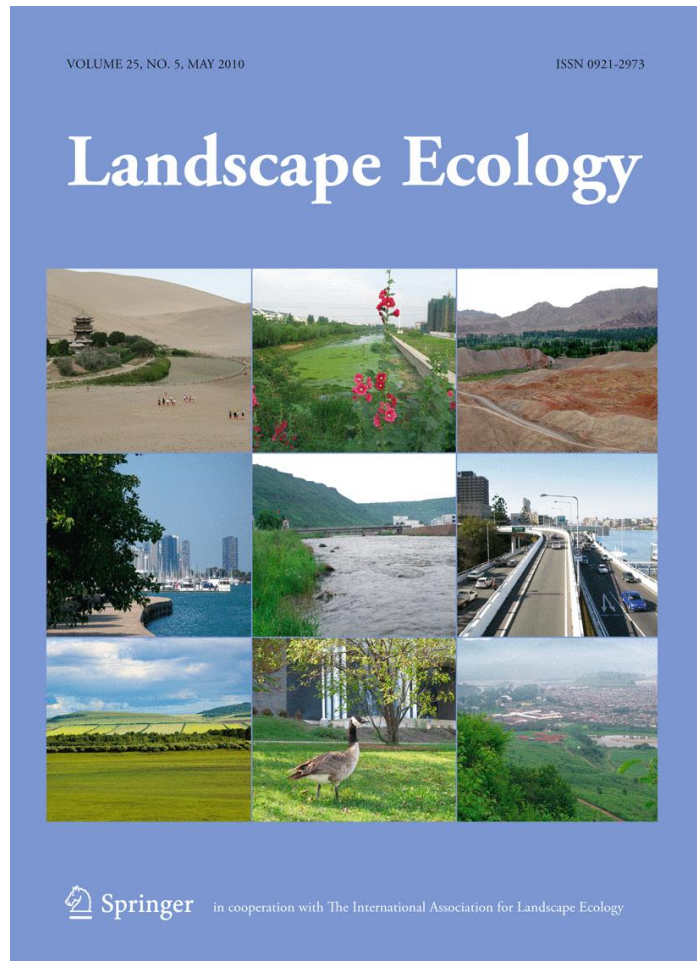


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Two multi-scale contextual approaches for mapping spatial pattern

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Abstract The majority of landscape pattern studies are based on the patch-mosaic paradigm, in which habitat patches are the basic unit of the analysis. While many patch-based landscape indices successfully relate spatial patterns to ecological processes, it is also desirable to use finer grained analyses for understanding species presence, abundance, and movement patterns across the landscape and to describe spatial context by measuring habitat change across scales. Here, we introduce two multi-scale pixel-based approaches for spatial pattern analysis, which quantify the spatial context of each pixel in the landscape. Both approaches summarize the proportion of habitat at increasing window sizes around each pixel in a scalogram. In the first regression-based approach, a third-order polynomial is fitted to the scalogram of each pixel, and the four polynomial coefficients are used as descriptors of spatial context of each pixel within the landscape mosaic. In the second shape-based approach, the scalogram mean and standard deviation, and the mean slope between forest cover at the smallest window size and each of the larger window sizes are calculated. The values emerging from these two approaches are assigned to each focal pixel and can be used as predictive variables, for example, in species presence and

abundance studies. We tested the performance of these approaches on 18 random landscapes and nine actual landscapes with varying forest habitat cover. Results show that both methods were able to differentiate between several spatial contexts. We thus suggest that these approaches could serve as a complement or an alternative to existing methods for landscape pattern analysis and possibly add further insight into pattern–species relations.

Keywords Landscape structure · Multi-scale · Spatial context, scalogram

Background

Landscape ecology has evolved around the patch-matrix paradigm (Forman 1995), which describes the landscape as consisting of habitat patches that are interspersed within a non-habitat matrix. One theoretical foundation of the patch-matrix paradigm is island biogeography theory (McArthur and Wilson 1967), which was extended to terrestrial landscapes by assuming that patches within the matrix are similar to islands (Haila 2002). Patch size and isolation thus explain species abundance, richness, and diversity (Ewers and Didham 2006). There are numerous methods and approaches to quantify landscape structure based on the composition and

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configuration of patches within the matrix (Gustafson 1998), and these are typically conducted at two spatial scales: the patch and the landscape. Patch-level analyses describe the size, edge, and shape of individual patches, while landscape-level analyses deal with the relative cover and density of patches, the distribution of patch size and shape, and the proximity/isolation of patches (McGarigal et al. 2002). Ultimately, the goal of landscape structure analyses is to relate landscape patterns to ecological processes, especially in the context of species abundance, richness, and diversity (Fahrig 2003). The relationship between pattern and species is well established, but as much as there are empirical results to support this theory, many studies still fail to confirm the relationship (Ewers and Didham 2006).

In recent years, landscape ecology has developed new approaches to measure landscape structure without identifying patches first (McGarigal et al. 2009). One motivation for these new approaches was to capture variability within patches better and to quantify gradual changes from patch to matrix. Landscape structure can be quantified from image texture of unclassified satellite imagery (St-Louis et al. 2006, 2009). Another approach, landscape gradients, calculates a new group of surface metrics that were adopted from the field of surface metrology (Hoechstetter et al. 2008; McGarigal et al. 2009). Surface metrics are landscape-scale analyses of continuous spatial data that are described by pixels, rather than patches. A third method, morphological spatial pattern analysis (MSPA; Vogt et al. 2007; Riitters et al. 2007), is a pixel-based approach that retains the binary habitat/non-habitat description of landscapes but does not define patches. Each pixel is assigned to a mutually exclusive thematic class according to its spatial context, or the structural role it has relative to its neighboring pixels. For example, habitat pixels adjacent to matrix pixels are defined as edges, internal patch pixels are defined as core, pixels that connect between disjoint cores are bridges, and matrix pixels are classified as background (Vogt et al. 2007; Riitters et al. 2007).

Most landscape metrics are calculated at a certain scale or window size. Many studies have attempted to relate landscape structure at given scales to species abundance and diversity (Fahrig 2003). Most of these studies used pattern at specific scales as their predictor variables. However, the scale that is most

important for predicting species abundance is often unknown (Marceau 1999; Li and Wu 2004), since the human perception of the landscape may be entirely different than those of other organisms (Wiens and Milne 1989; Manning et al. 2004). Moreover, many studies attempt to predict overall species richness using structure at specific scales; yet different species are known to be sensitive to landscape structure at varying scales (Milne 1992), making evaluation of multiple scales necessary for multi-species studies. Therefore, there are no general 'correct' scales for studying a given landscape, since the scale of analysis varies with purpose and application (Blaschke 2006).

Landscape analyses could potentially be improved with multi-scale landscape metrics, since landscape patterns and ecological processes vary in scales (Wiens 1989; Levin 1992). The majority of landscape metrics used for spatial pattern analysis operate at a specific spatial scale (i.e., the patch or the landscape), and most of these metrics are sensitive to scale (Wu 2004; Cushman and McGarigal 2004; Neel et al. 2004), as are the pixel classes used in morphological spatial pattern analysis (Ostapowicz et al. 2008). In the past decades, there have been several attempts to develop landscape metrics that characterize landscape structure at varying scales simultaneously and provide a spatial context of the location of each patch or pixel. Early attempts to define two-dimensional, multi-scale spatial patterns were based on fractals (Mandelbrot 1982). The fractal dimension of a landscape, i.e., the relationship among cover values at multiple landscape sizes, captures different landscape patterns in both real and simulated landscapes (Milne 1992) and is also related to, for example, the movement of tenebrionid beetles in micro-landscape experiments (Wiens and Milne 1989). Plotnick et al. (1993) used lacunarity indices to represent multi-scale pattern at the landscape level. Lacunarity is based on the frequency distribution of habitat pixels at various scales calculated with moving windows of various sizes. Another landscape-scale approach describes multi-scale pattern using conditional entropy profiles (Johnson et al. 2001). These are measures of entropy at a single scale relative to a subsequent coarser scale (generated by degradation of the finer scale map, in contrast to other approaches that retain the original pixel size), computed for a range of scales and plotted against the corresponding window sizes.

In addition to landscape-level multi-scale indices, there are also pixel-based multi-scale pattern analysis approaches. The multi-scale aggregation of every pixel in a landscape was quantified by generating windows of three, five, and nine pixels around each pixel and then assigning to each pixel the number of windows (generated around other pixels) that overlap it at a given scale (Milne 1992). The three resulting images were then displayed as an RGB image, and the aggregation context was visually interpreted. Forest cover and proportional adjacency of forest pixels (the probability that a forest pixel is adjacent to another forest pixel) have been analyzed at multiple scales over large areas and then classified into four thematic classes (core, patch, perforation or internal edge, and edge) to describe coarse-scale global (Riitters et al. 2000) and fine-scale continental (Riitters et al. 2002) forest fragmentation patterns. Vogt et al. (2007) generated similar pixel classes (and others) by applying mathematical morphology. Riitters (2005) also employed cluster analysis to differentiate between various contexts of spatial pattern, based on a multi-scale analysis of forest cover. Riitters (2005) was able to interpret several classes of context, including interior, small patches, concave edges, and convex edges. In a similar manner to Riitters et al. (2002) and Riitters (2005), the multi-scale pattern of disturbances in neutral and actual landscapes was assessed by applying a moving window analysis on binary disturbance maps, with window sizes from 3×3 to 21×21 pixels (Zurlini et al. 2007). A cluster analysis was then conducted to identify eight disturbance classes according to their pattern on different landscape sizes, and these were mapped back into geographic space to yield a thematic map of disturbance classes. The main advantage of the approaches of Riitters et al. (2002), Riitters (2005) and Zurlini et al. (2007) is the ability to account for different spatial scales simultaneously and thus to introduce a spatial context to each location (pixel) in the landscape. While the generation of thematic structure (Riitters et al. 2000) and disturbance (Zurlini et al. 2007) classes is appealing, especially for large-scale analyses, the classification or clustering eliminates much of the variation in the spatial information and result in categorical indices, and this may limit the potential to explain species abundance and diversity.

It is therefore desirable to develop methods to determine landscape structure at multiple scales that

measure landscape structure with continuous metrics. Such methods should determine for each pixel in the landscape its spatial context, i.e., where it is located relative to the surrounding areas of habitat and matrix. We present such a method, which analyzes multi-scale landscape pattern around each pixel, thus forming a scalogram. We propose two approaches to analyze scalograms. The first consists of fitting a polynomial curve to the scalogram and using the curve parameters as descriptors of context. The second approach describes the shape of the scalogram based on the slopes of the lines between the first entity of the scalogram (forest cover at the smallest window size) and each subsequent entity. In both approaches, a binary landscape map is transformed into a group of continuous maps that may be used as predicting variables for species studies.

Our goal was thus to develop two new approaches for Multi-scale Contextual Spatial Pattern Analysis (MCSPA), based on polynomial coefficients (MCSPA-P) and the shape of the scalogram (MCSPA-S). Both approaches quantify multi-scale landscape structure at the pixel level. Our objectives were to test these methods on both artificial and actual landscapes and explore their properties and limitations.

Methods

Scalograms: generation and properties

The starting point of our analysis is a binary map consisting of habitat ('1') and non-habitat ('0') pixels. A square moving window of width L is applied to every pixel (habitat and non-habitat) in the binary map, and the percentage of habitat pixels $P_h(L)$ within a window is assigned to its center pixel. The process is repeated with increasing window sizes, each time generating a new map, until a pre-defined maximum window size L_{\max} is reached. At the basic window size (focal window hereafter) $L = 3$, the window consists only of the eight immediate neighbors of the center pixel and the center pixel. If $L = 3$ and $P_h(3)$ is less than 100, the center pixel is an edge pixel since at least one of its immediate neighbors is a non-habitat pixel. For $L > 3$, $P_h(L)$ represents the percentage of habitat for larger neighborhood sizes beyond its eight adjacent pixels. The above process is similar to many previous multi-scale analyses and identical to the first

step in the methods by Riitters (2005) and Zurlini et al. (2007). It differs from the approach used by Milne (1992) to generate multi-scale aggregation maps (where the number of neighboring windows was tallied rather than the number of habitat pixels).

Once the moving window analysis is complete, there are $N = L_{\max}/2$ maps that originate from the original binary map. For each pixel in the landscape, we then generate a scalogram, i.e., a scatter plot of percent of habitat versus window size (or scale).

Scalograms of habitat cover have two interesting properties: [1] they may be locally linear, but globally non-linear unless their slope is zero; and [2] they exhibit autocorrelation. The former property occurs because a scalogram is constrained between a finite range of values, (0–100). Therefore, a linear function for all possible window sizes is impossible unless the slope is zero (i.e., an pixel in an infinitely large landscape with 100% cover or a pixel along a straight edge that separates large habitat and matrix areas). The second property, scalogram autocorrelation, emerges from the fact that their value at a given scale is based on a window analysis that contains all windows of smaller scales. The correlation between subsequent scalogram values increases with scale, since the ratio between the total number of pixels in subsequent window sizes decreases, and the number of new ‘habitat’ pixels in the larger window sizes has decreasing impact on the overall percentage of habitat with increasing scale.

Mathematically, the basic properties of scalograms can be described in the following manner. Assuming that the window size at scale i is denoted by L_i and the window size at a subsequent higher scale is L_{i+1} , the ratio between the number of pixels in subsequent window sizes is:

$$\lambda(L) = \frac{L_{i+1}^2}{L_i^2}$$

In case of a continuous increase in window size (odd numbers, steps of two pixels per window),

$$L_{i+1} = L_i + 2$$

Then,

$$\lambda(L) = \frac{(L_i + 2)^2}{L_i^2} = \frac{L_i^2 + 4L_i + 4}{L_i^2} = 1 + \frac{4}{L_i} + \frac{4}{L_i^2}$$

And therefore,

$$\lim_{L \rightarrow \infty} \lambda(L) = 1$$

Similarly, we can calculate δP_h , the difference in habitat cover P_h between subsequent window sizes L_i and L_{i+1} that contain $n(L_i)$ and $n(L_{i+1})$ habitat pixels, respectively, as:

$$P_h(L_i) = \frac{n(L_i)}{L_i^2}$$

$$P_h(L_{i+1}) = \frac{n(L_{i+1})}{L_{i+1}^2}$$

$$\begin{aligned} \delta P_h &= P_h(L_{i+1}) - P_h(L_i) = \frac{n(L_{i+1})}{L_{i+1}^2} - \frac{n(L_i)}{L_i^2} \\ &= \frac{n(L_i) + \delta n}{(L_i + 2)^2} - \frac{n(L_i)}{L_i^2} \end{aligned}$$

$$\delta P_h = \frac{n(L_i)}{(L_i + 2)^2} - \frac{n(L_i)}{L_i^2} + \frac{\delta n}{(L_i + 2)^2} \quad (1)$$

where δn is the additional number of habitat pixels gained by increasing the window size from L_i to L_{i+1} . The range of these values is:

$$0 \leq \delta n \leq 4L_{i+1} - 4$$

$$1 \leq n(L_i) \leq L_i^2$$

Therefore, as the window size increases, the values of the three components of Eq. (1) approach zero (the first two components cancel each other, and the third approaches zero). Hence, in large window sizes, there is little change in the value of a habitat cover scalogram:

$$\lim_{L \rightarrow \infty} \delta P_h = 0.$$

The polynomial approach

The first approach for describing the scalogram, MCS-PAp, was based on curve fitting. We used least squares estimation to fit a third-order polynomial function:

$$P_h = a_3 L^3 + a_2 L^2 + a_1 L + a_0 + \varepsilon \quad (2)$$

where a_0 , a_1 , a_2 , a_3 are the coefficients of the curve, and ε is the error term of the fit. We used a third-order polynomial because preliminary analyses with real-world maps revealed that first-order (linear) and second-order polynomials (parabolas) did not capture non-linear scalograms well, especially for pixels in and near convoluted edge areas. At the

same time, we did not use higher order polynomials, despite their better fit, because additional coefficients reduced the interpretability of our results. Following curve fitting, we use the coefficient of determination (r^2) to assess the goodness of fit of the curve for each pixel.

The four coefficients of the curve represent the spatial context of each pixel at varying scales. The zero-order coefficient a_0 is related to the percentage of habitat within the immediate neighborhood of the focal pixel (though in reality, it can be larger than 100% since it represents the intercept with the y -axis, while the lowest x -axis value of the scalogram is $3 \times 3 = 9$). In other words, the zero-order coefficient distinguishes habitat edge, habitat core pixels, and matrix core pixels. The first-order coefficient a_1 defines the linear trend of habitat with increasing neighborhood sizes. Positive values of a_1 denote cases where larger neighborhoods around the core pixel have a greater percent habitat than smaller neighborhoods. A value of zero denotes no scale effect on percent habitat, and negative values denote decreases in percent habitat with an increase in scale. The second-order coefficient a_2 introduces a non-linear effect in the scalogram and has two implications. First, the second-order coefficient denotes whether the rate of habitat gain or loss changes with scale (in contrast to the first-order coefficient that reflects only a constant rate of change). Second, it allows for the existence of an inflection point (minima or maxima of the curve) at which the direction of percent habitat change switches (more habitat with increasing scale to less habitat and vice versa). The third-order coefficient a_3 is highly and inversely correlated to the second-order coefficient, but it adds two more inflection points that are important for accurate description of highly complex habitat configurations where changes in the direction of percent habitat gain or loss occur more than once (although such complex configurations occur less often than simple ones, which are captured sufficiently well by a second-order polynomial).

Once the formula is applied and each pixel is characterized by the four coefficients, it is possible to depict the general multi-scale context of the landscape using the coefficients rather than using a large set of scale-specific maps. Therefore, four maps are created in which each pixel denotes the value of the polynomial coefficient of the relevant order, which

was generated by running the multi-scale analysis in its neighborhood.

Scalogram shape approach

In the second method, MCSPAs, we determine scale effects on change in habitat proportion. We calculate the average amount and the standard deviation of habitat proportion across scales, as well as the magnitude of change in habitat proportion among scales. The second approach is simpler than the polynomial approach and accounts solely for the shape of the scalogram, based on its average and standard deviation values and the average slope between the scalogram value at the focal window and any subsequent window size. There is no goodness of fit measure in the scalogram shape approach, since no curve fitting algorithm is applied. Resulting from the shape approach are three complementary metrics: [1] mean scalogram (S_0), which denotes the average amount of habitat with varying scales; [2] standard deviation of scalogram (S_1), which represents the variability of habitat amount through scales; and [3] mean slope (S_2), which represents the magnitude of habitat change through scales. They are calculated in the following manner:

$$S_0 = \frac{1}{k} \sum_{i=0}^k P(L_i) \quad (3)$$

$$S_1 = \sqrt{\frac{1}{k-1} \sum_{i=1}^k (P(L_i) - S_0)^2} \quad (4)$$

$$S_2 = \frac{1}{k} \sum_{i=1}^k \frac{P(L_i) - P(L_0)}{L_i - L_0} \quad (5)$$

where $i = 0$ is the index of the focal window, and k is the number of windows (or scales). S_0 ranges between zero and one, and its value is related to the percent cover of the entire landscape, coupled with its degree of aggregation. S_1 describes the general variability of the curve by distinguishing between scalograms that exhibit little change in habitat with scale versus curves that exhibit large-scale effects. The values for S_1 range between zero, denoting a linear curve with zero-slope, to positive numbers that increase as the curve slope deviates from zero, and scale effects are more pronounced. S_2 ranges from positive values that correspond to cases where habitat

increases with scale, through zero that represents cases where habitat is constant with scale (mainly core pixels, but possibly edge pixels located along straight boundaries), to negative values that denote cases where habitat decreases with scale. The lowest values of S_2 occur when the scalogram exhibits a non-linear decay pattern (rapid decrease of habitat at smaller window sizes, followed by smaller changes at larger window sizes).

Case studies

To test the performance of both approaches under various landscape configurations, we conducted analyses for 18 neutral landscapes and nine real-world landscapes that consisted of mosaics of forests (with forests corresponding to habitat hereafter) and agriculture (matrix) and represented a gradient of spatial pattern in terms of forest cover. Neutral Random landscapes were generated by MATLAB with varying patterns defined by percent of habitat cover. The size of each neutral landscape map was 332×333 pixels. We altered forest cover between 5% (open landscape) and 95% (closed landscape) in increments of 5%. To increase the interpretability of the results, we display results for forest pixels solely (i.e., matrix pixels were masked out in the following figures), even though the two approaches were run on matrix pixels as well and provide spatial context information for forest and matrix pixels alike.

Real landscape maps were obtained from the National Land Cover Dataset (Vogelmann et al. 2001) and represented areas of flat to rolling terrain in Wisconsin with forest cover ranging between 10 and 90% in increments of 10%. Each map had a spatial resolution of 30 m and covered a geographic extent of 10 by 10 km (332×333 pixels, same as the neutral landscapes). We converted the multi-class land cover map into a binary forest map by reclassifying the three forest classes (evergreen, deciduous, and mixed) into '1', while setting all other classes to '0'.

For each approach and every map, we calculated the mean polynomial coefficient values and mean S_0 , S_1 , S_2 . We also calculated the correlation between any pair of resulting maps from the same approach. In addition, we tested the effect of maximum window size on the above values by increasing the window size from 7 to 33 pixels per side, in increments of

two. In all cases, the scalogram contained all odd window sizes between the focal window and the maximum window size. To eliminate map boundary effects, we applied these methods only to pixels that were more than $L_{\max}/2$ (half the side of the largest window size) away from the outside edge of the map.

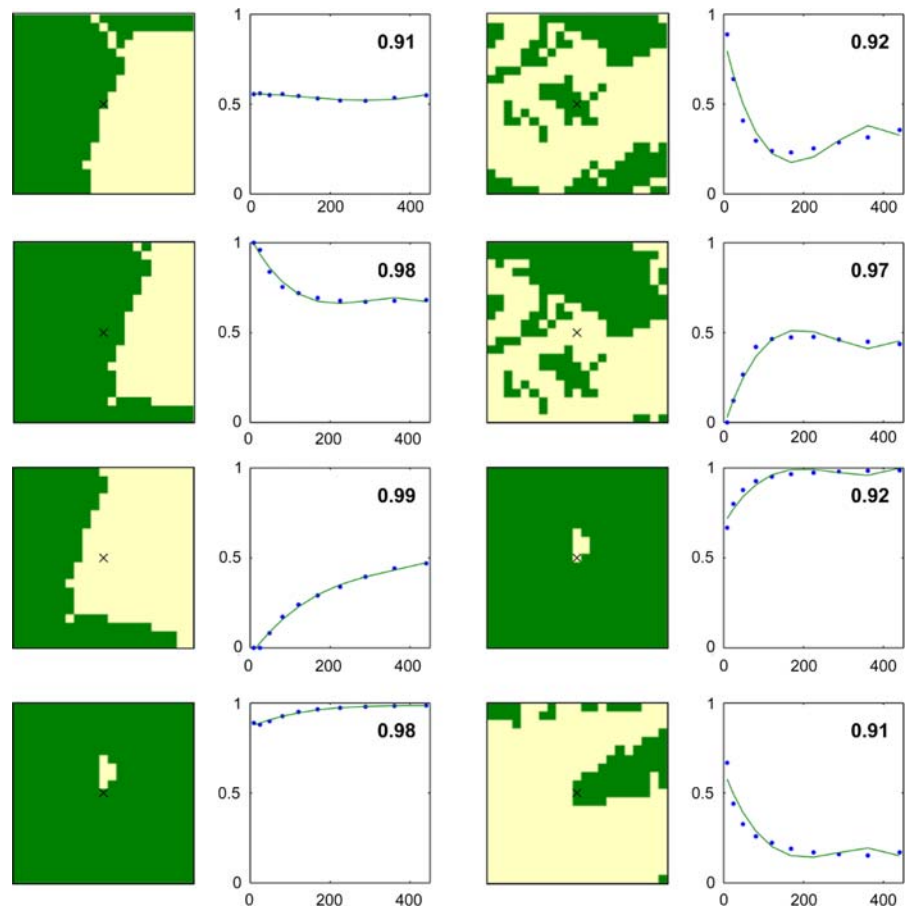
Results

The polynomial approach

Different pixels exhibited a wide variety of scalograms, ranging from simple linear forms to highly nonlinear and complex curves (Fig. 1). Straight lines with zero slopes occurred in three types of areas: [1] forest interior pixels for which the distance to the nearest edge was larger than maximum window size, which intercepted the y-axis at 100% cover; [2] matrix pixels for which the distance to the nearest forest pixel was larger than the maximum window size, which intercepted the y-axis at 0 % cover; and [3] edge pixels (forest or matrix) situated along straight edges between non-perforated core areas and clean matrix areas, which intercepted the y-axis at values between 11 and 88 % cover. All other spatial contexts formed more complex scalograms, either quasi-linear with non-zero slopes (in simple cases) or non-linear (in the majority of complex spatial contexts), but the majority of these scalograms had coefficient of determination values higher than 0.8 (Fig. 1).

The goodness of fit of the fitted polynomial curves was generally high in the actual landscapes, regardless of the amount of forest cover (Fig. 2a). In neutral random landscapes, the goodness of fit was moderate and was more affected by forest cover (Fig. 2b). The goodness of fit was also affected by the spatial context of the pixel (Fig. 3) and was generally lowest in places where changing neighborhood sizes resulted in strong nonlinear patterns with several critical points at which the direction of the spatial trend shifted. In such cases, the fit was still moderate, but the curves depicted a simplified version of the scalogram (i.e., the general trend was retained, but small-scale variations were ignored). The goodness of fit could have been increased by increasing the order of the polynomial to more than four, but this would have yielded a larger number of parameters

Fig. 1 Landscape blocks representing windows of 21×21 pixels and the scalograms of their center pixel. The y -axis represents forest cover, and the x -axis denotes window area (number of pixels). The third-order polynomial fit appears as a continuous line in each plot, and its goodness of fit (r^2) is noted above the plot



that are more difficult to interpret and may have limited ecological relevancy. We therefore decided to limit our analysis to the third-order polynomial form.

For all maps, the second- and third-order coefficients were highly correlated ($r > 0.99$). Both coefficients were also highly correlated with the first-order coefficient ($r > 0.9$) and moderately correlated with the zero-order coefficient ($r > 0.5$). We therefore questioned the need for the third-order coefficient in the model, but attempts to use only lower order polynomials resulted in lower goodness of fit (average r^2), especially for pixels that had complex scalograms (results not shown). In these cases, fitting first- or second-order polynomials severely decreased the goodness of fit (in the opposite case, increasing the polynomial order where the fit is already good does not change the goodness of fit, and the new coefficients are zero or very small). Thus, it was important to retain the

third-order polynomial form, even though its fitting capabilities only benefit the complex areas of the landscape, which are generally less abundant.

Interesting patterns emerged when the polynomial coefficients were depicted as maps (Fig. 4a–c). Zero-order coefficient values were sensitive to edges, and the maps resemble the output of a majority filter, with a window size of $L_{\max}/2$ (Fig. 4a). The first- and second-order coefficient maps (Fig. 4b–c) depicted similar patterns, owing to the high correlation between them. These coefficients reacted to protrusions from large forest areas (i.e., ‘forest peninsulas’), as well as to intrusions of matrix into the forest (i.e., ‘inlets’), and also differentiated between major and minor edges. Major edges are forest pixels adjacent to matrix with little or no additional forest pixels within the matrix at the distance of the maximal window size (i.e., boundaries between forests and large non-forest

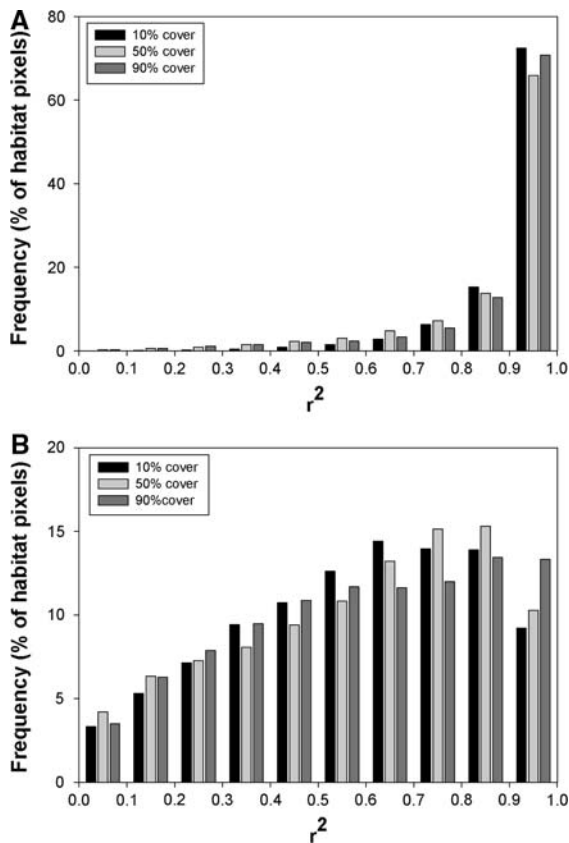


Fig. 2 The distribution of the goodness of fit (r^2) for actual landscapes (a) and neutral random landscapes (b), at three forest cover values

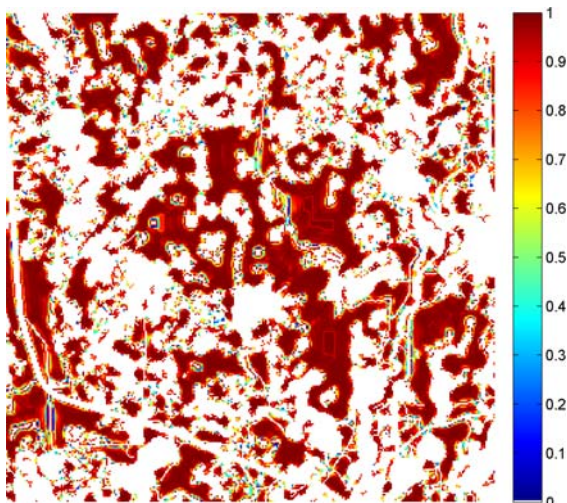


Fig. 3 Goodness of fit values (r^2) for an actual landscape with 50% forest cover

areas). Minor edges are forest pixels that border the matrix, and that have additional forest pixels within or beyond the matrix at distances smaller than the maximal window size. For example, forest pixels along forest roads are minor edges and so are edge pixels in areas of low-aggregation forest stands, forest pixels surrounding perforations (matrix ‘holes’ within forests), and inlets. Interior forest areas exhibited a gradient of coefficient values near edges, and the size of these gradients corresponds to the maximum window size.

The scalograms of these general context types differed, and distinctive polynomial curves were fitted to each scalogram with varying goodness of fit (Fig. 5). However, the general characteristics of the scalogram were retained even in cases with low goodness of fit. For example, scalogram B had an r^2 of 0.09, but the poor fit is largely the result of the local minima of the scalogram at the second smallest window size, which the polynomial function could not capture well. In other cases, the differences emerge from shifts in the local extreme points (maxima or minima, e.g.: scalograms A, C), a difference in their magnitudes between curves (A, E, D), or the addition of local extreme points that do not exist in the scalogram (A, E, D). Yet, the absolute difference in forest cover was never larger than 10%, so even in cases where the goodness of fit was low, the general properties of the scalogram were reasonably well described by the third-order polynomials.

The actual landscapes depicted spatial patterns that represent common forest-agriculture mosaics, in contrast to the neutral landscapes that represent random spatial patterns. However, actual landscape showed similar responses to changes in forest cover and maximum window size (L_{max}) as did the neutral landscapes, which are characterized by lower aggregation levels (Fig. 6). The average zero- and first-order coefficients increased linearly with forest cover, and the average second-order coefficient decreased linearly with forest cover.

The mean polynomial coefficients were non-linearly affected by the maximum window size (Fig. 6). The zero-order coefficient was less affected by maximum window size compared to the higher order coefficients, and the actual landscapes were more sensitive to window size than the random landscapes. The effect of maximum window size decreased with increasing forest cover.

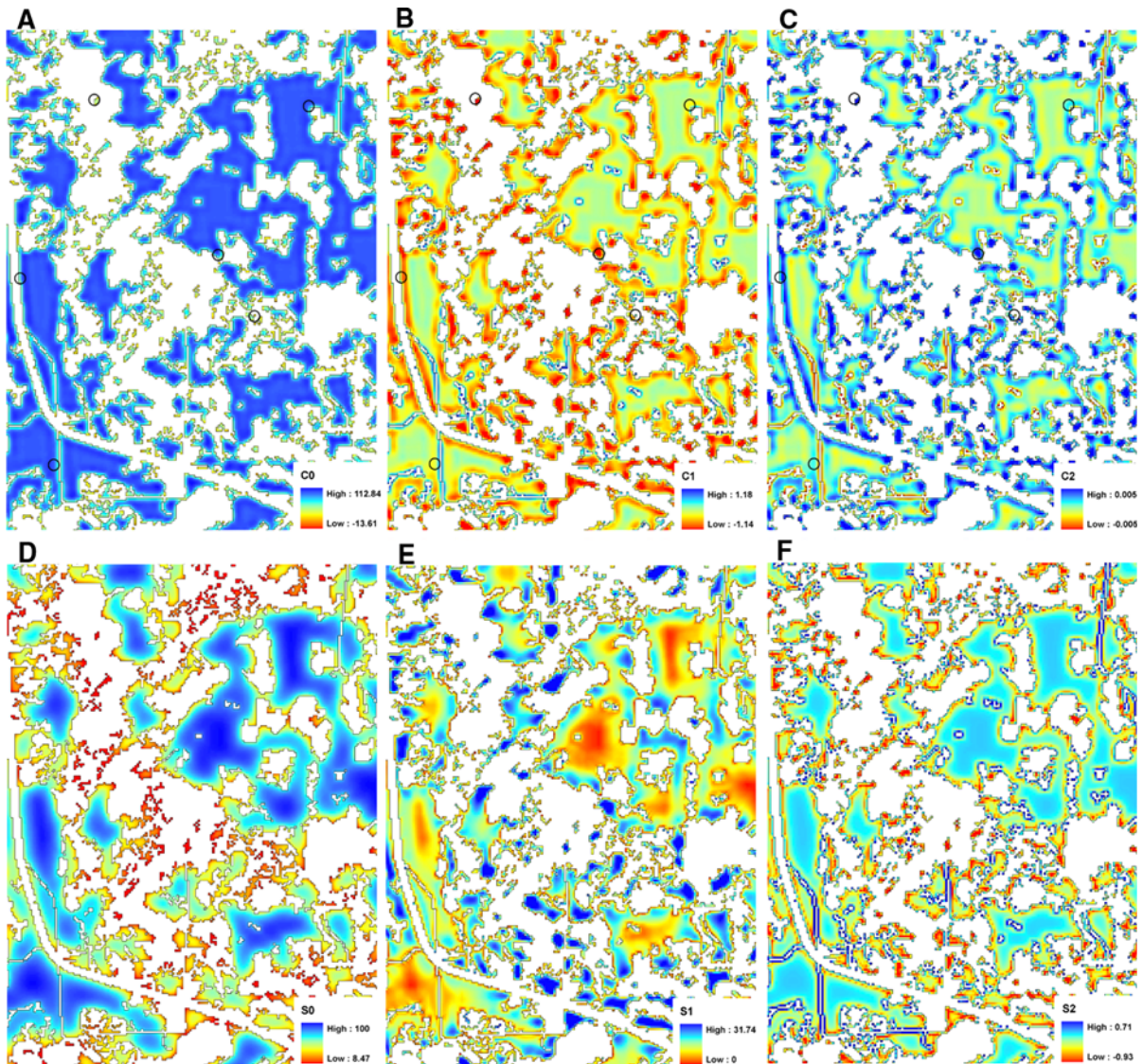


Fig. 4 MCSPap and MCSPAs maps for a landscape in Wisconsin with 50% forest cover: zero-order (a), first-order (b), and second-order (c) polynomial coefficient maps. *Bottom row*: S0 (d), S1 (e), and S2 (f) maps. The third-order

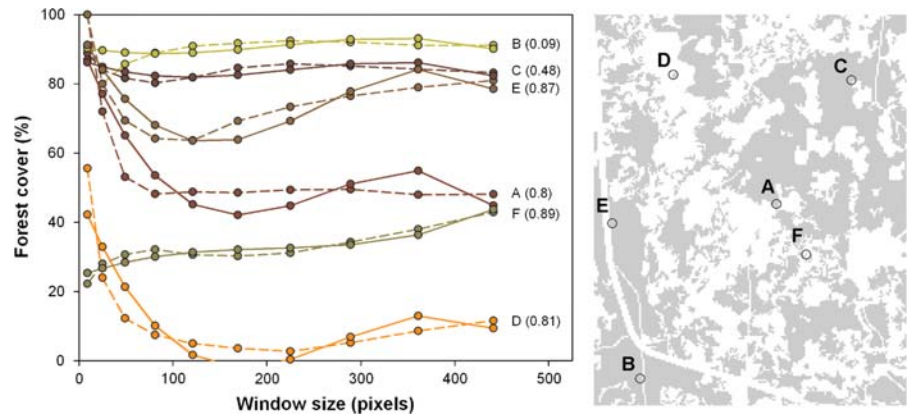
polynomial coefficient map is not depicted since the differences between it and the second-order map are minor. The circles in maps a–c correspond to the scalograms in Fig. 5

The scalogram shape approach

The scalogram shape maps depicted several spatial contexts (Fig. 4d–f). Pixels in the S0 maps highlighted effects of forest cover. Pixels in large, contiguous forest areas had higher S0 values, and S0 values decreased as pixels were closer to forest edges. Pixels along minor edges and small perforations had similar values to core forest pixels, since the scalogram was less affected by the small amount of

matrix in those areas. In contrast, pixel along major edges and large perforations exhibited lower values of S0, due to the impact of the matrix in their surrounding. There were two types of peninsula pixels: major and minor. Major peninsula pixels, which protruded from large forest areas, had intermediate S0 values. Minor peninsula pixels, protruding from major peninsulas, had very low S0 values. However, both types of peninsula pixels shared similar S0 values with intermediate-sized forest areas

Fig. 5 Real (dashed lines) and fitted scalograms (solid lines) of six pixels in a landscape with 50% forest cover. The scalograms are based on the center pixel in each of the six black circles in the right map, which corresponds to the six circles in Fig. 4a–c. The numbers in parentheses represent the goodness of fit between the actual data and the fitted polynomial (r^2)



(similar to major peninsulas) and small-sized forest areas (islands, similar to minor peninsulas).

The S1 maps highlighted in particular the core area contexts. Major peninsulas that emerged from large forest areas were highlighted more clearly than in the S0 maps, but S1 maps did not capture minor peninsulas. In small forest areas, the same S1 values represented core areas. Low S1 values most often represented core pixels of large forest areas, while intermediate S1 values depicted transition zones between core areas and peninsulas or edges. There was no explicit representation of edges in the S1 maps, and edges had relatively similar S1 values as cores.

The S2 maps depicted mainly different types of edges (Fig. 4f). Minor edges and small perforations that were unnoticed by S0 were clearly visible and had high values in the S2 maps. Major edges, on the other hand, had low S2 values. S2 exhibited also a more pronounced differentiation (compared to S0) between core pixels and pixels near (but not along) edges, which received positive and negative S2 values, respectively. The lowest values of S2 were related to pixels that were located in very small forest areas, as well as pixels that were directly adjacent to edge pixels in small forest areas and in peninsulas of large forest areas.

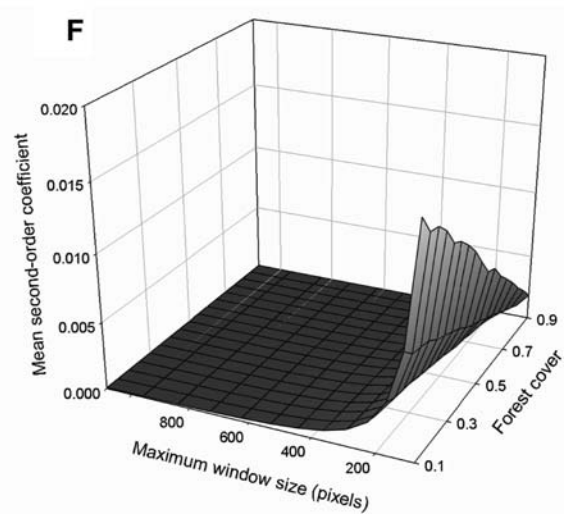
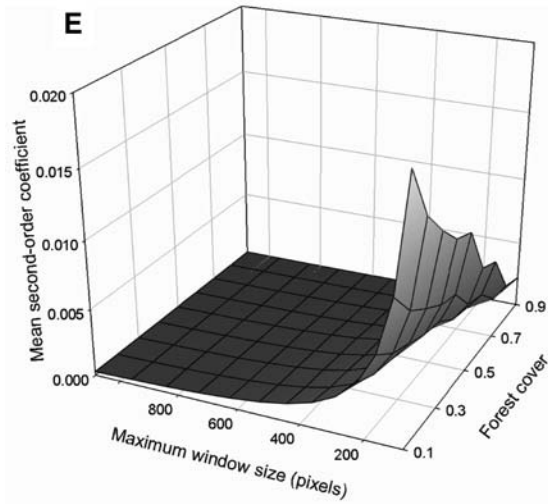
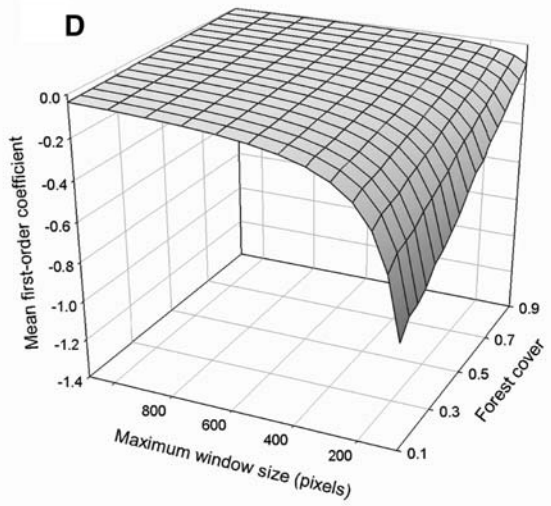
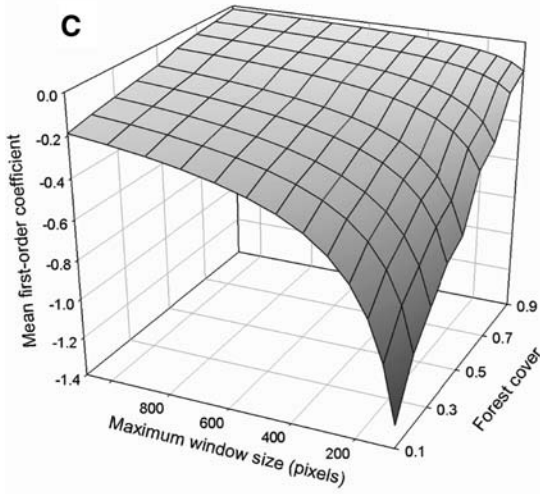
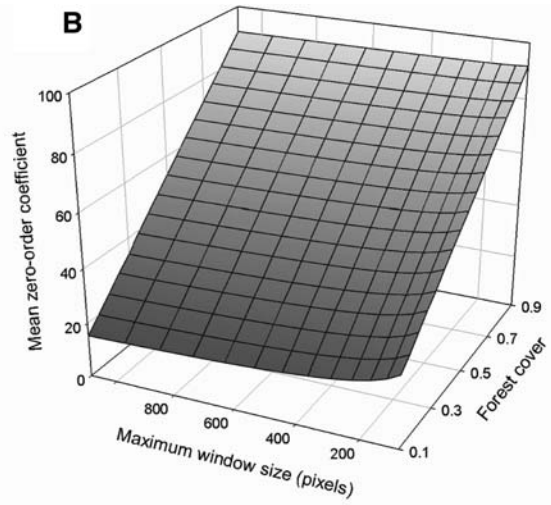
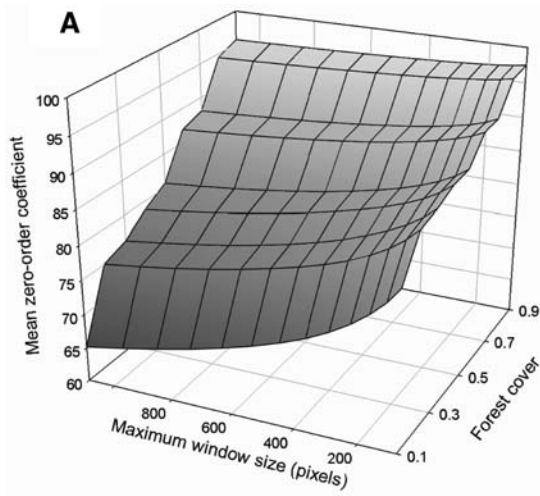
Maximum window size (L_{max}) and forest cover had varying effects on the average coefficient values. Mean S0 was linearly related to forest cover for all maximum window sizes (Fig. 7a–b). Mean S0 decreased non-linearly with maximum window size for the actual landscapes and was relatively unaffected at the random landscapes. The effect of maximum window size decreased with forest cover. Mean S1 was linearly related to forest cover for both actual and random landscapes, though the slope of the

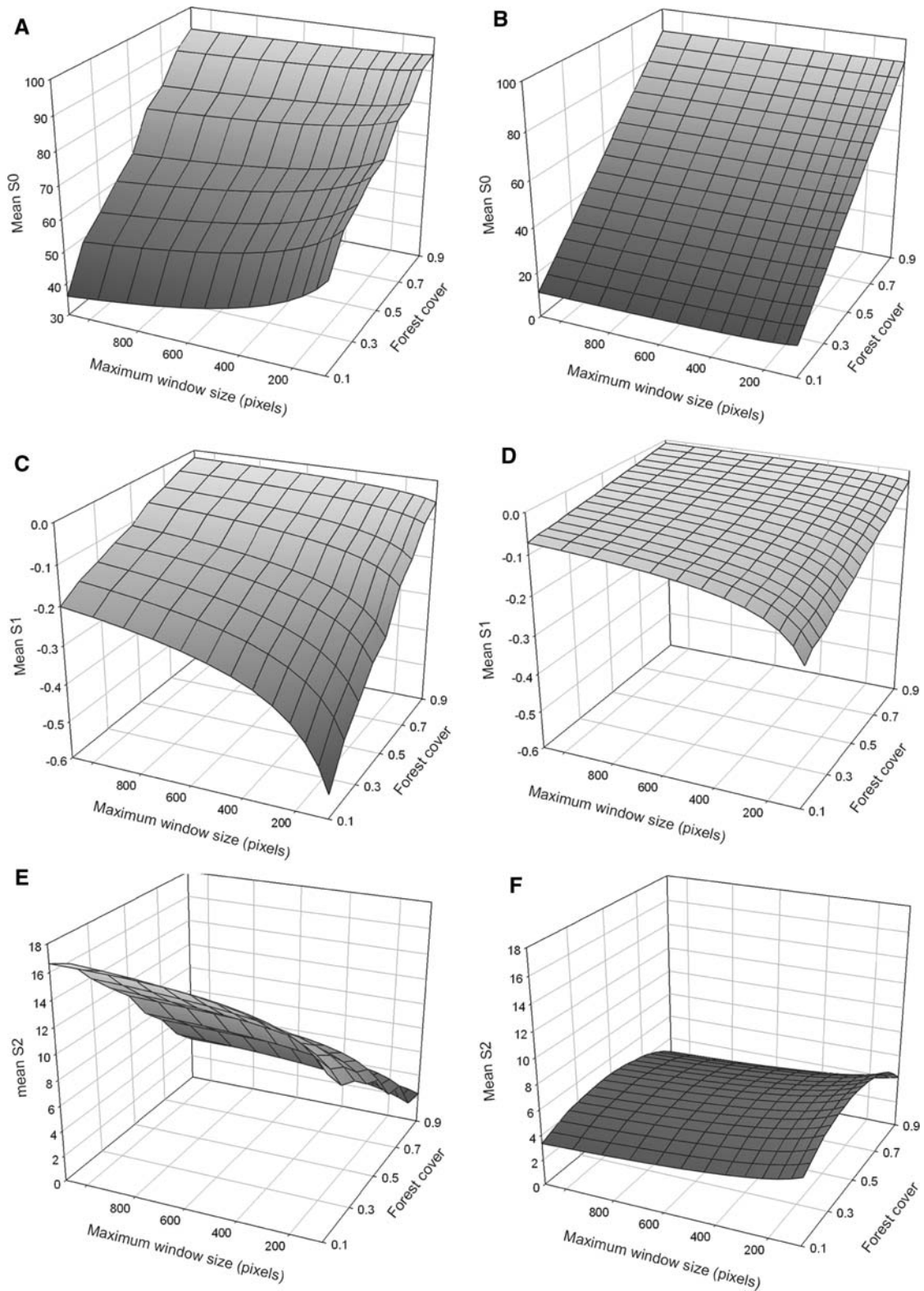
relation was larger for actual landscapes (Fig. 7c–d). Maximum window size had a non-linear effect on mean S1, and this effect decreased at higher forest cover values. The effect of maximum window size was smaller for random landscapes. In the actual landscapes, mean S2 decreased linearly with forest cover for all window sizes (Fig. 7e). The slopes of these relations increased asymptotically with maximum window size. In contrast, in random landscapes, mean S2 was non-linearly related to forest cover, having a parabolic form that peaked at 50% cover (Fig. 7f). These relations decreased asymptotically with increasing maximum window size.

Discussion

Landscape ecologists have greatly improved metrics to quantify landscape structure and to relate these metrics to ecological processes. The predominant theme behind the majority of these approaches is the patch-mosaic paradigm that examines the patch as the fundamental structural unit within the landscape. Finer grained units have been used as well in methods such as morphological spatial pattern analysis (Vogt et al. 2007; Riitters et al. 2007) and multi-scale analyses of disturbance (Zurlini et al. 2007). In both cases, the basic structural unit is the pixel, and its location within the patch-mosaic complex determines its class, either via its relationship to nearby pixel

Fig. 6 Effects of forest cover and maximum window size (L_{max}) on the average MCSPAp coefficients in actual (left column) and random (right column) landscapes. Rows represent: zero-order coefficients (a–b), first-order coefficients (c–d), and second-order coefficients (e–f)





◀ **Fig. 7** Effects of forest cover and maximum window size (L_{\max}) on the average MCSPAs indices in actual (left column) and random (right column) landscapes. Rows represent: S0 (a–b), S1 (c–d), and S2 (e–f)

classes (Vogt et al. 2007) or through the spatial characteristics of the surrounding landscape at varying spatial scales (Zurlini et al. 2007). Here, we built upon the pixel-based approach for landscape structure analysis and introduced two new approaches for describing the spatial context of each pixel in the landscape. MCSPAp fits empirical polynomial curves to scalograms to describe the multi-scale landscape structure around each pixel in the landscape. MCSPAs is a simpler approach, which describes the properties of scalograms based on the first- and second-order statistics and the mean value of the slope between the focal window and any other window size. Scalograms of habitat cover have two inherent characteristics—global non-linearity and autocorrelation—that may facilitate the usage of such mathematical tools to describe them in a relatively simple manner. Both MCSPA approaches describe the spatial context of matrix pixels as well, which may be important when matrix pixels are located in areas with high percentage of forest, and therefore may serve as complementary forest or movement pathways (Gustafson and Gardner 1996; Cook et al. 2002; Perfecto and Vandermeer 2002).

MCSPAp may be mathematically more elegant than MCSPAs, but it has inherent limitations. MCSPAp is appealing because the polynomial framework is able to describe the scalogram in a holistic manner, accounting for the change of habitat at all scales simultaneously. However, MCSPAp has several limitations that emerge from the necessity to fit third-order polynomial curves to often noisy scalograms, with varying goodness of fit. In addition, a fixed third-order polynomial is fitted to all pixels, for three reasons: [1] straightforward interpretation of coefficients; [2] relatively high goodness of fit; and [3] assigning polynomial order to pixels on a case-by-case basis based on maximizing goodness of fit would introduce an element of arbitrariness that would make interpretation of coefficients intractable. The majority of spatial contexts were successfully described by a third-order polynomial, while other contexts were poorly described. However, we found that even curves that had a low goodness of fit including important context information, such as the general

trend of habitat change through scales and the magnitude of change. The low goodness of fit values often resulted from noisy scalograms, rather than a curve that could not capture the general pattern in the scalogram well.

MCSPAs, though being a simpler approach, appeared to capture more spatial contexts than MCSPAp. This result is based on visual interpretation (i.e., which landscape ‘features’ emerge from the S0, S1, and S2 maps), which is constrained by the number of landscapes analyzed and their characteristics. The simplicity of the approach may be one of its great strengths, since there is no error in quantifying metrics (as there is in MCSPAp due to the curve fitting stage), and no need to make a priori decisions about parameters (as is the case of cluster analyses of scalogram values). On the other hand, the main limitation of this approach is that pixels with different spatial contexts may have similar metric values. This problem may be reduced by using all three metrics simultaneously (S0, S1, S2).

There are several issues that need to be considered when applying either MCSPA approach. The first is the choice of ‘habitat’ (forest) among all land cover classes. Though this is the standard in landscape ecology studies, it is based on a simplistic human perception that may be different than the species perception of landscapes (i.e., ‘*Umwelt*’; Manning et al. 2004). While attempting to predict the occurrence of specific organisms, a careful selection of the relevant habitat types should precede the analysis, based on a priori ecological knowledge (Li and Wu 2004). In addition, the response of different species to landscape context is often unknown. Some species may be sensitive to certain types of context (e.g. edge-preferring or edge-avoiding species in a simple case), while other are insensitive to context. And last but not least, species reaction to context may vary during different life cycles such as nesting, feeding, or breeding. Careful selection of the appropriate land cover classes to be included in the habitat category thus is always a required first step of any landscape structure analysis.

A pixel-based approach for landscape description is not inherently superior to the patch-based approach, but it may be more suitable in cases where the ecological process of interest is sensitive to landscape variability or context at a scale smaller than the patch. One strong benefit of using pixels versus patches is

their ability to describe spatial heterogeneity beyond the capability of patches. Pixels may also be used to quantify structural differences between different patches with similar patch-based metric values. In contrast, a criticism of pixel-based approaches is that they do not represent real-world objects (pixels can only be interpreted in terms of their class value and spatial context; Lang 2008), but a sampling of the landscape (depending on pixel size), and as such are less meaningful than studies of image objects or patches (Hay et al. 2003). Therefore, the choice of pixel size (and consequently, the maximum window size) has to be related to the characteristics of the ecological process (or organism) of interest (Marceau 1999), just as the scale of the analysis of a patch-based study should correspond with its application (Blaschke 2006). For small organisms with limited dispersal range, pixel size should be small since using large pixel sizes will represent context that may be ecologically irrelevant. Also important to consider is that larger pixels may contain a mixture of landscape (or habitat) types, and as such introduce bias into the analysis since the map representation of the landscape is not a reliable depiction of the actual landscape (Fisher 1997; Townsend et al. 2000).

A potential application of MCSPA beyond quantifying spatial context per se would be assessment of multi-scale connectivity. Based on percolation theory, binary landscapes become connected once a certain proportion of habitat exists, and this proportion is defined as the percolation threshold (Gardner et al. 1987). Habitat pixels may be connected to other habitat pixels at a given landscape size (L) in which the percolation threshold is exceeded ($Ph(L) >$ percolation threshold), but not connected at larger landscape sizes. Conservation planning would benefit if connectivity was measured at multiple scales simultaneously, and MCSPA combined with percolation theory may offer a suitable methodology to meet this need.

The main assumptions behind both MSPA approaches are that the scalogram is a good descriptor of spatial context in landscapes and that spatial context may be an advantageous predictive variable of ecological processes. Just like any other landscape metric, a single scalogram may be representing different spatial contexts, though when looking at the coefficient maps, it is clear that scalograms are able to successfully represent spatial context. Therefore, the major challenge in multi-scale spatial pattern

analysis is finding robust ways to successfully describe the properties of scalograms. The two approaches developed here, MCSPAp and MCSPAs, offer two alternative ways to do so, and as such can offer further insight into how ecological processes, and particularly species distribution and movements, are affected by spatial patterns.

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