, 76.4$, to give $n = 765$. We then generated a random number series $z_1, \ldots, z_{765}$ where z was normally distributed with $\mu = 0$ and $\sigma^2 = 1$. The simulated series, SIM, was calculated as:

$$\mathrm{SIM}_i = y_i + z_i$$

for $i = 1$–765. One hundred iterations of SIM were produced using the same base sine wave with the addition of a different set of random numbers for each iteration.The function

$$f(x) = \sin(ax)$$

has a period of $2\pi/a$ and thus, by substitution, our sine wave should exhibit a period of π^2 or ~9.9.

3.3. Expected scales of pattern

Based on our knowledge of the landscape, we expected the datasets collected along a transect, TSPACE and SHANND, to show patterns of structure at scales of: (1) approximately 220 m, corresponding to the average width of management categories in the landscape, or (2) <100 m, corresponding to the sizes of the largest group of management patches (6 of 17 patches were <100 m; Saunders et al., 1998). We thought larger scales of pattern, from four management patches >450 m wide, might be detected in analysis of SHANND. However, we did not expect temperature patterns along the transect to resolve at the scale of these large management zones, except at very coarse resolutions. Features, such as roads, which bisect some management patches, create thermal patches within these vegetation zones which tend to persist even at resolutions greater than 400 m (see Saunders et al., 1998). For the series TTIME, we expected to detect a dominant scale of pattern of 24 h, reflecting temperature cycles through the course of a day.

Because the field data were collected along a single transect, we did not examine information on anisotropy that could be detected by the three methods. Field data collected at such a broad extent and at such fine resolution are, by necessity, limited to one or a few transects, and we present this analysis as an example of the level of information that can be derived from similar, empirical field data (in contrast to two-dimensional field data collected over a smaller extent (e.g., Csillag and Kabos, 2002), or remotely sensed two-dimensional data).

For the simulated data, SIM, we expected to be able to detect a scale of pattern of approximately 9.9 units, associated with the periodicity of the sine wave. We also hoped to distinguish the abrupt step at $x = 30.00$ (unit 300, see Fig. 1D). Analyses were conducted on all 100 iterations of SIM, to determine the influence of the random component of the series on the ability to detect the known features within the base series.

3.4. Data analysis

All four datasets were analyzed using lacunarity, spectral, and wavelet analysis. We compared the information on structure that could be obtained from the different techniques. We expected that analyses using these different techniques would provide complementary information about the scale of structure within datasets. For example, more global techniques, such as lacunarity or spectral analysis, might indicate scales at which to examine wavelet transforms of position variance for specific features in the data that appear to create repeating patterns. Lacunarity and wavelet techniques might provide parallel and complementary information on the hierarchical structure of data, or the multiple resolutions across which patterns are propagated in space or time. Wavelet transforms can be relatively difficult to interpret due to the volume of information (i.e., coefficients at multiple scales) along a data series. However, because they can be linked to geographical or temporal distance, wavelet transforms (and the averaged position variance) can help elucidate fine-scale features or processes that contribute to overall (broader) scales of pattern in the data, indicated by wavelet variance or the other methods examined here, and suggest experimental approaches to examine these relationships.

3.4.1. Lacunarity

Lacunarity analysis was performed on using STRATISTICS (for TTIME, TSPACE, and SHANND), provided by R.E. Plotnick (personal communication) and PASSAGE (Rosenberg, 2001). Dominant scales of pattern were inferred to occur at scales (box sizes) where there were breakpoints (i.e., abrupt (maximal) changes in the slope of the relationship between lacunarity and box size (see Plotnick et al., 1996)). To highlight locations where changes in slope were subtle, we examined the difference in slope at a point as a percentage of the average slope of lacunarity plots at surrounding points ($n = 5$). Similarly, subtle difference in decay curves of lacunarity can be detected by examining the percent deviation in lacunarity from self-similarity across scales (a straight line) and the first derivative of this value (see Dougherty and Henebry, 2002).

3.4.2. Spectral analysis

Spectral analysis was completed using the SPECTRA procedure of SAS (SAS, 1990). For SIM, we first removed the nonlinear trend:

$$f(x) = c + (ax) + (bx^2)$$

using the Marquardt iterative method of PROC NLIN (SAS, 1990) and subsequent spectral analysis was performed on the residuals. We confirmed that data series were still nonrandom using the WHITENOISE option (Bartlett's Kolmogorov–Smirnov statistic with Bonferroni corrected $P < 0.05$). Detrending apparently reduced nine of the 100 iterations of SIM to whitenoise, and spectral analysis was limited to the remaining 91 iterations. For analysis, we centered data about the mean, and specified a three-term moving average with equal weights for all terms when smoothing the periodogram to produce the spectral density estimates. We hoped to thus minimize bias introduced by the smoothing (e.g., see Priestley (1981), for discussion of bias from kernels and weighting) and render output from this technique more comparable to the wavelet analyses.

We plotted spectral density estimates against frequency to locate peaks that indicated dominant scales (wavelength of time or linear distance) in the pattern of the data. We recorded the frequency of up to four dominant peaks in spectral density for a data series. To determine whether the frequencies we detected graphically were creating the dominant pattern in the data, we used these candidate frequencies to fit the Fourier transform equation and estimate sine and cos coefficients (see Section 2.2) to our original data using PROC NONLIN in SAS. We then retested the residuals to determine if they had been reduced to white noise by removal of these frequencies of pattern from the data. We calculated the Fourier transform first using the frequency that displayed the highest spectral density. If the pattern was still nonrandom, we removed subsequent candidate frequencies in the order of the magnitudes of their spectral densities, until residuals represented a random series or until we had removed (up to) the four recorded frequencies.

Period, or scale of pattern, was calculated initially in "units" (there are 765 units or sample points in all data series analyzed) from the values of frequency at which peaks in spectral density occurred (i.e., period = $(2\pi/\text{frequency})$). We then converted values of period into the appropriate units for each dataset; one unit is 5 m for TSPACE and SHANND, 0.25 h (15 min) for TTIME, and 0.1 for SIM. So, for example, to determine the period of pattern in hours for the series TTIME, we multiplied the period calculated in units by 0.25, as there are 0.25 h represented by each sample in the series TTIME.

3.4.3. Wavelet analysis

We performed wavelet analysis using S-Plus Wavelets for PC, Version 1.0 (Bruce and Gao, 1994). The datasets were imported as regular time series signals. We first conducted some exploratory wavelet analyses to choose our final, analyzing wavelet for the comparison with spectral and lacunarity analysis: (1) we produced the discrete wavelet transform of each dataset with the Haar, Daublet, Symmlet, and Coiflet families of analyzing wavelets; (2) the best fit (i.e., best ability to approximate the data) among these wavelet families was assessed by reconstructing the original data from the transform using: (a) all coefficients, and (b) (up to) the top 150 coefficients; (3) we then examined the reconstruction of the original data visually and by computing the relative error between the original and the reconstructed data series (see Bruce and Gao, 1994); (4) we repeated (1) to (3) for different sets of wavelets from the Daublet Symmlet, and Coiflet families to choose the level of smoothness and width of the final analyzing wavelet. The Haar wavelet produced the smallest relative error between original and reconstructed data for all four datasets (see Fig. 2). Thus, subsequent examinations of wavelet transforms were based on using a Haar analyzing wavelet.

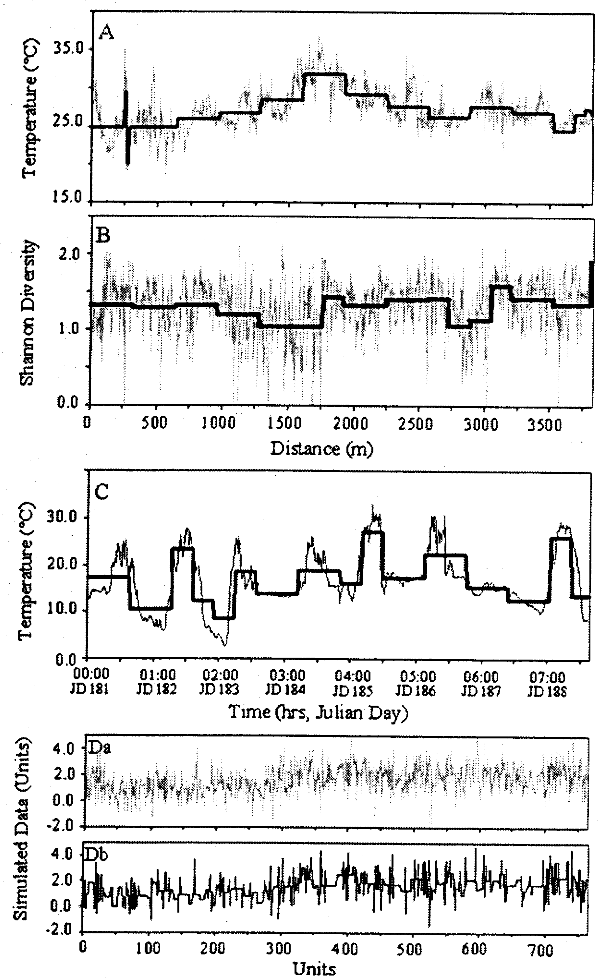

Fig. 2. Reconstruction of data series from the discrete wavelet transforms produced using the Haar wavelet. This wavelet produced the smallest relative error between the original and reconstructed data for all four data series. The original data (thin gray line) and the reconstructed series using the top 16 coefficients of the discrete wavelet transform (thicker, black line) are shown for (A) air temperature at the ground surface over space (TSPACE); (B) Shannon diversity of understory plant species over space (SHANND); (C) air temperature at the ground surface over time (TTIME); and (D) a simulated data series of same length (SIM, Da), reconstructed with 153 coefficients (Db) to account for the same percentage of energy compacted by 16 coefficients for the three empirical data series. $n = 765$ evenly spaced points for all series.

We used plots of the cumulative proportion of energy (i.e., the sum of all squared normalized coefficients; Bruce and Gao, 1994; Csillag and Kabos, 2002) accounted for by successive wavelet coefficients to determine the scales at which the dominant coefficients (those accounting for the majority of the energy) occurred. For the three field datasets, the wavelet transform compacted approximately 95% of the energy of the original data series into 15–20 coefficients. Twenty wavelet coefficients concentrated only 74% of the energy of the simulated dataset, TSIM, and 153 coefficients were required to incorporate 90% of the energy in this series. Further analysis of the scale and location of coefficients was restricted to a subset of the top 16 coefficients.

We calculated wavelet variance and position variance for the three sets of field data and 100 versions of SIM using PASSAGE (Rosenberg, 2001). Plots of wavelet variance were used to examine the average contribution of the coefficients at each scale to data structure, and thus identify scales that dominated patterns in the datasets. Position variance was examined to find locations within the series of data points that had relatively strong influences on the overall pattern averaged across scales.

4. Scales of pattern detected for the datasets

4.1. TSPACE, temperature across linear transect

Lacunarity and spectral analysis indicated similar scales of structure for the transect temperature series, TSPACE. The lacunarity plot of TSPACE had its

Table 2
Dominant scales suggested by three analysis techniques (wavelet, lacunarity, and spectral), for three series of field data collected in the Chequamegon National Forest, northern Wisconsin and a simulated series of the same length. TSPACE is air temperature at ground surface recorded every 5 m for 3820 m along a linear transect. SHANND is Shannon–Wiener diversity of understory species calculated at the same points as TSPACE was recorded. TTIME is air temperature at ground surface recorded every 15 min at one point on the transect. See text for explanation and equations for simulated data, SIM. $n = 765$ for all datasets. Values in brackets refer to log(box size) (lacunarity), scale (wavelet variance) or frequency (spectral analysis) indicated by arrows in Fig. 3. Values given for SIM are medians from analysis of 100 iterations

Analysis technique	Scale of pattern detected (m, h, or unitless[a])
TSPACE	
Lacunarity	555 (2.045)
Spectral analysis	425 (0.074), 1912 (0.016)
Wavelet variance	240 (48), 1210 (242)
SHANND	
Lacunarity	N/A
Spectral analysis	N/A
Wavelet variance	460 (92), 1100 (220)
TTIME	
Lacunarity	7.5 (1.477), 19.8 (1.898)
Spectral analysis	23.9 (0.066)
Wavelet variance	25.0 (100)
SIM	
Lacunarity	2.8 (1.447), 11.1 (2.045)
Spectral analysis	0.6 (0.977), 1.9 (0.337), 10.9 (0.058)
Wavelet variance	4.4 (44)

[a] Meters for TSPACE; meters for SHANND; hours for TTIME; unitless for SIM.

maximum change in slope (breakpoint) at a scale of 555 m (log box size = 2.04; Table 2, Fig. 3-A1). Spectral analysis indicated a scale of pattern of 425 m (frequency = 0.074) (Table 2; Fig. 3-A2), similar to that found with lacunarity analysis. The periodogram also suggested a possible, second, larger-scale pattern at about 1912 m (frequency = 0.016).

Wavelet variance suggested two scales of pattern (240 and 1120 m) dominating TSPACE (Table 1; Fig. 3-A3). These results differed from those of both lacunarity (555 m) and spectral analysis (425 and 1912 m). Wavelet analysis indicated that two percent ($n = 16$) of the total ($n = 765$) coefficients of the wavelet transform could explain 99% of the energy (variance of pattern) in the data signals for TSPACE. The discrete wavelet transforms approximated our data series as a set of Haar wavelets through "smooth" scaling coefficients, $s_{j,k}$, and detail coefficients, $d_{j,k}$, where $j = 1, 2, \ldots$. The smooth coefficients determine the underlying, coarse-scale pattern of the data and the detail coefficients recreate progressively finer-scaled deviations of the data from this overall smooth pattern. The coefficients exist for scale (or dilation) factors 2^j and translation (i.e., location or position along the data series) parameters $2^j k$ (Bruce and Gao, 1994; Csillag and Kabos, 2002). For TSPACE, the 12 most important coefficients for approximating the pattern were the smooth (s6) coefficients at a scale of $2^6 = 64$ units (320 m). The strongest of these coefficients, suggesting an abrupt or edge feature, occurred at 1920 m along the dataset; note that spectral analysis suggested a scale of pattern of 1912 m. TSPACE also had two d3 (scale = 40 m), one d4 (scale = 80 m), and one d5 (scale = 160 m) coefficient in the largest 16 coefficients of its transform function. Only one of these detail (d3) coefficients appeared to be a true signal effect whereas others occurred at the edges of the data and may have been artifacts of the lack of boundary correction in the analysis.

The position variance of TSPACE showed a strong peak at 1530 m (location 306 in the series; Fig. 4A) and lesser peaks at 1100 m (location 222) and 2475 m (location 495).

4.2. SHANND, plant diversity across linear transect

For SHANND, the shape of the relationship between log(lacunarity) and log(box size) was concave upward (Table 1, Fig. 3-B1), suggesting randomness of data (Plotnick et al., 1996). The periodogram for SHANND exhibited a noisy pattern with alternating high and low peaks of spectral density from scales of 3820 through 325 m i.e., there were no obvious peaks (Fig. 3-B2). Thus, both techniques suggested a lack of dominant scale of pattern in the diversity data.

Wavelet variance again indicated different scales of pattern for SHANND than did lacunarity or spectral analysis. Wavelet variance was the only technique that suggested recurrent patterns in SHANND, at scales of 460 and 1100 m (Table 2, Fig. 3-B3). Ninety-three percent of the energy in the pattern of SHANND was expressed using 16 wavelet transform coefficients, slightly less than could be compressed by the same

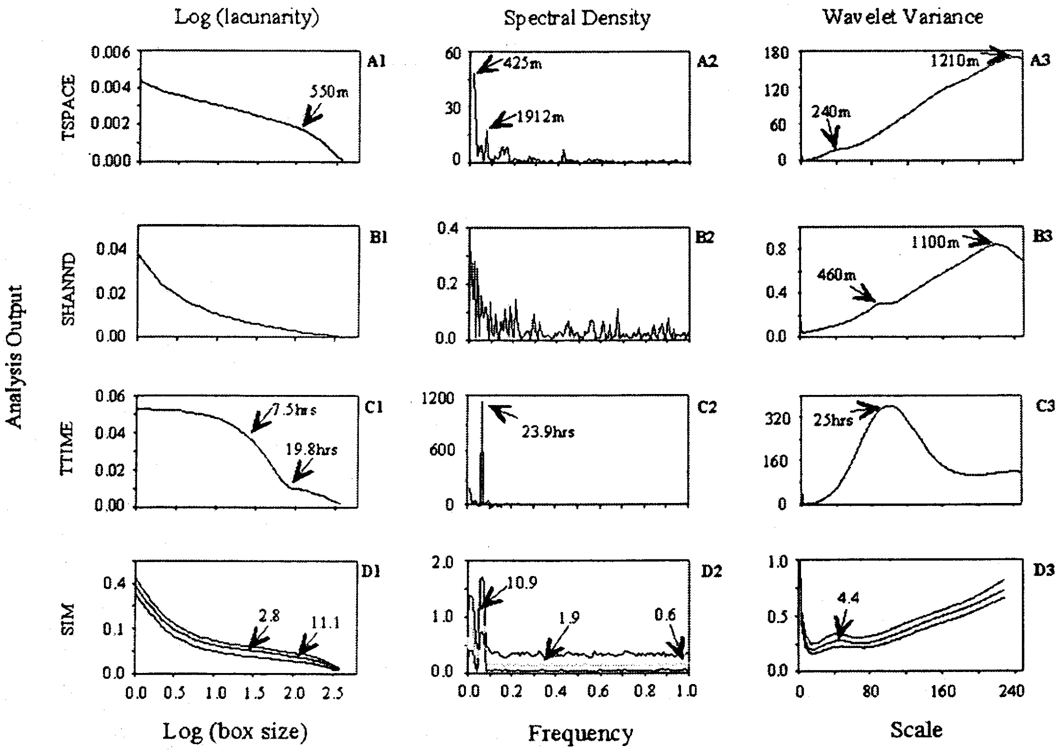

Fig. 3. Log(lacunarity) (1), spectral density (2), and wavelet variance (3) for air temperature at the ground surface every 5 m along a transect (A; TSPACE); morning air temperature at ground surface for a single point, every 15 min (0.25 h) over 8 days (B; TTIME); understory plant diversity (Shannon–Wiener index) every 5 m along a transect (C; SHANND); and a simulated data series (D; SIM). Dominant scales of pattern suggested for a data series by each of the analyses are indicated with arrows (see also Table 2). For SIM, 5th, 50th, and 95th percentiles are presented for each analysis and dominant scales are indicated on the median series. For lacunarity, the *x*-axis is log(box size), where box size ranges from 0 to 765 units and one unit is 5 m for TSPACE and SHANND, 15 min for TTIME, and 0.1 for SIM. Spectral density is shown as a function of frequency along the *x*-axis. The period (calculated as 2π/frequency) of the peaks in spectral density indicates dominant spatial or temporal scales of pattern in the data. To calculate the period in units appropriate to a series, a unit is 5 m for TSPACE and SHANND, 15 min (0.25 h) for TTIME, and 0.1 for SIM. The scale (*x*-axis) for wavelet variance is a distance measure (meters = scale 5) for TSPACE and SHANND, a temporal measure (hours = scale 0.25) for TTIME, and a unitless measure (units = scale 0.1) for SIM.

number of coefficients for the other two field datasets. Again, the top 12 coefficients were at the coarsest scales of analysis, s6 ($2^6 = 64$ units, or 320 m; Fig. 5B). Of the remaining four of the top 16 coefficients for SHANND, three were at the coarsest level of the detail coefficients (d6) and one, which appeared to be an edge effect, was at the d3 level ($2^3 = 8$ units, or 40 m).

The position variance for SHANND was highest at 1760 m (Fig. 4B). Lesser peaks were apparent at 1125 and 1475 m. Though even smaller, spikes of position variance did also stand out at 1620 and 2835 m (Fig. 4B).

4.3. *TTIME, temperature over time*

Lacunarity indicated scales of pattern in TTIME of 7.5 h (log(box size) = 1.5) and 19.8 h (log(box size) = 1.9; Table 2, Fig. 3-C1). Spectral analysis suggested one dominant scale of pattern, 23.9 h (frequency = 0.065; Fig. 3-C2).

The wavelet variance of TTIME had a single, strong peak (dominant scale) at 25 h (Table 2, Fig. 3-C3). Here, all three techniques indicated a repeating pattern with a period of approximately 1 day, as expected. The scale of pattern detected by lacunarity deviated the most from this expected value. Two percent ($n = 16$) of the

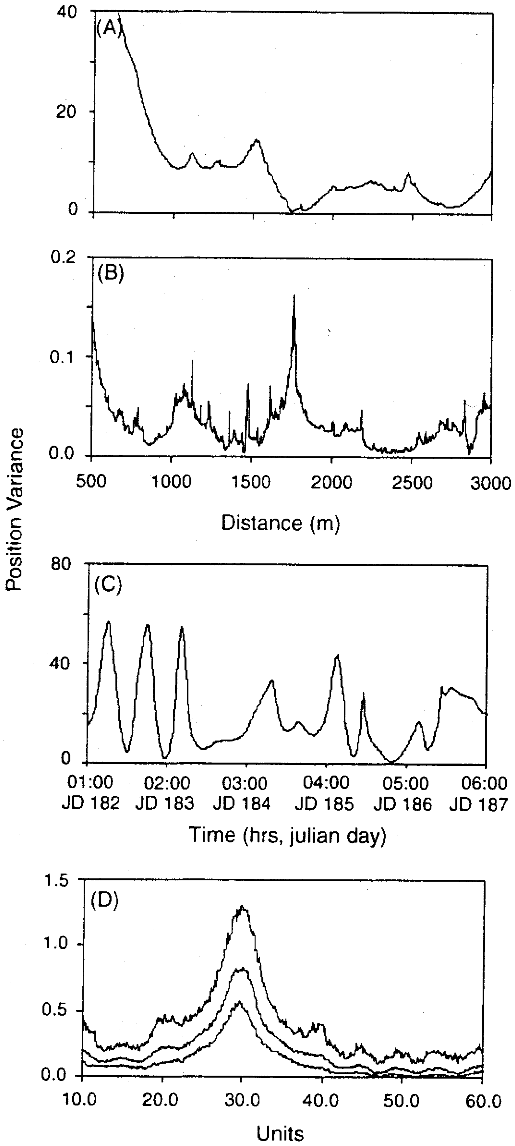

Fig. 4. Position variance, calculated using Haar wavelet, for: (A) TSPACE, average morning (05:00–11:00 h) surface temperature (°C) along a transect; (B) SHANND, understory plant diversity (Shannon–Wiener index) from 1 m^2 quadrats along a transect; (C) TTIME, surface temperature (°C) across time at a single point; and (D) SIM, a simulated dataset (see text for details). The x-axis is truncated to positions 100 through 600 for all series, to show areas not edge-influenced during analysis. For SIM, position variance is shown for the 5th, 50th, and 95th percentiles of 100 iterations of the data (see text for details).

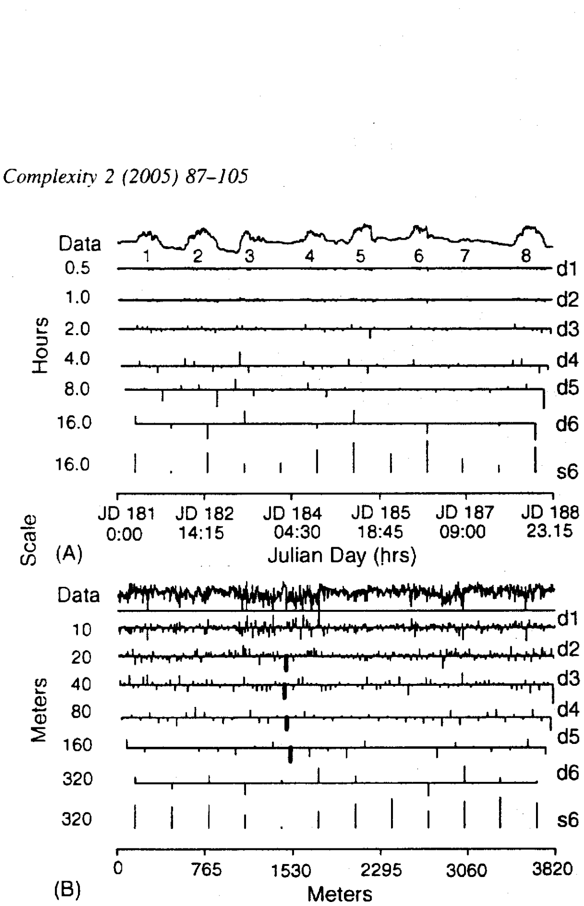

Fig. 5. Original data and coefficients of the wavelet transform (produced with the Haar wavelet function) for (A) air temperature at the ground surface every 15 min for 191.25 h (TTIME); and (B) Shannon diversity of understory plants measured every 5 m for 3820 m along a transect (SHANND). All coefficients are detail coefficients except for the bottom row in both panels, which shows smooth (coarse-scale) coefficients. Relative size of coefficients is indicated by length of the line at each position. Both the detail and smooth coefficients at the coarsest (d6 and s6) levels are shown on a separate measurement scale to the other (finer-scale) coefficients. The thicker, gray lines in panel (B) indicate relatively strong coefficients that occurred across multiple scales for SHANND. n = 765 for both datasets.

coefficients of the wavelet transform could explain 95% of the pattern in TTIME. The top 12 coefficients were at the coarsest scales (Fig. 4A), as for TSPACE and the remaining four of the 16 coefficients were at the coarsest detail scale, d6 (i.e., 2^6 or 16 h).

Position variance showed seven relatively strong peaks at: 07:15 h, Julian Day (JD) 182; 19:15 h, Julian Day 182; 06:00 h, JD 183; 10:45 h, JD 184; 07:00 h, JD 185; 15:00 h, JD 185; and 15:45 h, JD 186 (Fig. 4C).

4.4. SIM, simulated data

For SIM, both lacunarity and spectral analysis indicated structure at scales close to the period of the regular sine wave (period = 9.8). The scale at which this breakpoint was detected in lacunarity varied from 8.4 units (5th percentile) to 11.4 units (95th percentile) over the 100 iterations of SIM (median = 11.1 units; Table 2, Fig. 3-D1). Spectral density showed the strongest peak at a scale between 8.5 units (5th percentile) and 10.9 units (95th percentile and median) for 85 of 91 iterations (recall nine series were random after detrending and were not analyzed; Fig. 3-D2). Five of the remaining six series showed a strong peak in this range, though the greatest peak was closer to the origin, at a period of 25.5–76.5 units. Finer patterns were noted at scales between 1.8 and 5.1 units (median = 1.9 units, Fig. 3-D2) for 56 series, and between 0.2 and 0.7 units (median = 0.6 units) for 82 series, perhaps associated with the random noise component of the signal. This was less consistently apparent (occurred in fewer decay curves) from lacunarity analysis. For curves in which this structure was noted, the scale ranged from 1.6 units (5th percentile) to 3.1 units (95th percentile), with a median value of 2.8 units (Fig. 3-D2). Neither lacunarity nor spectral analysis detected the abrupt step in the data at 30.0 units.

Spectral density was maximal at a scale of 8.5, 9.6, or 10.9 units for 85 of our analyzed SIM iterations. Removal of the Fourier transform of the series at this scale from the original data reduced the series to white noise in 58 of these 85 cases. Interestingly, for 17 of these 58 cases, the series was randomized by removing a pattern with period of 9.6, though the strongest peak in spectral density was at a value of either 10.9 or 8.5 units. An additional seven series were randomized by removal of a second dominant scale of pattern; two were randomized by removal of the top three scales of pattern. Of the 91 iterations of SIM, 24 were not reduced to white noise by removal of (up to) four dominant scales of pattern detected through our spectral analysis procedure.

Wavelet variance suggested only one prominent scale of pattern for SIM (Table 2, Fig. 3-D3), after which variance continued to climb with no indication of leveling by the maximum scale analyzed (30% of series length). Mode scale for which the peak in variance occurred was 4.2 units ($n = 14$), with a range in values from 4.0 units (5th percentile) to 5.5 units (95th percentile) and a median of 4.4 units (Table 2, Fig. 3-D3). These values are approximately half the length of the full period of the sine wave, the width detected for each repeating peak and trough in SIM. Eighty-seven of 100 iterations showed this same pattern of wavelet variance; there were 13 cases for which no obvious scale of pattern occurred.

For SIM, only 74% of the energy in the data pattern was accounted for by the top 16 (2%) of the wavelet transform coefficients. The 12 s6 ($2^6 = 64$ units or scale of 6.4) coefficients were the largest, incorporating 73% of the energy in the original data; one coefficient at the d1 level (2.0 scale) and three at the d2 (4.0 scale) level were also in the strongest 16. Within the coarsest, s6 level, the strongest seven coefficients all occurred after the abrupt step in the series at 30 units (location 32 units along the data series and after), suggesting the presence of this feature in the series. We had expected, however, only the coefficient closest to that location in the data series, rather than all that occurred after it, to be relatively prominent. For the discrete wavelet transform, the number of coefficients at any scale is related to the width of the analyzing wavelet; $n/2^j$ terms (and coefficients) are required to cover the length of the data series (Csillag and Kabos, 2002). For the Haar wavelet, the coefficients are plotted at the middle of the wavelet function that is used to approximate that portion of the data (e.g., Fig. 5; and Bruce and Gao, 1994). Thus, the plotting of the coefficients is constrained, by the discrete nature of the transform (and the data), to occur every 6.4 units along the data series SIM; the ability to detect a sine wave of period 9.8 is accordingly restricted.

Examining position variance for SIM, 98 of 100 iterations of the data showed a single, dominant peak, as shown in Fig. 4D. The mode location along the series at which this peak occurred was 29.5 units ($n = 7$); median location = 29.7 units, 5th percentile = 28.0 units and 95th percentile = 31.3 units (Fig. 4D). Two iterations of SIM did not have an obvious peak in position variance.

5. Summary and discussion

Lacunarity and spectral analysis gave the most consistent results, indicating similar scales of structure for the transect temperature series, temperature over time, and the simulated dataset. As would be expected for temperature over time, both methods indicated a repeating pattern with a period of approximately 1 day, though spectral analysis indicated a temporal scale closest to the expected diurnal pattern in this case. Neither lacunarity nor spectral analysis identified dominant scales of structure in Shannon diversity across space. Lacunarity gave relatively consistent results across iterations of SIM. However, the dominant scales of pattern suggested by periodograms were more variable. Eighty-five of 91 iterations analyzed (93%) had a clear peak in their periodogram associated with the base sine wave. However, removal of the (apparent), dominant frequencies of pattern did not reduce over one quarter of the iterations to white noise. Further, 29% of those randomized could only be so by removing a pattern with frequency adjacent to that which had the strongest value of spectral density. These results illustrate some difficulties inherent in distinguishing dominant, underlying patterns in data with this technique. Because the coefficients of the Fourier transform are not well localized (in space or time), even minor changes (or minor random variation) can influence the coefficients and pattern detection (see Percival, 1993, for an illustration of this effect). In the case of SIM, we expected that a specific period of pattern would contribute most of the energy to the process and could reasonably test this. However, when using spectral analysis as an exploratory process to question whether a process has periodic structure, or to rule out competing a priori hypotheses regarding scales of pattern, lack of clear dominance in spectral density will be confounding.

The results of wavelet analyses contrasted with the results of the other two techniques for the transect datasets (both TSPACE and SHANND), though relatively similar results were obtained for TTIME and SIM. The wavelet variance suggested two prominent scales in the pattern of understory plant diversity (at 460 and 1100 m), in contrast to the lack of structure found using lacunarity or spectral analysis. Brosofske et al. (1999) also found a double-peaked pattern in wavelet variance for a different set of Shannon diversity values calculated for the same landscape. Through the current study, two scales of patchiness were also indicated by wavelet variance for temperature across space, 240 and 1210 m. The broader scale is substantially smaller than the larger patch size determined from the periodogram and the finer scale approximately half the breadth of the finer scale patterns suggested by the other two analyses (Table 1). This disparity between the wavelet variance output for some series and the relatively similar outputs of the lacunarity and spectral analyses across datasets might tend to build confidence in the latter two techniques. However, the wavelet variance did provide an estimate of the period closer to that expected for the temporal dataset (25 h) than did lacunarity (19.8 h). Wavelet variance also suggested a repeating pattern of 4.4 units for SIM, which would suggest a sine wave period of approximately 8.8 units, closer to the expected value of 9.9 than the other techniques. Further, lacunarity has been cited as imprecise at determining scale in patterns with known structure (Dale, 2000), suggesting caution should be used when interpreting output of analyses.

There were no apparent broad-scale features in the field, such as repeating topography or overstory management that readily explained patterns in TSPACE at scales >1000 m (all techniques). However, the pattern at a scale of 240 m (detected by wavelet analysis) may correspond to the average overstory patch size of ~220 m along this transect (Saunders et al., 1998). The apparent 400–550 m scale of patterning (lacunarity and spectral analyses) could be associated with the influence of four management patches (60-year red pine, retention jack pine, 12-year-old red pine, and clearcut) that each extended >450 m along the transect. However, previous analyses of data from these landscapes suggested that the thermal environment existed in finer patches than overstory structure at all but the coarsest scales of analysis. Though there was strong suggestion of a process structuring the transect temperature data at this scale, we also considered that long memory (i.e., slowly decaying autocorrelations) was responsible for the strong peak in spectral density near the origin (and the conclusion of scale of pattern at a frequency of 425 m). Existence of a straight line pattern with negative slope in the log–log plot of a periodogram can indicate long memory correlations (Beran, 1994; Beran and Ghosh, 2000). Our examination of the log–log plot and residuals suggested a linear regression was not the most appropriate fit for the relationship and, along with supporting results from lacunarity analysis, encouraged consideration of ecological explanations for this periodic pattern.

We expected the broad management patches of approximately 400–500 m in length to influence strongly the scale of pattern of the SHANND data series. In contrast to results for the TSPACE data, this scale of pattern was only indicated by the wavelet variance for understory plant diversity. These discrepancies highlighted the importance, when analyzing field data, of interpreting the results from these analysis techniques in concert with each other and with examination and ecological understanding of the original data.

The wavelet analysis provided additional information about these data and the potential reasons for the scales of pattern that were observed. The wavelet transform showed that even for a relatively cyclic phenomenon, such as diurnal temperature change, not all patches contribute similarly to a data signal. For example, the coefficients for the transform of TTIME were unequal across time at the coarsest scales of analysis (d6, s6; Fig. 5A). The largest three coefficients corresponded to the relatively sharp drop in temperature during the sixth, fifth, and eighth days in the series (Julian Days 186, 185, and 188, respectively). Other days contributed relatively little to the overall pattern or exhibited relatively smooth temperature gradients (rather than abrupt, step-like changes) and had small coefficients at the coarse scales of analysis e.g., Days 3 and 7 (see Fig. 5A). Thus, variation in even coarse-scale temperature patterns was highlighted. This information was augmented by examination of position variance, for which strong peaks indicated sudden changes (either increase or decrease) of temperature in time. Again, peaks were unequal across days; Julian Days 182 and 185 had higher position variances than Julian Days 184 and 186 (Fig. 4C). One could examine local weather station data, for example, to see if broad changes in weather could account for the irregularities in contributions of different days to the overall variation in surface temperature data. One would expect a cloudy day, with lower variation in temperature over 24 h than a sunny day, to contribute less to the total variation in these data, and have correspondingly smaller transform coefficients along the series of temperature in time. Similar variation occurred within the other two field data series but examination of lacunarity or spectral output, or the wavelet variance in isolation from the transform, suggested only the global pattern within any of these series.

This variation in the wavelet transform across the data series further facilitated the examination of features for their effects on patterns at specific scales of space or time. For example, the relatively strong changes in broad-scale pattern towards the center of the TSPACE data series (Figs. 1A and 2A) may be related to a specific patch type. Of the 16 coefficients we examined, all of those falling within clearcuts or retention cuts (i.e., open canopy stands) were stronger than those located within closed canopy stands. Averaging the transform across scales, position variance indicated strong influence of a road at 1100 m (Fig. 4A), though no obvious feature could be associated with peaks at 1530 or 2475 m. Similarly, for the Shannon diversity series, it appeared that specific cover types of patches were influencing patterns detected by wavelet variance, suggesting future datasets or experimental manipulations to analyze with these techniques for comparison to our initial results. Position variance also highlighted the effect of structural features on data pattern. Strongest peaks for SHANND (Fig. 4B) occurred in proximity to roads: gravel road at 1755 m, sand road at 1125 m, and ATV trail at 1455 m.

For SIM, the strongest wavelet transform coefficients at the s6 (coarsest) level of analysis all occurred after the abrupt step in the series at 30 units, suggesting detection of a feature in the data series at this point. This feature in the data was clear from position variance (Fig. 4D). Position variance did not point out the underlying sine wave of SIM.

Examination of the wavelet transform coefficients suggested hierarchical structure for some datasets. For example, some propagation of pattern across scales was indicated for SHANND by the relatively strong transform coefficients in close spatial proximity at scales d2 (2^2 units or 20 m) through d3, d4 and d5 (2^5 or 160 m scale) (thick, gray line in Fig. 5B). The relationship between apparently minor structural features on the landscape and pattern across multiple (coarser) scales has been suggested by wavelet analysis of vegetation patterns in other landscapes (Brosofske et al., 1999; Chen et al., 1999).

The data reduction capabilities of wavelet analysis have implications not only for understanding dominant scales of pattern, but also for data collection, compression and archiving. One can assess how many scales retain a desired level of detail within a dataset, and examine the degree of homogeneity among scales of information, determining the relative importance of fine versus coarse-scale heterogeneity in contributing to patterns. At least 93% of the energy – or dominant pattern – in any of the three empirical datasets could be expressed with only 16 coefficients using the Haar function. All 16 of these coefficients for the field data, and 12 of 16 top coefficients for the simulated data occurred at the two coarsest scales of analysis, suggesting that the finer scales (less than 160 m (transect datasets), 8 h (temporal sets), or 64 units (simulated data)) contributed relatively little to the patterns in these data. The exception may be for SIM, which had four of 16 of its largest coefficients at the scale of two and four units. Such fine scales of repeating pattern were also suggested by lacunarity and spectral analyses (Table 1, Fig. 3D), possibly reflecting the random noise imposed on the sine curve in this series. Thus, wavelet analysis allowed us to retain information on the heterogeneity of patterns at coarse scales, and propose management features or ecological processes that might create that heterogeneity, but clarified those scales that require less attention for understanding patterns in our data. That large amounts of variation in the data could be explained by few transform coefficients, particularly relative to the simple, simulated data series, sustained our expectation that features such as roads, and regular extents of vegetation management patches, impose a strong signature in the pattern of other ecological variables. The need to assess the contribution of finer scales to overall data patterns will be augmented by the increasing use of relatively coarse-resolution, remotely sensed data in ecology.

Lacunarity, wavelet and spectral analyses provided complementary information regarding our data. The utility of combining multiple methodologies to understand patterns in ecological phenomena was similarly noted by Nezlin and Li (2003). They found that spectral analysis, lagged correlations analysis, and wavelet analysis used in concert revealed different aspects of the abiotic influences on coastal phytoplankton dynamics. Dale (2000) suggested that estimates of scales of pattern identified by lacunarity have low precision and the technique does not consistently detect known features in multiscaled patterns. However, lacunarity detected similar, multiple scales of pattern in our simulated dataset, SIM, to both wavelet variance and spectral analysis. In contrast, the scale of pattern indicated by lacunarity for TTIME was the furthest of any technique from the expected, 24 h period for TTIME. Thus, precision may depend on the nature of the pattern being examined.

Similar to the lacunarity output, wavelet variance suggested the presence of dominant scales in the data. In contrast to lacunarity, the wavelet transform can indicate both the scales of patchiness and positions in space or time that contribute to the data structure and pattern without comparison to data of a known structure. Wavelet analysis did not, however, provide insight into random versus regular distributions of data patches. Further, to avoid analytical artifacts in the absence of any edge correction, wavelet analysis must be restricted, at coarser scales (i.e., wider analyzing wavelets), to the central portion of a series. Spectral analysis is sensitive to nonstationarity of a data series in addition to being influenced by data edges. This contrasts with lacunarity, which requires no edge correction.

The appropriate technique to use in assessing the scale of pattern is dependent on the type of data being analyzed, the detail of information required, and the study objective. Tradeoffs exist among acquiring: (1) relatively detailed information on a subset of the data (wavelet analysis); (2) more global information on a subset of the data (spectral analysis); or (3) relatively coarse information on the full set of data (lacunarity analysis). None of these techniques appeared superior in identifying the scales of structure across all four datasets. Differences in the scales of pattern detected emphasized the importance of matching the analysis technique to the expected nature of pattern in the data. For example, as expected, spectral analysis provided the closest assessment of the (predicted) periodicity of pattern in our most uniformly repeating and cyclical data series, diurnal temperature. This suggested that a smooth wavelet function would provide a good fit to the temporal data. The strong approximation to all our datasets obtained using the Haar wavelet indicated that even diurnal cycles of temperature could be abrupt and variable. All three techniques approximated the scale of the sine wave in the simulated data; however, only the wavelet transform (along with wavelet position variance) provided information on the abrupt "step" feature in these data. The graphical outputs of lacunarity and the wavelet and position variances were, perhaps, the most easily interpreted, but gave only an average or global understanding of data. Spectral analyses also provided an "overall" assessment of scales of structure. The abilities of the wavelet transform to compress data and retain locational information provided further detail on dominant scales, hierarchical structure, and specific points in space or time that strongly influenced the global pattern of the data. When information on the average sizes of the patches and gaps is inadequate or one wishes to investigate changes in pattern across multiple scales, wavelet analysis provides a promising alternative. These comparisons emphasized the: (1) importance of using multiple techniques to examine scales of pattern in ecological data (Dale, 2000; Perry et al., 2002); (2) utility of interpreting output of analysis in concert with ecological knowledge of the original data; and (3) usefulness of some of the techniques for directing subsequent descriptive and experimental examination of features or processes inducing scales of pattern.

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