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Spectral representation of neutral landscapes

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Abstract

Pattern in ecological landscapes is often the result of different processes operating at different scales. Neutral landscape models were introduced in landscape ecology to differentiate patterns that are the result of simple random processes from patterns that arise from more complex ecological processes. Recent studies have used increasingly complex neutral models that incorporate contagion and other constraints on random patterns, as well as using neutral landscapes as input to spatial simulation models. Here, I consider a common mathematical framework based on spectral transforms that represents all neutral landscape models in terms of sets of spectral basis functions. Fractal and multi-fractal models are considered, as well as models with multiple scaling regions and anisotropy. All of the models considered are shown to be variations on a basic theme: a scaling relation between frequency and amplitude of spectral components. Two example landscapes examined showed long-range correlations (distances up to 1000 km) consistent with fractal scaling.

Introduction

Landscape ecology is the study of the reciprocal interaction between spatial pattern and ecosystem process. To understand and rigorously test the effects of landscape pattern on ecological processes requires that we define suitable models of spatial pattern. One class of spatial models employed in landscape ecology are neutral landscape models (Gardner et al. 1987; Turner et al. 1989; Gardner and O'Neill 1991; Milne 1992; O'Neill et al. 1992; With and King 1997). Neutral landscape models attempt to capture a minimal set of constraints dictating landscape pattern and assign the remaining pattern to a purely random process. For example, the simplest neutral landscape model can be generated by assigning cells in a lattice the value 1 with probability p and 0 with probability $1 - p$. These are the percolation maps discussed by Gardner et al. (1987). Percolation maps were used as simple models of physical phase-transitions (Stauffer and Aharony 1985; Goldenfeld 1992) prior to their use in landscape ecology. Despite the simplicity of percolation models, they exhibit a surprising variety of spatial patterns and sudden changes in connectivity with changing p (Stauffer and Aharony 1985; Gardner et al. 1987).

Neutral landscape models were originally introduced to generate spatial patterns in the absence of any structuring process (Gardner et al. 1987). More recently, the use of neutral landscape models has evolved to include additional constraints on the patterns generated (Gardner and O'Neill 1991; Milne 1992; Milne et al. 1996; Plotnick et al. 1996). Neutral models are also increasingly being used as input to spatial simulation models (Palmer 1992; Keitt and Johnson 1995; With and Crist 1995; Moloney and Levin 1996). These more sophisticated neutral landscape models appear less-and-less like random neutral models and increasingly like explicit models of spatial pattern. However, it should be noted that random need not imply uniform random. Any of a large variety of random distributions including Gaussian, exponential, and gamma distributions can be used in the construction of neutral landscape models. Spatially correlated patterns can also be random in the sense that any one pattern is drawn from an ensemble of correlated random landscapes. For example, self-similar or fractal (Mandelbrot 1982) patterns can be considered to be the result of a single structuring process operating at all scales in a landscape. Thus, fractal patterns can be considered neutral with respect to multiple structuring processes that induce different landscape patterns at different scales. To avoid semantic confusion, I will simply refer to neutral landscape as any stochastic model of a spatial pattern where the value $X(t)$ assigned to any location t in the pattern can be considered a random variable, regardless of any constraints placed on that variable such as spatial autocorrelation.

Neutral landscapes in ecology

There are a number of potential uses for neutral models in the study of landscapes. First, neutral models can be the objects of study themselves. In this capacity, neutral models serve as a baseline to generate expected spatial patterns from random processes (e.g., Gardner et al. 1987). Second, neutral models may be used to compare random patterns to real landscapes to evaluate whether spatial patterns in empirical landscapes are consistent with simple, random processes (Milne et al. 1996). A third use of neutral models is as a means of generating replicate landscapes that share statistical properties with an empirical landscape of interest. These replicate landscapes can then be used to study statistical outcomes over a large ensemble of landscapes. Finally, neutral models can be used as input to simulation models to explore ecological dynamics in heterogeneous landscapes (Gardner et al. 1989; Gardner et al. 1992; O'Neill et al. 1992b; Palmer 1992; Keitt and Johnson 1995; With and Crist 1995; Lavorel et al. 1995).

Whereas percolation maps were the first neutral models considered in landscape ecology, other neutral models are capable of generating more complex spatial patterns. A variant of the standard percolation model involves a linear decrease of the p-value across the lattice producing a gradient percolation-map (Milne et al. 1996). Gradient percolation maps vary from high density of ones on one side of the map to a low density of ones on the other, with intermediate densities in between. The underlying gradient of p-values can be more complex and include quadratic and higher-order polynomial surfaces (A. Johnson, personal communication). Gradient maps have been used to study the geometry of ecological transitions or ecotones (Milne et al. 1996).

Another variation on random neutral models is to introduce contagion or autocorrelation in the resulting spatial pattern. These neutral models emulate the effects of localized ecological processes (e.g., dispersal) that create clumped or spatially correlated patterns. The most commonly used neutral model exhibiting contagion is a surface created via a fractional-Brownian process (or fractional-Brownian motion, often abbreviated fBm). Fractional-Brownian processes exhibit self-affine or fractal scaling properties (Mandelbrot 1982), and are thus useful for modeling fractal landscape patterns (Burrough 1983a, b; Palmer 1988; Milne 1992). The most popular method of generating fBm is the mid-point displacement method (Peitgen and Saupe 1988) in which line segments are recursively broken at their mid-points. Each mid-point is then randomly displaced a distance that depends on the length or scale of the segment. Fractional-Brownian surfaces have been used as neutral models to study the influence of correlated spatial patterns on species coexistence (Palmer 1992), predator-prey interactions (Keitt and Johnson 1995), and disturbance ecology (Moloney and Levin 1996). Other methods of producing autocorrelated maps include adjacency biased percolation maps (Gardner and O'Neill 1991) and random fields constrained by a particular semivariogram (Cressie 1993).

A neutral model that generates hierarchical patterns is the random curds (Mandelbrot 1982) described by O'Neill et al. (1992). Random curdling recursively subdivides the plane into blocks. At each level of the recursion, blocks survive with a probability p and are subdivided again at the next level. Blocks that don't survive are assigned a value 0 and are thereafter ignored. The process is repeated until a minimum block size is obtained. The resulting curds are fractal in structure.

Although neutral models have been useful in the study of landscapes, there has been little mathematical synthesis of various neutral models. Synthesis can often be achieved by adopting an alternative representation of a problem. Here, I synthesize existing neutral models by considering their properties in terms of a spectral representation and show how the spectral representation unifies concepts of pattern and scale in landscape ecology. I discuss a number of extensions, not discussed by previous authors, to spectral synthesis methods with direct applications to neutral landscape models. I also extend spectral methods to include other frequency-based transforms such as the wavelet transform (Daubechies 1992).

Spectral representation of landscapes

When considering pattern in landscapes, one commonly thinks of a sequence of landscape attributes repeated through space. A canonical example is the cosine function that repeats itself in intervals of 2π. The scale of the pattern is the distance over which the pattern repeats itself or, in this example, the period of the cosine function. (Notice that the frequency is the inverse of the period so that high frequency implies fine-scale pattern.) The intensity of the pattern is the variation of the pattern or the amplitude of the cosine curve.

Typically, landscapes exhibit pattern not on a single scale, but on multiple scales simultaneously (Milne 1992). Spectral representation of a multi-scaled pattern is illustrated in Figure 1. The spectral representation contains a number of spectral coefficients, each one specifying a cosine curve with a given amplitude and frequency (Renshaw and Ford 1984). The summation or synthesis of the spectral components reproduces the original landscape. The set of all spectral components form the basis of the spectral representation and are sometimes referred to as a set of spectral basis functions. A common spectral transform, called the Fourier transform, represents patterns in terms of cosine functions. However, the number of suitable bases for spectral representation is essentially unlimited and can include step-functions and spatially localized wavelets (see section 5).

To generate a spectral representation of a pattern, we must first define an appropriate basis. If the pattern is self-similar, the basis functions must posses the property that any one spectral component is identical to a rescaled version of any other component. For example, given two cosine curves g_0 and g_1, then

$$g_1(x) = (a_1/a_0)g_0(fx + \phi),$$

where a_1/a_0 is the ratio of amplitudes, f and ϕ are the frequency and phase of g_1. The set of cosine functions with frequencies $1, 2, 3, \ldots N/2$ forms the Fourier basis.

In fractal landscapes, the amplitudes of the components are coupled to their frequencies via a power-law. For a 1-D transect across a landscape,

$$E(a_f) \propto f^{-5/2-D}$$

where $E(a_f)$ is the expected amplitude of spectral components with frequency f and D is the fractal dimension of the landscape (Peitgen and Saupe 1988). Thus, in the spectral representation, the self-similarity

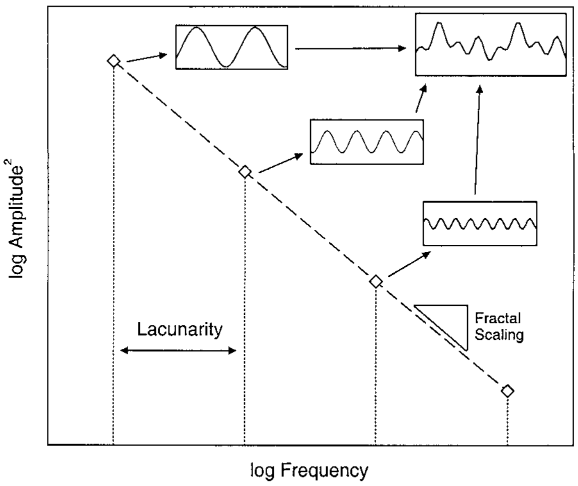

Figure 1. Spectral representation of pattern and scale. Each diamond represents a spectral component of the landscape. In fractal landscapes, amplitude decreases as a power-law function of the frequency. The log-transformed slope of the relationship is related to the roughness or fractal dimension of the surface. The change in frequency between successive spectral additions is related to the lacunarity of the surface.

exhibited by fractals is equivalent to a scaling-relation between the amplitude and frequency of components – as the scale of the components decreases, their amplitudes decrease at a rate determined by the fractal dimension. Of course, spectral methods need not be limited to fractal patterns. As long as a suitable basis is defined, any pattern may be represented in that basis.

A concept related to fractals is the lacunarity of a pattern (Mandelbrot 1982; Allain and Cloitre 1991). Roughly speaking, lacunarity refers to the amount of variation among adjacent sites in a pattern. For example, checker-board pattern have high lacunarity, whereas random patterns will have somewhat lower measures of lacunarity. A number of definitions exist for lacunarity (Mandelbrot 1982; Peitgen and Saupe 1988). However the most commonly used is the variance among the means taken in overlapping windows (Plotnick et al. 1993; Plotnick et al. 1996). Lacunarity also has an interpretation within the spectral representation (Figure 1). An index of lacunarity is the width of gaps between successive spectral components in a pattern (Peitgen and Saupe 1988). Thus, lacunarity in natural landscapes reflects a limited number of processes, each generating pattern within a tightly restricted range of scales. Lacunarity can have important consequences for ecosystem processes. Holling (1992), for example, has suggested that lacunary landscape patterns, by influencing foraging success, can result in discontinuous body-size distributions in animals.

Scaling in ecological landscapes

Fractal pattern in landscapes often arises when a single structuring process operates over many scales. For example, tectonic faulting can lead to fractal topographic relief and a power law distribution of earth quake energies (Feder and Feder 1991; Olami et al. 1992; Geller et al. 1997). Forest fires are another structuring process that can generate fractal patterns (Malamud et al. 1998). Disturbances, such as tree fall gaps have also been shown to exhibit fractal scaling Solé and Manrubia (1995).

To illustrate scaling in ecological landscapes, I plotted the spectral decomposition (power spectrum) of forest density for two regions of the continental U.S., each covering greater than one million square kilometers (Figure 2). The resulting spectra were power law over nearly three orders of magnitude in scale. The Southwest forest data exhibited scaling with $S(f) \propto 1/f^{1.57}$ or $H = 0.29$; the Eastern forest data was $S(f) \propto 1/f^{1.21}$ or $H = 0.11$. The larger Hurst exponent in the Southwest reflects the strong dependence of forest distributions on montane environments. The pattern of mountain ranges in the Southwest increased the variation in forest density at low frequencies, thereby increasing the slope of the spectral density plot. The Eastern forests were much more evenly distributed. Thus, low frequency variation was less prevalent in the Eastern data which resulted in a smaller Hurst exponent.

Spectral synthesis methods

Spectral representation not only provides a conceptual framework for understanding pattern and scale, but can also generate many classes of rugged landscape patterns. The method of generating neutral landscapes via spectral means is known as spectral synthesis. The approach revolves around generating random Fourier coefficients with a know distribution and then applying an inverse Fourier transform to produce the landscape in the spatial domain. In essence, the process is just that illustrated in Figure 1: successive addition of cosine functions with random phases and frequency-scaled amplitudes. Generally speaking, spectral synthesis is not restricted to Fourier transforms, nor sine or cosine functions, but can be considered to include any spectral method such as wavelet transforms.

Synthesis of fractional Brownian landscapes

A class of correlated landscapes easily generated via spectral methods is fractional-Brownian surfaces (Peitgen and Saupe 1988; Hastings and Sugihara 1993). Fractional Brownian motion is an extension of regular Brownian random walks in which the correlation between successive steps is controlled by a parameter H known as the Hurst exponent (Mandelbrot 1982). Unlike a standard first order autoregressive process, fractional Brownian motion exhibit correlations that do not decay rapidly with distance, but are instead present at all spatial or temporal scales.

The Hurst exponent defines a scaling relation

$$E[(X_t - X_{t'})^2] \propto (t - t')^{2H}, \tag{1}$$

where $E[(X_t - X_{t'})^2]$ is the expected variance of successive increments X_t and $X_{t'}$ of the random walk spaced a distance $t - t'$ apart. The left-hand side of equation 1 is also known as the semivariance, a measure commonly employed in geostatistics (Cressie 1993). A more complete description of fBm includes: (1) The mean of the increments is zero, (2) the increments are normally distributed, (3) the variance of the increments scales with distance according to equation 1, and (4) properties 1–3 are stationary and isotropic with respect to distance or time. Note that because the expected mean of fBm is zero, the variance of the increments is equivalent to the semivariance used in geostatistics. Whereas semivariance analysis usually identifies a scale above which the semivariance remains constant, the semivariance of fBm increases with the length of the sequence. In the limit of infinitely long sequences, fBm has infinite variance (Mandelbrot 1982).

The Fourier transform of fBm is best understood in terms of its spectral density. The spectral density is simply the square or modulus of the complex Fourier coefficients. The spectral density of a fractional-Brownian sequence scales as

$$S(f) \propto 1/f^{\beta} \tag{2}$$

where f is frequency and $\beta = 1 + 2H$. The Hurst exponent controls the degree of correlation in the landscape: a large Hurst exponent, $H \rightarrow 1.0$, results in relatively smooth, correlated sequences, whereas for $H \rightarrow 0.0$ produces highly rough, uncorrelated sequences.

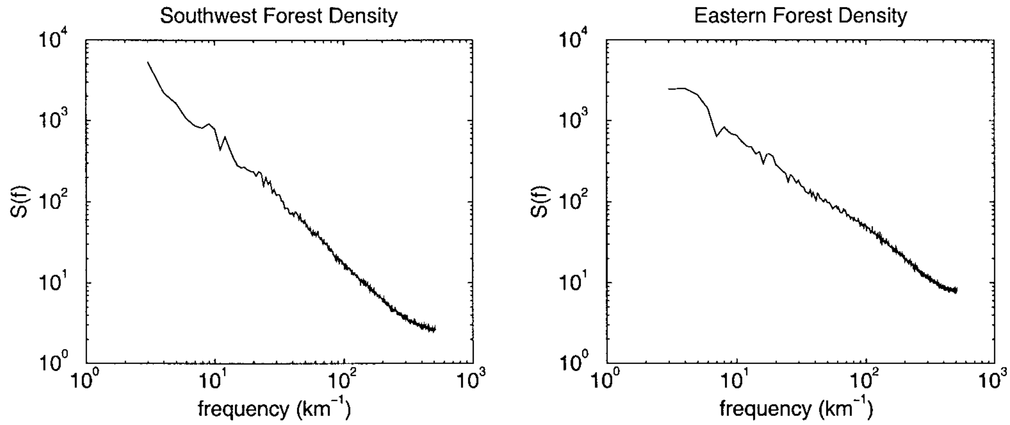

Figure 2. Spectral density plots of forest density over 1.0^6 km^2 regions in the Southwestern U.S. and the Eastern U.S [data from Evans et al. (1993)]. Both plots show distinct power-law scaling. The slope of the Southwest was $\beta = 1.57$, and for the East $\beta = 1.21$.

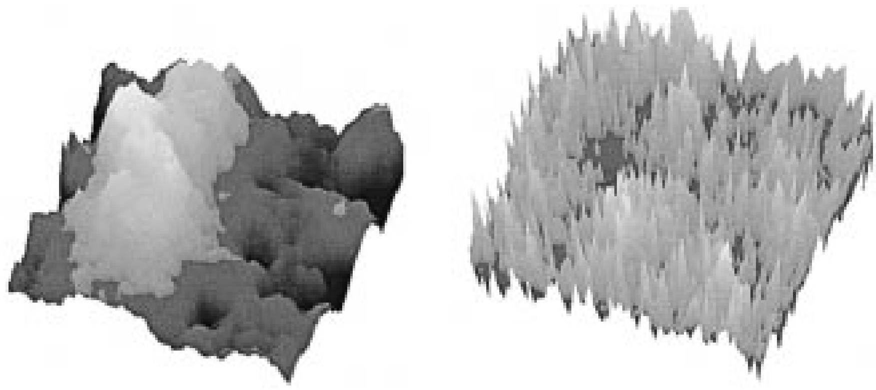

Figure 3. Fractional-Brownian surfaces. Left side: Hurst exponent = 1.0; Right side: Hurst exponent = 0.0.

Limitations and alternate methods

A property of fBm generated by the Fourier synthesis method is that the sequences will be periodic, i.e., a 1-D sequence lies on a circle with the end-points adjacent, a 2-D surface forms a torus, and so on. This causes the variance of the increments to increase according to equation 1 only up to distances $L/2$ for a sequence of length L. For distances beyond $L/2$, the variance will begin to decrease. The periodicity of Fourier generated landscapes is easily circumvented by generating a large sequence and retaining only the first $\frac{1}{2}$ or $\frac{1}{4}$ of the data.

The periodic nature of Fourier synthesis can be quite useful when generating landscapes for input to spatial simulation models. If the simulation uses periodic boundary conditions (i.e, the simulated landscape is wrapped on a torus such that both the left and right edges and the top and bottom edges are adjacent), the use of periodic neutral landscapes avoids sudden changes when an individual crosses from one edge of the landscape and reappears on the other.

An alternative method of generating fBm that does not produce periodic sequences is the mid-point displacement method (Peitgen and Saupe 1988). Mid-point displacement generates fractal landscapes be recursively breaking line segments and displacing the mid-points a random distance. The variance of the displacements is scaled as a function of the length of the line segments; each recursion reduces the segment length (or scale) by $\frac{1}{2}$. The result is an approximation of fBm that is not periodic. Mid-point displacement also produces artifacts: because each point is displaced only one time, the resulting distribution of increments is non-stationary. Furthermore, mid-point displacement involves a geometric progression of frequencies (i.e., $f_{n+1} = rf_n$) and is thus related to Weirstrauss functions (Mandelbrot 1982), whereas Fourier synthesis builds sequences from a linear progression of frequencies. Either method is sufficient for most uses in modeling. However, when validating mathematical theory, the biases introduced by various methods of generating fBm need to be considered.

The dimension of fBm

Given a support $\vec{t} \in R^N$ with dimension N, a plot of $X(\vec{t})$ versus $\vec{t}$ is contained in $E = N + 1$ dimensions: N dimensions for $\vec{t}$ and one for $X(\vec{t})$. The quantity E is referred to as the embedding dimension of the sequence $X(\vec{t})$. For an fBm with embedding dimension E, the fractal dimension of the surface is approximately given by $E - H$ (Mandelbrot 1982). However, some care is necessary in defining the fractal dimension of fBm because fractional-Brownian surfaces are not, strictly speaking, self-similar, but rather self-affine (Barnsley 1988). Under successive magnifications, a fBm will scale differently with respect to space or time t than with respect to height $X(t)$. Given a fBm $X(t)$, if one rescales the sequence by a factor $0 < r < 1$ such that $X'(t') = rX(rt)$, the increments will not be properly rescaled. In order to preserve the original scaling properties, the increments must be rescaled by the factor r^H such that $X'(t') = r^H X(rt)$.

The lack of self-similarity in fBm leads to some ambiguity in defining a fractal dimension. A more precise definition stems from the concept of a zero-set Z (Mandelbrot 1982). The zero-set of a fractal embedded in E-dimensions is simply the set of all zero-valued points in the sequence, i.e., $\vec{t} \in Z$ if $X(\vec{t}) = 0$. Since taking the zero-set removes the height dimension, the remaining spatial dimensions can be rescaled at will; hence the zero-set is self-similar and has a well defined fractal dimension $D = E - 1 - H$ (Peitgen and Saupe 1988).

H and $1/f$ noises

Spectral approximation of fBm is most accurate for $0 \leq H \leq 1$. In practice, H can be varied outside this range to produce highly smooth sequences and highly rough sequences. However, for $0 > H > 1$, one is no longer dealing with approximations to random walks and the relationship given in equation 1 does not hold. Furthermore, setting $H = 0$ does not produce random white-noise. From equation 2, note that $H = 0$ results in a 1-D spectral density of $1/f$, whereas a purely random sequence results in a $1/f^0$ spectrum which would require an H equal to -0.5. According to equation 1, $H = -0.5$ implies a decreasing variance with increasing distance, which is of course untrue for a purely random sequence.

The relationship between $H < 0$ and fBm is resolved by noting that a Brownian random-walk $(1/f^2)$ is the integral of white noise $(1/f^0)$. White noise is discontinuous and nowhere differentiable; however, it's integral, a Brownian walk, is continuous, yet still nowhere differentiable. The transition from continuous sequences for $H \geq 0$ to discontinuous sequences for $H < 0$ explains why equation 1 no longer applies. Thus, one can define a set of discontinuous fractional white noises with $-1 \leq \beta < 1$ whose integrals are fractional-Brownian sequences (Feder 1988).

Multifractals and wavelet synthesis

Multifractal sets are the composition of fractal sets, each with a different scaling relation (Feder 1988). Thus, for multifractal patterns, the Hurst exponent H can be replaced by a family of exponents $H(q)$. The spectrum of scaling exponents is usually found by examining the power-law relationship between scale and various statistical moments of local measures on the multifractal pattern (Feder 1988; Milne 1992; Ott 1993). In other words, unlike fBm, multifractal scaling is non-stationary with respect to space or time: each spatial location can have a different scaling exponent. Multifractal patterns can arise in situations where local contingencies affect the processes generating landscape pattern. Localized patterns can simply be the result of historical landscape features created by ecological processes operating at widely different time scales. For example, Solé and Manrubia (1995) have suggested that variation in the recolonization rate of tree-fall gaps in tropical forests can result in multifractal patterns.

The wavelet transform is an ideal spectral method for analyzing multifractal patterns (Arneodo et al. 1988; Muzy et al. 1991, 1993) and other hierarchical pattern in landscapes (Bradshaw and Spies 1992; Bradshaw and McIntosh 1994; Dale and Mah 1998). Wavelet transforms are closely related to Fourier transforms, but involve the use of spatially localized spectral components. The mathematics of wavelets are quite technical [a thorough introduction can be found in Daubechies (1992)]. However, programs for computing wavelet transforms are widely available. Roughly speaking, the wavelet transform represents a pattern as a set of localized spectral components (i.e., wavelets), each weighted by a wavelet coefficient $a_\phi(t)$ where ϕ is the scale or level of the transform and t is the spatial location or translation of the wavelet.

The actual transform involves two filters: a scaling function or father wavelet is used to average the data at each level (in effect rescaling the data) and a mother wavelet (or just wavelet) which extracts detail from the sequence. The output from the scaling function is used as input to the next level of the transform, and the output from the wavelet filter is the wavelet coefficients. To synthesize random patterns, the $a_\phi(t)$ are chosen from a random distribution and then inverse wavelet-transformed.

Wavelet synthesis has a number of advantages over Fourier synthesis. Because wavelet coefficients can be specified locally, it is possible to generate fractal patterns where the Hurst exponent varies across the landscape. A non-stationary Hurst exponent corresponds to a multifractal pattern. In general, to precisely reproduce multifractal patterns, one should constrain all of the moments q of the input noise to match the desired spectrum $H(q)$ for a given multifractal pattern. For demonstration purposes, it was sufficient to vary H in a simpler manner. Figure 5 shows a multifractal fBm where H has been varied from 0.0 along the centerline of the image to 1.0 along the edges. The result is reminiscent of tectonic faulting.

Another advantage of wavelet synthesis is the wide range of choices of wavelet bases. Wavelet bases are constrained by certain mathematical requirements. As a result, there is a trade-off between the smoothness of the wavelet and its size. Compact wavelets tend to be sharper and less continuous, whereas longer wavelets can be relatively smooth (see Figure 4). The choice of wavelets allows one to alter the texture of generated sequences, independent of scaling properties. Low-order wavelets will produce rougher, more discontinuous sequences. Longer high-order wavelets can produce smoother images.

O'Neill et al. (1992) introduced a neutral landscape model based on Mandelbrot's (1982) random curds. Random curdling recursively subdivides the plane into blocks. At each level of the recursion, blocks survive with a probability p and are subdivided again at the next level. Blocks that don't survive are assigned a value 0 and are thereafter ignored. The resulting pattern is a fractal dust related to Cantor sets (Mandelbrot 1982). A variant of curdling retains the pattern generated at each scale and adds them together to produce a fractal pattern. This form of random curdling has a natural spectral representation in the Haar wavelet basis (first row in Figure 4). Examples of these curd-like fractals are shown in Figure 6.

Periodicity is a property shared by both Fourier and wavelet transforms. Periodicity in the output image can be corrected by generating a large image and retaining only $\frac{1}{2}$ or $\frac{1}{4}$ of the original. However, periodicity is not intrinsic to the wavelet transform; it is possible to construct non-periodic wavelet transforms (Daubechies 1992) thereby eliminating any periodicity in synthesized patterns.

Discussion

Despite the apparent differences among the models discussed here, they can all be considered to be variations on a common theme. In the spectral representation, it becomes clear that all of these models can be defined in terms of a spectral basis and a scaling relation between the amplitude and frequency of spectral components (Table 1).

The importance of a common mathematical description of neutral models is that it allows one to consider independently different aspects of pattern, texture, and scale, and their influence on the spatial properties of ecological landscapes. For example, wavelet-based models could be used to analyze stationarity, isotropy, fractal-scaling, and continuity of spatial patterns. In addition, understanding the relationships among various landscape models allows one to cast these analyses in much broader context; the idiosyncrasies of a particular model is no longer a deterrent to generalizing results across different landscapes and different ecological processes.

Although not the main topic of this paper, spectral methods may also be used for analysis of landscapes as well as sythesizing artificial landscapes. Scaling exponents may be estimated by fitting models to the power spectrum of a landscape. Generally overlooked are measures of the precision of such estimates and methods for hypothesis testing. The application of bootstrapping and Monte Carlo techniques to the wavelet transform is particularly promising. Because spectral transforms are linear, traditional inference methods such as ANOVA may be applied to the Fourier transform of a spatial pattern (Dutilleul 1998). ANOVA of the Fourier transform is mainly used to assess differences in periodicity among levels of the classification factors and to determine if replicate time series share similar periodicities. Fraction-Brownian noise is not strictly speaking periodic. However, there is no reason these methods cannot be generalized to study spatial scaling. There is in fact an enormous literature on

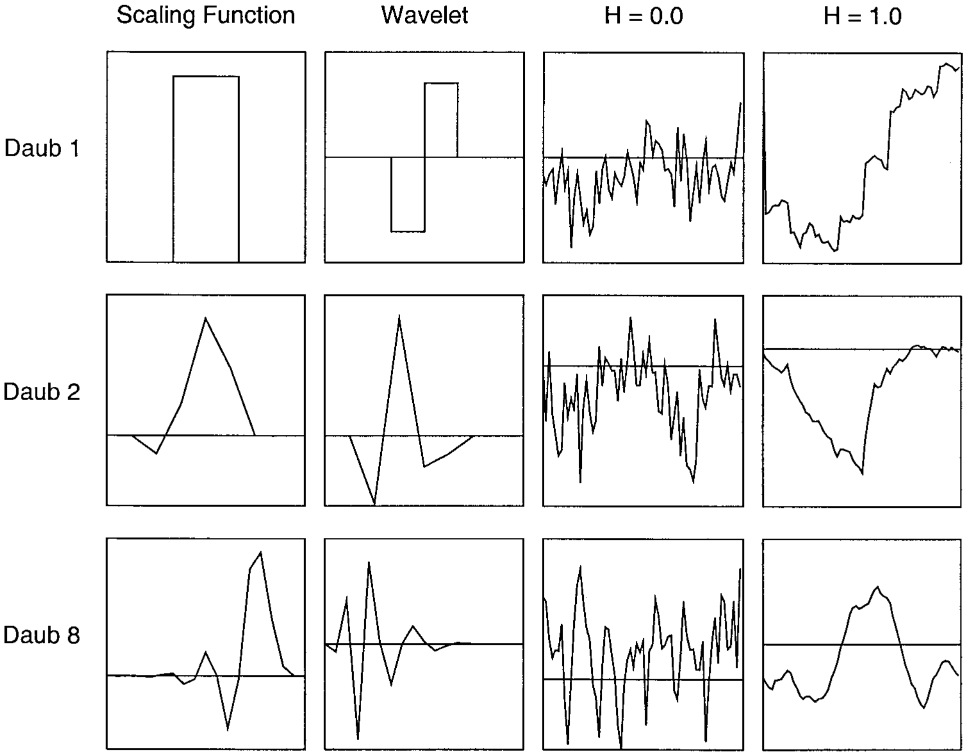

Figure 4. Wavelet synthesis of 1-D transects. Wavelet bases are the Daubechies (1992) series of order 1, 2, and 8. Wavelet order determines the texture of the pattern: lower-order wavelets produce sharper edges; higher-order wavelets are more continuous.

spectral analysis of time series and spatial processes. With respect to landscapes, an extensive review of analysis methods was recently given by Gustafson (1998).

In many respects, researchers have only scratched the surface in the application of fraction-Brownian landscapes and their derivatives (Appendix B). Most studies have focussed on binary maps with suitable habitat embedded in a mosaic of unsuitable habitat. The real power in fractal landscapes may be as models of complex gradients. The emerging synthesis of evolutionary and ecological theory strongly emphasizes the importance of regional landscape mosaics in the organization of biological diversity. For example, Thompson (1994) discusses many examples of species that evolve quite different coevolutionary specializations in different parts of their geographic range. The spatial structure of landscapes is a key component that determines the context in which these coevolutionary specialization occur. Recent theoretical work has supported the idea that coevolutionary relationships can vary along gradients, and in some cases, the direction of the interaction may even reverse (Hochberg and van Baalen 1998). A promising area for future modeling efforts would be to investigate whether the introduction of complex gradients, such as fractional-Brownian surfaces, alters the predictions of these models.

Appendix

Spectral synthesis methods

The (continuous) Fourier transform of a sequence $X(t)$ of length T is

$$F(f) = \int_0^T X(t)e^{-2\pi i f t}\,\mathrm{d}t, \qquad (3)$$

where f is frequency, t is displacement in time or space, and i represents the imaginary number $\sqrt{-1}$. By Taylor expansion of the complex exponential, it can be shown that

$$re^{i\phi} = r\cos\phi + ri\sin\phi$$

thus relating equation 3 to a spectral representation composed of sine and cosine functions. The result

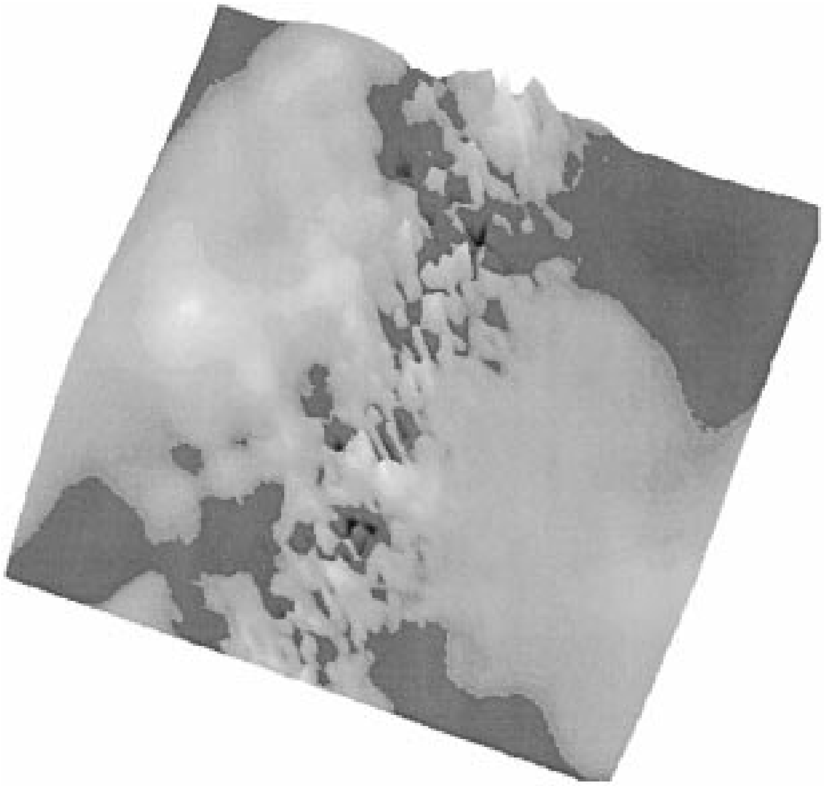

Figure 5. Multifractal surface generated via a wavelet synthesis. A 2nd-order Daubechies wavelet was used. Hurst exponents vary from 0.0 at the center and 1.0 at the left and right edges.

Figure 6. Curd-like fractals generated via a Haar wavelet synthesis. Hurst exponents are 0.0, 0.5, and 1.0 from left to right.

Table 1. Summary of neutral landscape models

Model	Spectrum	Parameters	Properties
Percolation map	Segmented $1/f^0$	$0 \le p \le 1$	Critical p produces spanning cluster
Fractal curd	$1/f^\beta$, Haar wavelet basis	$1 \le \beta \le 3$	Rectilinear texture, fractal scaling
Fractional-Brownian	$1/f^\beta$	$1 \le \beta \le 3$	Continuous, nowhere differentiable
Segmented fBm	Segmented $1/f^\beta$	$0 \le \beta \le 2$, $0 \le p \le 1$	Patch edges have dimension $D = 2 - H$
Multifractal fBm	$1/f^\beta$, varies spatially	$H(q)$ spectrum	Fractals within fractals

of Fourier transforming a time series or spatial transect is a set of complex coefficients $a_f \exp(i\phi_f)$ with amplitudes a_f and phases ϕ_f.

Using equation 2, one can generate fractional-Brownian sequences and surfaces via the method of spectral synthesis. For a 1-D fBm, the steps in the procedure are

1. determine the Hurst exponent H;
2. generate M random phases $\phi_1 \ldots, \phi_M$ uniformly distributed on $[0, 2\pi]$;
3. generate M normally distributed random numbers $x_1, \ldots, x_M$; multiply each x_f by $1/f^{\beta/2}$ to form the amplitudes a_f;
4. form the complex coefficients $a_f \exp(i\phi_f) \equiv a_f \cos\phi_f + i a_f \sin\phi_f$;
5. take the inverse (discrete) Fourier transform of the coefficients (many software packages have a routine for the discrete fast Fourier transform or FFT);
6. convert the complex valued result to a real valued result by dropping the imaginary part.

The procedure is easily extended to higher dimensions by setting the amplitude proportional to the length of the vector of frequencies such that

$$S(\vec{f}) \propto \left(\sum_{n=1}^{N} f_n^2 \right)^{-\frac{1}{2}\beta}$$

where N is dimension of the support, i.e., the size of the vector $\vec{f}$. Note that the number of spectral coefficients required in the transform increases as M^N; thus, the exponent β must be adjusted to reflect the increase in the number of spectral components. For a fBm with support $\vec{f} \in R^N$, $\beta = N + 2H$. Examples of $N = 2$ fractional-Brownian surfaces are shown in Figure 3.

Extensions of fractional Brownian models

The introduction of fractal neutral models is an important contribution because it allows one to incorporate spatial correlations into simulations and neutral studies of spatial pattern. Increasingly complex models of spatial pattern can be generated by relaxing certain assumptions of fBm such as isotropy or stationarity. Despite the increasing complexity of these models, they can still be considered neutral in the sense that the models represent random ensembles of landscapes whose properties are described by statistical averages. These more complex neutral models could, for example, be used to generate expected patch size distributions for landscapes that are fractal and stationary, but non-isotropic, or any other appropriate combination of parameters. In the following, I describe several useful extensions of fBm for modeling landscape pattern.

Segmented fractional-Brownian landscapes

For simulations, it is often convenient to segment fBm (Figure 7) to create landscapes of ones and zeros corresponding to habitat and non-habitat (e.g., Keitt and Johnson 1995). To segment a fBm, all points above some height are assigned a 1 and all points below are assigned 0. Letting the critical height be X_c, then the landscapes are indexed by the parameter p defined as the probability of a randomly chosen X being less than or equal to X_c. For $p = 1.0$ the entire image is filled with ones; for $p = \frac{1}{2}$ half are ones, etc. A variation slices the fBm into multiple levels and assigns a different label to each level.

The dimensions of the resulting clusters will be somewhat higher than for the zero-set, since the interior spaces of the zero-set are filled-in with ones. Furthermore, the dimension of segmented fBm will depend on the parameter p. At the extreme values of $p \to 0.0$ and $p \to 1.0$, the dimension of the clusters must approach 0.0 and 2.0 respectively, because in the former case the set of ones is empty and in the latter, the set of ones fills the entire plane.

Piece-wise log-linear scaling

In many cases, natural landscapes do not exhibit constant scaling over all scales. Instead, scaling exponents may differ across regions of the frequency spectrum (Krummel et al. 1987). Multiple scaling regions result because different ecological and environmental processes operate at different scales, each generating a different scaling relation. The complete landscape pattern is in effect the synthesis of the patterns generated by these processes. It is simple to generate piece-wise log-linear neutral landscapes via spectral synthesis by taking advantage of the linearity of Fourier transforms.

From equation 3, note that the Fourier transform is defined by an integral, or for discrete transforms a summation. Integrals and sums are linear operations, hence, Fourier transforms (and their inverses) have the following properties

$$\begin{aligned} F(rX) &= rF(X), \\ F(X+Y) &= F(X) + F(Y). \end{aligned}$$

Thus, given the second property, one can simply construct a series of landscapes, each filling in a region of

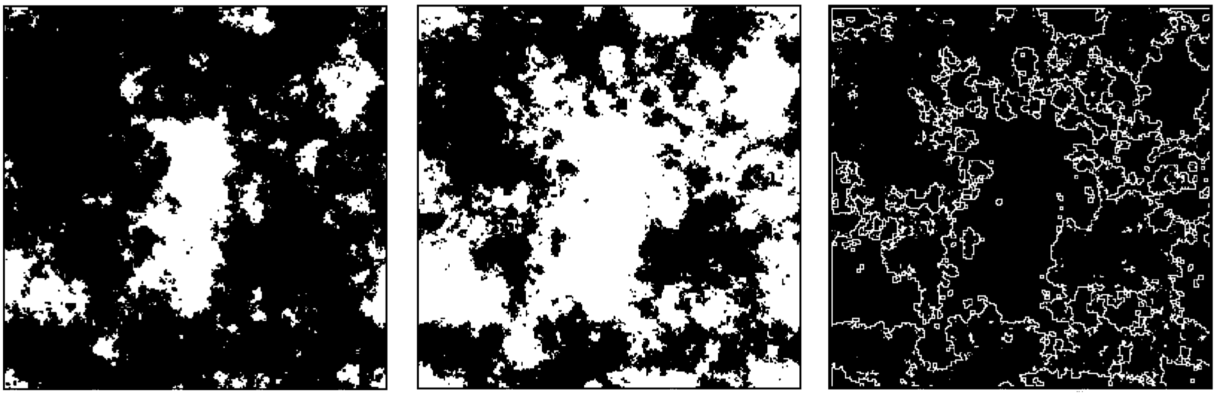

Figure 7. Segmented fractional-Brownian surfaces ($H = \frac{1}{2}$). From left to right: $p = 0.2$, 0.5, zero-set.

the spectrum according to particular scaling exponent, and then adding all the landscapes together. An example using two scaling regions is shown in Figure 8. To produce the landscapes, the frequency spectrum was broken into two regions, one containing the high frequency components and the other, the low frequency components. High and low regions were scaled with Hurst exponents equal 1.0 or 0.0; spectral coefficients were set to zero outside the scaling region for a given sequence. The final images were created by adding high and low frequency landscapes together.

Direction-dependent scaling

Natural processes that produce landscape pattern are not necessarily isotropic: pattern forming processes can be strongly direction dependent. Prevailing wind direction, sun angle, water drainage down-slope, and animal dispersal patterns can all exhibit direction dependence. To model direction dependent scaling using spectral synthesis, one only need introduce a different Hurst exponent for each orthogonal direction. For example, the Fourier transform of a 2-D surface generates 2-D coefficients $c(f_x, f_y)$. Thus, to generate a 2-D surface, one must specify coefficients in both the x and y direction. Let H_x be the Hurst exponent in the x direction and H_y be the Hurst exponent in the y direction, then

$$H_{xy}(f_x, f_y) = \frac{f_x H_x + f_y H_y}{f_x + f_y},$$

where f_x is the frequency of the spectral component in the x direction and f_y is the frequency of the spectral component in the y direction. To fully specify the Fourier coefficients, it is necessary to compute H_{xy} for all combinations of f_x and f_y. The resulting plane of 2-D Fourier coefficient can then be inverse transformed to produce direction-dependent scaling. An example is shown in Figure 9.

Spatio-temporal landscapes

Natural landscapes are not static, but evolve through time. It is therefore natural to consider dynamic neutral-landscape models. Spectral synthesis methods can be extended to high dimensional spaces and thus, can also generate spatio-temporal landscapes with two spatial dimensions and a time dimension. Furthermore, using direction dependent scaling, it is possible to decouple temporal scaling from spatial scaling. To model, for example, a landscape that had high rates of disturbance and thus, low temporal correlation, one can generate a series of landscapes with the appropriate spatial scaling and tune their temporal correlation by adjusting the Hurst exponent in the time dimension. Two example landscapes are shown in Figure 10.

Lacunarity

Mandelbrot (1982) coined the term lacunarity to describe the extent to which a pattern contains gaps or holes. Checkerboards, for example, have high lacunarity, whereas uniform random patterns have low lacunarity. Lacunarity can also be applied to fractal patterns; two fractal landscapes can possess the same scaling exponents, but vary in their degree of lacunarity. In terms of landscape pattern, high degrees of lacunarity indicate a scenario in which different ecological processes generate pattern within restricted and strongly separated scaling regions. For example, the distribution of piñon-juniper woodlands in the Southwest is likely controlled at fine scales by biotic

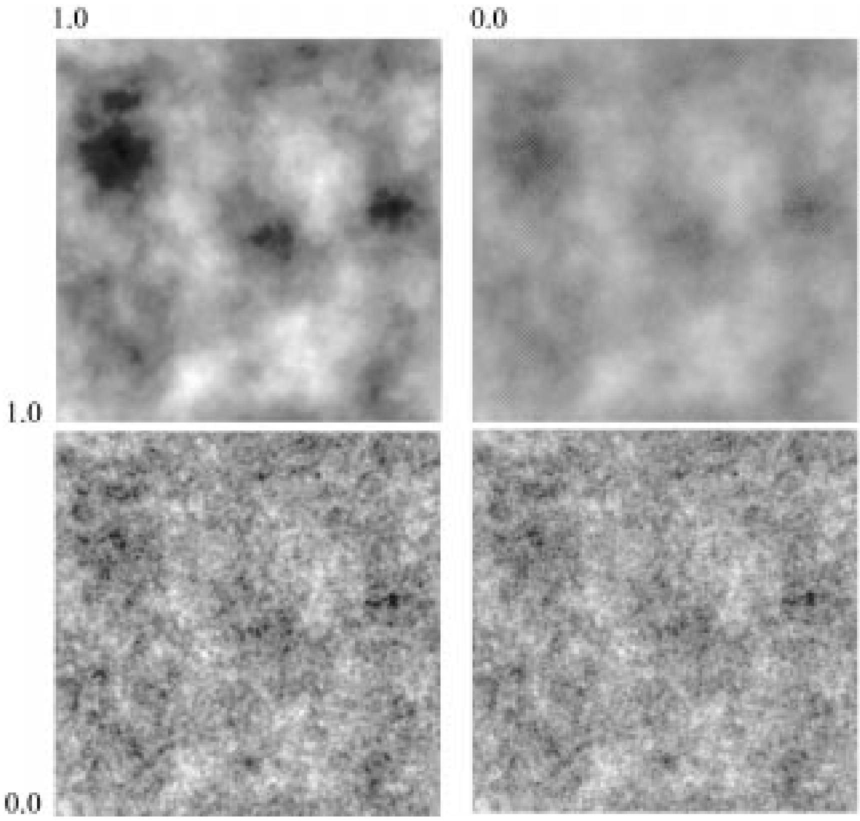

Figure 8. Piece-wise log-linear surfaces. The Hurst exponent of the lower $\frac{1}{2}$ of the power spectrum (i.e. low frequencies) is given before each row; the exponent for the upper $\frac{1}{2}$ of the spectrum is given atop each column.

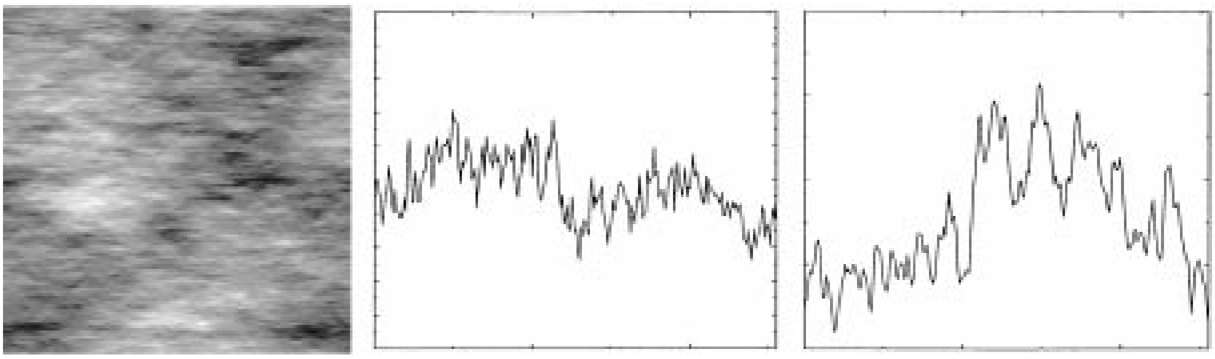

Figure 9. Direction-dependent scaling with vertical ($H_v = 0.0$) and horizontal ($H_h = 1.0$) transects.

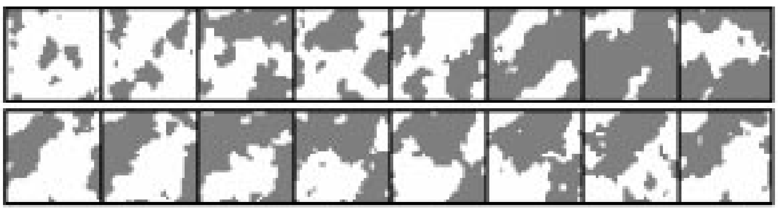

Figure 10. Correlated spatio-temporal landscapes. Time runs from left to right. The upper panel shows an uncorrelated temporal sequence; the lower panel, a correlated temporal sequence.

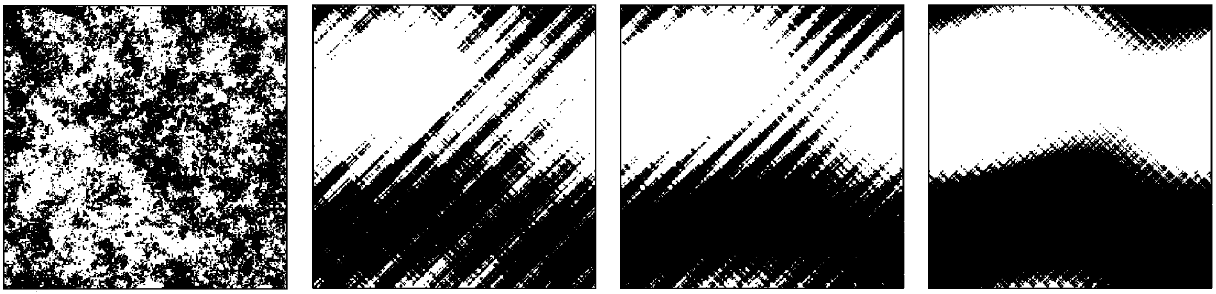

Figure 11. Segmented landscapes with varying degrees of lacunarity. Lacunarity indices (r_L) from left to right were 1, 0.2, 0.1, 0.05. The landscape share the same scaling relation ($H = 0.0$) but differ in texture.

processes such as dispersal and seed predation, but at broad scales by climate (Milne et al. 1996). Processes acting on a pattern at widely different scales can lead to strongly lacunary landscape patterns (Plotnick et al. 1996).

From the standpoint of spectral representation (Figure 1), lacunarity is correlated with the size of gaps between successive spectral additions (Peitgen and Saupe 1988). For Weirstrauss functions, the scale of each spectral addition follows a geometric series such that the nth spectral component has a frequency proportional to $1/r^n$ with $0 < r < 1$, and the variance of the increments scales proportional to $1/r^{2Hn}$. For values of r near zero, successive spectral additions are spaced far apart in their frequencies. Thus, r can be used as and index of lacunarity (Peitgen and Saupe 1988).

For Fourier methods, it is more appropriate to define the lacunarity index in terms of a linear sequence of frequencies. Letting $f(n)$ be the frequency of the nth spectral component, one can define a lacunarity index

$$r_L = \frac{1}{f(n+1) - f(n)} \tag{4}$$

For $r_L = 1$, each successive spectral component has a frequency one greater than the last, and results in the standard approximation to fBm. For smaller values of r_L, the resulting images will exhibit increasing patchiness or gappiness (Figure 11). For clarity, I refer to the geometric lacunarity index defined in Peitgen and Saupe 1988) as r_G and the linear index defined in equation 4 as r_L.

Wavelet synthesis

The wavelet transform can be used to generate fractional-Brownian noise (Figure 4). First, I define the wavelet spectral density as $S_W(\phi) = E[a_\phi(t)^2]$. The wavelet transform reduces the data sequence by 1/2 at each level; thus, the frequency f is related to the level of the transform by $f = 2^\phi$. In this sense, the wavelet transform is related to the Weirstrauss function or "lacunary" Fourier transform (Daubechies 1992) because it involves a geometric progression of frequencies. As with the Fourier synthesis method, it is necessary to define a scaling relation between frequency and spectral density – for wavelets the same expression can be used:

$$S_W(f) = 1/f^\beta = 1/2^{\phi\beta} \tag{5}$$

where $\beta = N + 2H$ as previously defined. A useful property of the wavelet transform is that the wavelet coefficients of a pattern share the same scaling relation as the pattern itself (Arneodo et al. 1988). Thus, to generate fBm using wavelet synthesis, one simply have to choose random wavelet coefficients and scale the variance at each level according to equation 5. A simple method of generating fBm via wavelet synthesis is as follows:

1. choose the Hurst exponent H,
2. choose a wavelet basis for the transform,
3. wavelet transform a white noise signal ($1/f^0$),
4. multiply the wavelet coefficients at level 0 by $1/2^0$, level 1 by $1/2^\beta$, level 2 by $1/2^{2\beta}$, and so on,
5. apply the inverse wavelet transform.

Confirmation of the correct $1/f^\beta$ distribution of fluctuations can be achieved by estimating the slope of the log-transformed Fourier power-spectrum.

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