Plant Ecology **156:** 89–103, 2001.

Measuring the abruptness of patchy ecotones

A simulation-based comparison of landscape pattern statistics

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Key words: Boundaries, Ecotones, Landscape statistics, Simulation, Spatial analysis

Abstract

The use of statistics of landscape pattern to infer ecological process at ecotones requires knowledge of the specific sensitivities of statistics to ecotone characteristics. In this study, sets of patch-based and boundary-based statistics were evaluated to assess their suitability as measures of abruptness on simulated ecotone landscapes. We generated 50 realizations each for 25 groups of ecotones that varied systematically in their degree of abruptness and patchiness. Factorial ANOVA was used to evaluate the sensitivity of statistics to the known differences among the simulated groups. Suitability of each index for measuring abruptness was evaluated using the ANOVA results. The statistics were then ranked in order of their suitability as abruptness statistics based on their sensitivity to abruptness, the consistency of the relationship, and their lack of sensitivity to patchiness. The two best statistics for quantifying abruptness were those we developed based on lattice delineation methods, and are called cumulative boundary elements and boundary element dispersion. The results of this research provide support for studies of ecotone process that rely on the interpretation of patch or boundary statistics.

Introduction

Ecotones are zones of transition between adjacent ecosystems. Their characteristics are uniquely defined by the interactions between the ecosystems (Holland 1988). Ecotones under the above definition have also been referred to as edges (Orloci & Orloci 1990), transitional areas (Kent et al. 1997) and boundaries (Wiens et al. 1985). Although these alternative terms often imply abruptness, an ecotone may be abrupt or gradual and may be highly heterogeneous or less heterogeneous depending on the ecological processes acting on it.

This research focuses on the measurement of ecotone abruptness, which is thought to be representative of specific ecological processes operating at the alpine treeline ecotone. *Abruptness* refers to the rate at which one ecosystem spatially transitions to another across the ecotone; for example, abrupt alpine treeline ecotones change rapidly from trees to alpine tundra while gradual treelines are characterized by gradual interspersion of types and a decrease of tree cover until trees are completely absent. Abrupt ecotones may result from abrupt environmental gradients. However, abrupt ecotones may also occur along gradual environmental gradients, suggesting the action of ecological processes such as species competition (Armand 1992; Malanson & Butler 1994) and positive feedback mechanisms (Wilson & Agnew 1992; Malanson 1997). One approach to testing hypotheses about these processes is to quantitatively compare the level of abruptness that results from spatial process models that include varied process assumptions and to compare model results with observations of real ecotones (e.g., through remote sensing). Quantitative comparisons, however, require statistics of pattern that measure the property of interest (e.g., abruptness). The goal here is to investigate multiple statistics and determine which are most suitable for quantifying ecotone abruptness for use in model and observation comparison.

Patchiness across an ecotone can confound attempts to detect differences in ecotone abruptness. For this reason, the best statistics for measuring abruptness will be those that are sensitive to abruptness, but relatively insensitive to patchiness. Ecotone *patchiness* is defined as spatial heterogeneity or the degree of spatial randomness in the pattern; an ecotone is patchy when neighboring sites (e.g., grid cells) tend to be dissimilar.

Landscape statistics can be computed from spatial representations of a landscape through a variety of approaches. We focus on two approaches that involve identifying (a) homogeneous patches on the landscape or (b) locations of rapid change on the landscape (boundaries). This research evaluates patch and boundary statistics with the goal of selecting those most suitable for quantifying abruptness. The goal is to evaluate the statistics in an experiment where patchiness and abruptness characteristics are controlled through simulation of ecotones, modeled according to alpine treeline ecotones observed in a satellite image. This approach allows for an objective comparison among statistics and provides evidence of the information content and behavior of the statistics with respect to abruptness when applied to ecotones with varying degrees of patchiness. The experiment also allows for an examination of the interacting effects of abruptness and patchiness on each set of statistics.

Following a general description and definition of terms associated with patch and boundary statistics, we describe our approach to simulating ecotones at multiple levels of abruptness and patchiness and analyzing 11 different statistics for their suitability as abruptness measures. The results of an analysis of variance are presented for evaluating the suitability of the statistics as abruptness measures based on their sensitivity to abruptness, the consistency of the relationship, and their lack of sensitivity to patchiness. Finally, a discussion of the importance of understanding the interacting effects of patchiness and abruptness and choosing the appropriate statistic is followed by our concluding remarks.

Patch statistics

The patch approach to describing landscapes typically involves classifying satellite imagery or aerial photography to produce a map in which similar types of ecological communities or vegetation types are grouped together. These groups, referred to as classes, are represented within a raster map and used to identify contiguous clusters of cells, called patches. After classification, patches are considered internally homogeneous and the boundary between patches of different classes is a distinct one. The programs SPAN (Turner 1990), r.le (Baker & Cai 1992) and FRAGSTATS (McGarigal & Marks 1993), which are compatible with geographic information systems (GIS), generate a variety of patch statistics that mathematically define the spatial pattern of a landscape. Among the characteristics that patch statistics represent are patch density, patch size, patch shape and patch variability, landscape edge, landscape core area, landscape diversity, contagion and interspersion (McGarigal & Marks 1993).

Baker & Weisberg (1995), in Rocky Mountain National Park, CO, and Allen & Walsh (1996), in Glacier National Park, MT, used the patch approach to quantify landscape pattern at the alpine treeline ecotone. Both were able to discern 6 unique types of alpine treeline ecotone using a cluster analysis of patch statistics. Each study found ecotone types that were best described according to their patchiness and abruptness characteristics. Baker & Weisberg (1995) found ecotones that were 'long' and 'short' with variable amounts of patchiness, while Allen & Walsh (1996) differentiated ecotone patchiness and abruptness by labeling types as 'heterogeneous' or 'highly heterogeneous' and 'moderately zonal' or 'zonal', respectively.

A central element of the patch approach is the classification and patch delineation necessary to compute patch statistics. The patch approach uses a line of zero thickness to represent the transitions between adjacent patches. Because many ecotone-related questions address the contrast and spatial rate-of-change between adjacent ecosystems the classification procedure represents a loss of relevant information (Johnston & Bonde 1989; Wood & Foody 1989; Brown 1998). At best, only the length of the ecotone and the classes that it separates can be directly quantified. There is no way to represent a gradual transition between neighboring patches using this approach.

Boundary statistics

Boundary statistics can avoid the classification step by measuring information about boundaries that are based on the spatial rate-of-change, i.e., slope, of a continuous variable surface. Many ecological surfaces possess the mathematical property of continuity and have only one value at any point. Surfaces of ecologically relevant variables are frequently approximated using satellite imagery; examples include percent vegetative cover, the Normalized Difference Vegetation Index (NDVI) and Leaf Area Index (LAI) (e.g., Brown, in press). The ecological surface is approximated as a regularized grid where each cell of the grid contains a unique data value.

Legendre & Fortin (1989) provide a review of methods for analyzing surfaces that employ spatial autocorrelation coefficients, correlograms, variograms, spectral analysis, and the Mantel test to measure spatial pattern. Kent et al. (1997) review similar methods with respect to ecotone analysis. Among the several surface-based methods available, one group, the boundary statistics, focuses on transitional areas and relies on the methods of boundary detection. The goal of boundary detection is to locate discontinuities along transects (Ludwig & Cornelius 1987) or within two-dimensional maps (Johnston et al. 1992) using algorithms that accentuate areas with high rates of change on a given variable or set of variables mapped over the landscape. Womble (1951) proposed a method of boundary detection within two-dimensional maps that has been modified by Barbujani et al. (1989), Fortin (1994), and Jacquez & Maruca (1998). The method is commonly called either Wombling or lattice delineation and identifies boundaries as spatially contiguous locations with high rates of change. The location, width, shape, or distribution of these boundaries can be used to characterize the transition.

While boundary statistics have been found to be effective in determining the significance of detected boundaries (Fortin 1994; Fortin & Drapeau 1995), less is known about how the boundary statistics can be used to quantify specific boundary characteristics or landscape patterns. For instance, a small number of long boundaries may indicate that an ecotone is abrupt, while a large number of shorter boundaries may indicate that an ecotone is more gradual.

A limitation of the lattice delineation approach is the arbitrary nature of the gradient threshold used to define boundaries. A method that uses the lattice delineation approach to obtain boundary statistics at multiple gradient threshold levels may avoid the limitations of an analysis at only one threshold level. We developed the cumulative boundary elements (CBE) statistic to take advantage of this approach and to measure ecotone abruptness. CBE is tested for its suitability as an abruptness statistic along with other patch and boundary statistics.

Methods

The research was conducted in three phases. First, ecotone surfaces with known patchiness and abruptness characteristics were simulated, classified, and organized into a matrix structure that facilitated a factorial analysis of variance (ANOVA) experimental design. Second, patch and boundary statistics were calculated on the simulated data. Finally ANOVA was conducted and interpreted for comparison between groups of simulated ecotones and among statistics.

Simulation

A goal of the simulation was to create ecotone data similar to what would be obtained from a LANDSAT Thematic Mapper (TM) satellite image. Inspection of alpine treeline ecotones captured in a TM scene of Glacier National Park (GNP), MT provided a visual model for the simulations. A majority of the treelines examined in the TM image had transition lengths less than approximately 600 m. Transition length was defined as the distance between closed canopy forest and open alpine tundra as measured along the profile of vegetation change. The extent of the areas used in the simulations was set at 630 m $\times$ 630 m to accommodate the maximum transition lengths observed in the image. The simulated data set used a cell size of 30 m, which corresponds to the cell size of TM. The size of each simulated ecotone was approximately 40 ha, which was comparable to some of the smaller two-dimensional transects used by Baker & Weisberg (1995). The GNP TM scene was consistently referred to throughout the development of the simulation to assure, at the very least, that the simulated ecotones visually resembled real ecotones (Figure 1).

Simulated data were used to control the patchiness and abruptness characteristics of each ecotone by systematically altering the parameters of the simulation. The simulation produced values of a hypothetical continuous variable for each cell in a square grid that mimicked a real world study area containing an ecotone. High variable values were intended to represent more tree cover while low variable values represented lower tree cover and more tundra, bare soil or rock.

We used simulation to produce 2 sets of maps, a continuous set (Figure 2) and a classified set (Figure 3), each representing 25 different types of ecotones. The 25 types resulted from unique combinations of 5 levels of patchiness and 5 levels of abruptness. The simulation was repeated 50 times for each type in

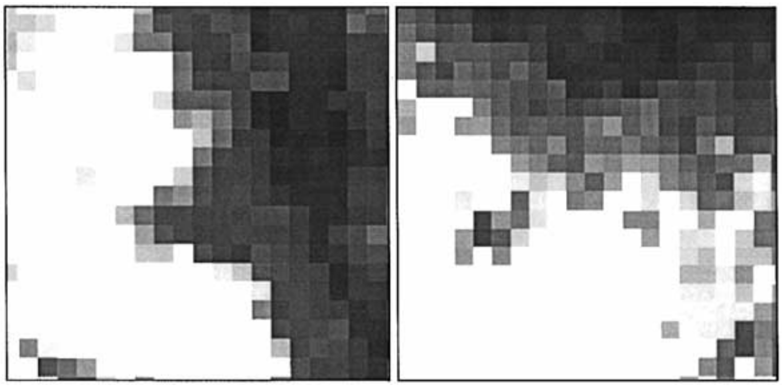

Figure 1. Two sample alpine treeline ecotone sites from a Landsat image of Glacier National Park, Montana, USA. The images represent estimates of the average leaf area index (LAI) of trees within each 30 m pixel, following Brown (in press).

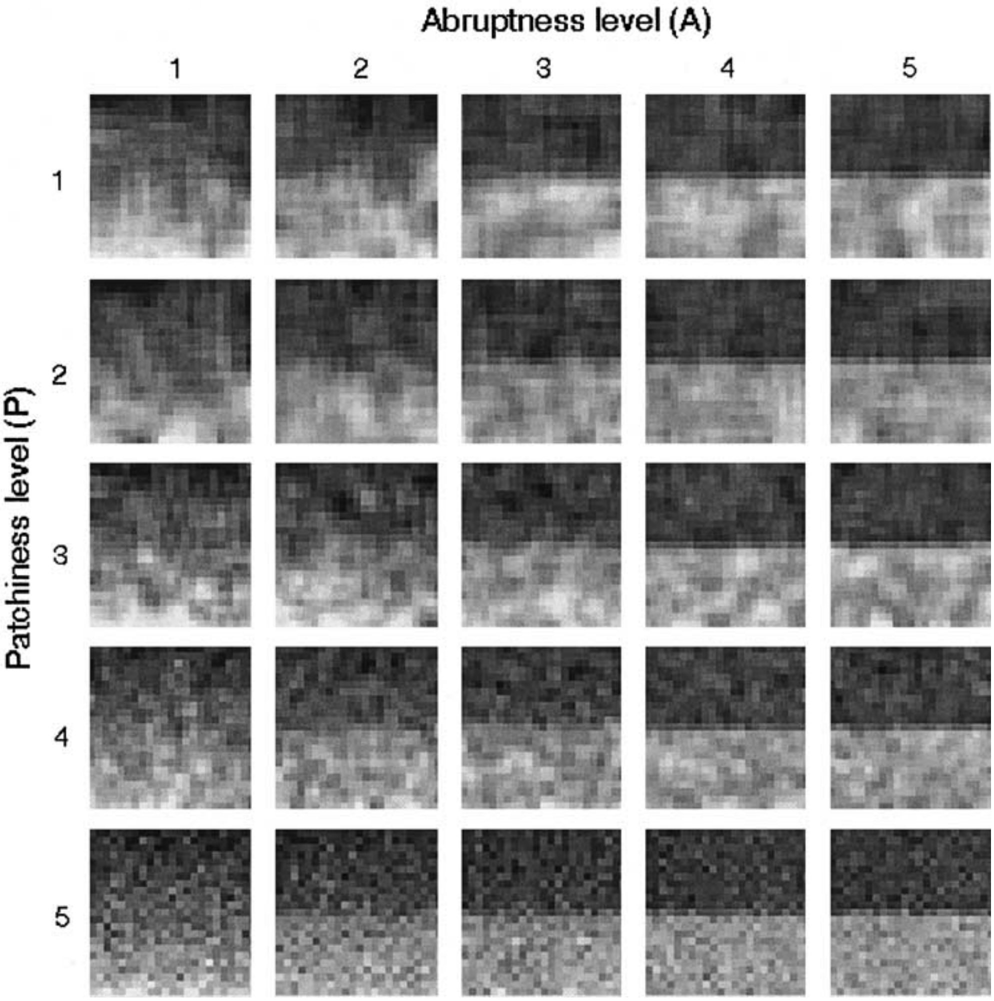

Figure 2. An example of the simulated ecotone surfaces from each of the 25 groups. Each surface is the result of adding a perturbation surface of a given patchiness level to a deterministic surface of a given abruptness level. The brightness of the surface shading represents the strength of tree presence.

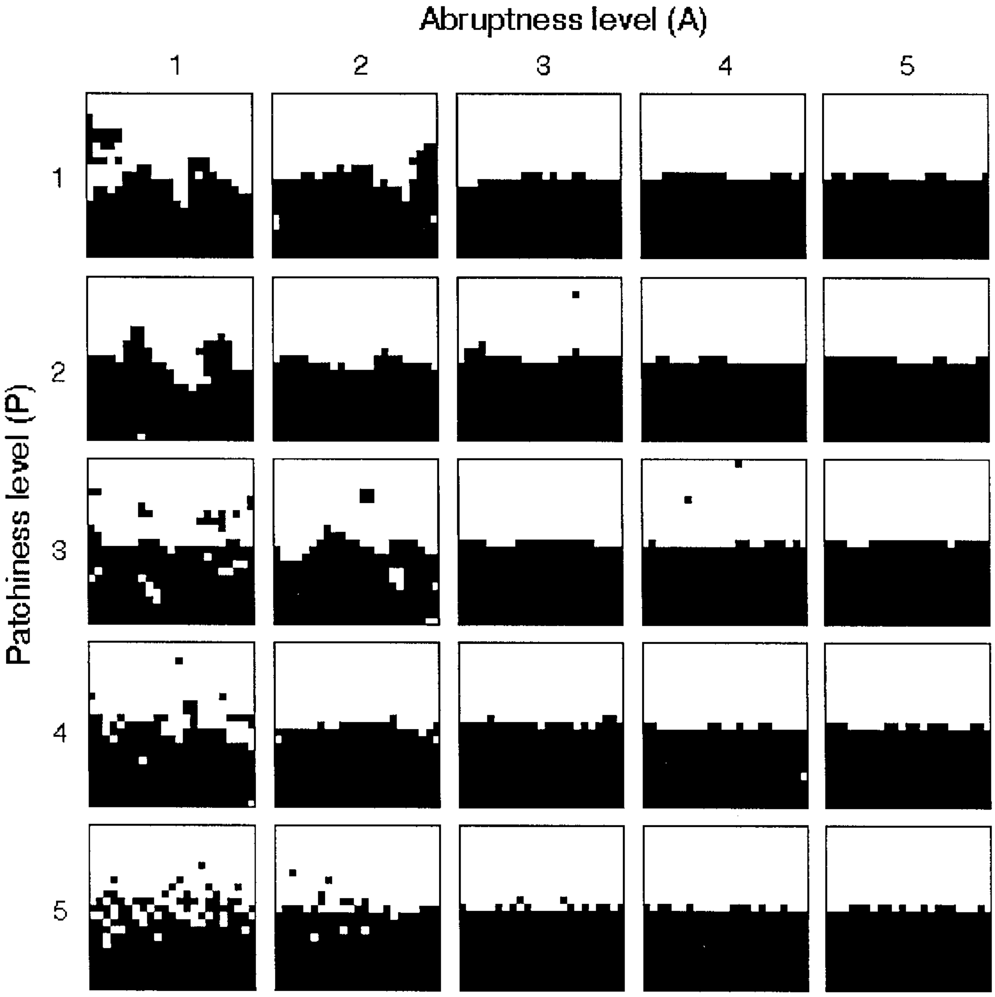

Figure 3. An example of the simulated ecotone surfaces that have been classified into tree presence/absence from each of the 25 groups. Black represents tree presence, white represents tree absence (i.e., tundra species, rock, and bare soil).

order to obtain replicates for statistical analysis. Accordingly, 1250 simulated maps of each type (continuous and classified) were produced. For the remainder of this text, the 50 ecotones that were simulated to be of the same patchiness and abruptness level are said to belong to the same 'group'.

Abruptness was controlled using a deterministic function, which is in the form of a sigmoid curve:

$$z = \mathrm{sign}(y) \cdot |y|^n \cdot 0.5, \qquad (1)$$

where z is the surface variable, sign is an operator that returns the sign (i.e., $+$ or $-$) of y, y is the position along the transition, and n is the slope (or abruptness) parameter. This function was chosen for its ability to model a smooth transition from low values of a variable to high. In a similar fashion, Churkina & Svirezhev (1995) and Timoney et al. (1993) used sigmoid functions to mathematically model ecotones; however, their work was done at the biome scale and not a local scale, as is the case here. The function used here is capable of modeling transitions of variable abruptness without a change in the minimum and maximum z values.

Four values for the slope parameter (n) were used to generate two-dimensional maps of varying degrees of abruptness: 1, 0.5, 0.25 and 0.0625. This was accomplished by mapping the value of the function on y over the interval $[-1, 1]$ at 0.1 unit increments to consecutive cells in each row of the two-dimensional map. Each of the four resulting deterministic surfaces had a value range $[-0.5, 0.5]$. Lower magnitude slope terms produced surfaces on which the transition from high to low variable values was more abrupt. Using a slope term of 1 produced a planar transition. A fifth deterministic surface was created manually, so that the transition between -0.5 and 0.5 occurred over one incremental unit. All of the surfaces lacked planform curvature (i.e., change in slope in the direction parallel to elevation contours) while profile curvature (i.e., change in slope perpendicular to elevation contours) was dictated by the parameters of the deterministic function used.

Patchiness was introduced to the simulation by creating perturbation surfaces that were later added to each of the five deterministic surfaces through map algebra. The level of spatial autocorrelation of the perturbation surfaces was adjusted to represent variations in landscape patchiness. First, surfaces containing normally distributed spatially random cell values were generated to represent the most patchy condition. Next, positive spatial autocorrelation was added to the random surfaces by using a variable-size square averaging filter kernel. Larger kernels had a larger smoothing effect, and the resulting surface had a greater degree of spatial autocorrelation and less patchiness. Five different levels of patchiness were simulated using the unsmoothed random surfaces, plus surfaces smoothed with four kernel sizes: 2×2, 3×3, 4×4 and 5×5 cells. The random surfaces were adjusted prior to smoothing, through multiplication by a scalar value, so that their means and standard deviations after smoothing were approximately equal across all perturbation surfaces. The adjusted surface values were all in the range $[-0.5, 0.5]$ after smoothing. Since both the perturbation and deterministic surfaces were in the range $[-0.5, 0.5]$ the simulated ecotone surfaces, after adding the surfaces together, had values in the range $[-1, 1]$.

We used Moran's I, a coefficient of spatial autocorrelation, as an indication of spatial pattern that resulted from the simulations and to verify that the groups displayed differences in spatial pattern before testing the landscape statistics on them. Moran's I is positive when positive spatial autocorrelation (i.e., clustering) is present in a pattern and negative when negative spatial autocorrelation (i.e., regularity) is present. It varies from -1 to $+1$. A value close to zero suggests that the pattern is spatially random.

All of the simulated ecotone surfaces were then transformed into binary representations of tree presence and absence to create classified maps of the ecotone. The classification was accomplished by mapping all surface variable values above the median surface value into a class of tree presence and all values below the median into a class of tree absence. This method assured that for each map approximately 50% of the ecotone was classified as trees and 50% as not trees.

Patch statistics

FRAGSTATS (McGarigal & Marks 1993) was used to calculate the patch statistics used in the analysis. Each of the classified ecotone maps was submitted to FRAGSTATS and the landscape-level statistics listed in Table 1 were calculated. The small size of sample sites limited the value patch statistics for characterizing pattern because:

- large patches at the site borders result in patch edges that are artifacts and not real landscape edges,
- at 50% trees in each simulated site, the number of distinct patches is too small, and
- the small number of grid cells (21 by 21) introduces cell-based artifacts (e.g., stair-step edges) into the patch-delineation process.

Nonetheless, we present the analysis of patch-based statistics, bearing these limitations in mind, because they are commonly used in landscape studies and their value in studies of treeline ecotone pattern has been demonstrated (Baker & Weisberg 1995; Allen & Walsh 1996).

The area weighted shape statistics (AWMPFD and AWMSI), contagion (CONTAG) and total edge (TE) were expected to be useful for measuring abruptness, but not without some sensitivity to patchiness. Values of AWMPFD and AWMSI should decrease with abruptness. Patches in gradual ecotones were expected to form shapes that were more complex because they are not confined by a steep gradient and tend to spread out on the landscape. As abruptness increases the complexity of patch shape should decrease as patches are confined to smaller areas of transition. However, as ecotone patchiness increases, the potential for patches to form convoluted shapes increases also. Therefore, values of AWMPFD and AWMSI were expected to increase with increasing patchiness. Higher values of CONTAG were expected as abruptness increased, while lower values were expected as patchiness increased. Since CONTAG measures the degree to which patches of different classes are intermixed, or patch interspersion, it should also be affected by patchiness. Patch interspersion increases, and CONTAG decreases, as patchiness increases es-

Table 1. Patch and boundary statistics evaluated for suitability as abruptness measures. All statistics were hypothesized to be sensitive to ecotone abruptness.

Patch statistics	Abbr.	Description
Area-weighted mean patch fractal dimension	AWMPFD	Average fractal dimension over all patches weighted by area. Fractal dimension is a measure of the degree of complexity of planar shapes. A shape with a high fractal dimension is more plane filling than a shape with a low fractal dimension.
Area-weighted mean shape index	AWMSI	Average perimeter to area ratio for all patches weighted by area.
Contagion	CONTAG	Measures both patch interspersion (the intermixing of different patch types) and patch dispersion (the spatial distribution of a patch type). Low values of CONTAG are equated with a high degree of patch interspersion and/or dispersion.
Total edge	TE	Absolute measure of total edge between all patches.

Boundary Statistics		
Number of Boundary Elements	BE	Count of boundary elements (ROC locations) selected during lattice delineation
Number of subgraphs	N	Count of subgraphs, two or more connected boundary elements
Minimum length	LMIN	Minimum number of boundary elements in any one subgraph
Maximum length	LMAX	Maximum number of boundary elements in any one subgraph
Mean length	LMEAN	Average number of boundary elements per subgraph
Subgraph dispersion	DISP	The average distance of each BE from the centroid of all BE combined. The distance used is the y distance from the centroid of all BE to the centroid of each BE.
Cumulative boundary elements	CBE	Area under curve of BE versus slope threshold level.

pecially when only two classes are present. Total Edge (TE) measures the length of the boundaries between all patches of different classes. TE was expected to decrease with increasing abruptness. An abrupt transition should form patches without complex shapes and therefore generally less edge. As patchiness increases, the number of patches increases and patch size will decrease leading to an increase in the amount of edge between patches.

Boundary statistics

Lattice delineation was performed using the capabilities of ARC/INFO geographic information system (GIS) and two supplemental programs written in C. The work of Fortin (1994) and the alpha version of the program BoundarySeer (Jacquez & Maruca 1998), were used as a template for the ARC/INFO and C routines in this study.

First, two surfaces related to the spatial change in the variable surface were computed for each simulated surface: gradient and aspect. The gradient surface represents the magnitude of spatial change while an aspect surface represents the compass direction of change. All locations with gradient values greater than a given threshold were identified. These locations, termed *boundary elements*, became candidates to form *subgraphs*. Subgraphs are created to represent the boundaries on the landscape. Subgraphs were formed by joining neighboring boundary elements (i.e., cells with gradient values above the threshold) that were within a minimum angular divergence of aspect (Jacquez et al. 2000).

Threshold value selection is subjective. Conventional rules-of-thumb commonly suggest the selection of the top 5 or 10% of locations with the highest gradient values as boundary elements (Barbujani et al. 1989; Fortin 1994; Fortin & Drapeau 1995) and the use of 30 deg as the aspect threshold for boundary element connection (Barbujani et al. 1989; Jacquez et al. 1998). Here, instead of selecting locations of high rate-of-change until an area threshold is met, the range of values in each gradient surface was divided into 20 equal intervals and the threshold is based on the lower limit of one of the intervals. This method of threshold selection produces what we call *slices* of the gradient surface, where each slice represents all locations whose value is equal to or greater than the lower limit of a particular interval. Lattice delineation and subgraph formation was performed for each of the 20 slices. We selected slice level 9, about mid-range, for calculating most of our statistics because the average number of boundary elements at or above that level was close to 10%.

The numbers of boundary elements (BE) and subgraphs (N) and descriptive statistics on subgraph length (LMEAN, LMIN, and LMAX) were calculated for each ecotone (Table 1). These statistics were all thought to have some sensitivity to the level of ecotone abruptness. As an ecotone becomes more abrupt, the area of transition decreases, which means the number of locations of high gradient value should also decrease. For this reason, BE and N at or above any given level of steepness were expected to decrease as abruptness increased. Abrupt ecotones should have distinct transition areas that result in boundary elements with similar aspects. Therefore, boundary elements of abrupt ecotones should have a higher connectivity, which also translates into fewer subgraphs (N) per ecotone.

LMAX, LMEAN and LMIN were expected to be useful for measuring abruptness, but also affected by patchiness. They were all expected to increase as abruptness increased because abrupt transitions should have similar aspect values and thus be more connected. As patchiness increases, LMAX, LMEAN and LMIN were expected to decrease because of the negative effect patchiness has on the connection of boundary elements into long subgraphs.

We developed two new statistics based on the lattice delineation method for the express purpose of measuring ecotone abruptness from images. The first of these, called dispersion (DISP), was developed to measure the degree of boundary element clumping in the direction of the ecotone transition. DISP measures the average distance of each BE from the centroid of all BE combined. The more clumped boundaries produced by abrupt ecotones were expected to form boundary element patterns that resulted in low DISP values.

The second new statistic, the cumulative boundary elements (CBE), uses data from each of the 20 slice levels, avoiding the need to choose one specific gradient threshold. CBE approximates the integral of the response curve produced by plotting the number of BE versus gradient slice level. Ecotones with different abruptness characteristics should produce noticeably different response curves and the integral of these curves would provide a numerical means to differentiate them (Figure 4).

Analysis of variance

The calculated statistic values were organized to facilitate a two-way factorial ANOVA experiment (Bhattacharyya & Johnson 1977). The ANOVA was used to determine whether the statistics were sensitive to differences resulting from simulated combinations of unique patchiness and abruptness levels. The unique combinations of abruptness and patchiness are called treatments and the quantitative differences in abruptness and patchiness themselves are known as treatment effects.

The main effects of the factorial design were examined first to determine whether the statistics were sensitive to abruptness, patchiness, or both. The main effects tested the null hypothesis that the mean statistic values observed across factor levels are equal when the effects of the second factor are disregarded. Rejection of the null hypothesis indicates that the statistic was capable of detecting differences in either abruptness or patchiness.

Interaction occurs when the affect of one factor on the dependent variable changes at different levels of the other independent variable (Keppel 1991). The null hypothesis is that interaction is not present. Rejection of the null indicated significant interaction. The presence of interaction did not allow for a simple interpretation of the main effects. Significant interaction meant that the statistic being tested did not perform consistently across all levels of one or both of the independent variables. For example, a statistic may have been more sensitive to abruptness at lower levels of patchiness than at higher levels of patchiness.

Four component sources of variance contributed to the factorial experiment: the variance due to abruptness treatments (σ_a^2), patchiness treatments (σ_p^2), the interaction of patchiness and abruptness ($\sigma_{p\times a}^2$), and experimental error ($\sigma_{\mathrm{error}}^2$). An index, called Omega Squared, was used to compare the relative strength of the relationships between statistic values and abruptness levels (Keppel 1991):

$$\omega_a^2 = \sigma_a^2/(\sigma_a^2 + \sigma_p^2 + \sigma_{p\times a}^2 + \sigma_{\mathrm{error}}^2). \quad (2)$$

To evaluate the influence of patchiness on the statistics, we used this same equation, with σ_p^2 in the numerator. Omega squared ranges from 0 to 1, with

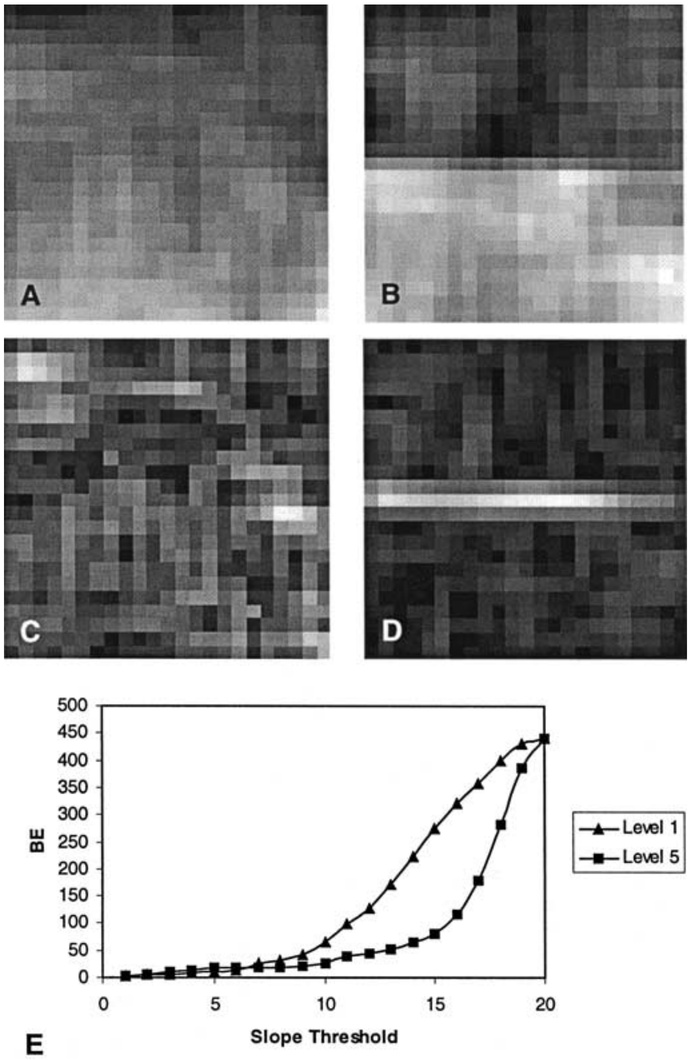

Figure 4. Illustration of the cumulative boundary elements statistic. (A) A surface variable with an ecotone exhibiting low abruptness (level 1); (B) A surface variable with an ecotone exhibiting high abruptness (level 5); (C) and (D) The slope surfaces corresponding to the surfaces in A and B. (E) The cumulative boundary element curves for each ecotone.

higher values representing stronger statistic sensitivity. Sensitivity to the differences produced by the simulation is directly related to the Omega squared values they produce.

By decomposing the factorial ANOVA into 5 single-factor ANOVA experiments, we analyzed the abruptness simple effects of each statistic. Each single-factor ANOVA was equivalent to holding the level of patchiness constant while studying the effects of abruptness. In each of the single factor ANOVAs there were only two variance components, variance due to abruptness (σ_a^2) and variance due to experimental error (σ_{error}^2). Therefore, the Omega squared for the single factor ANOVAs is:

$$\omega_a^2 = \sigma_a^2/(\sigma_a^2 + \sigma_{\text{error}}^2).$$

For each of the single factor ANOVAs, pairwise multiple comparisons between factor levels were conducted using the Bonferroni method (Keppel 1991). Bonferroni comparisons tested for significant mean difference between each pair of abruptness levels. The sign of the mean differences was used to determine whether the statistic responded to abruptness as expected (i.e., it was externally consistent) and whether its response was consistent across patchiness levels (i.e., it was internally consistent). As an example of external consistency, the number of boundary elements (BE) was expected to decrease with increasing abruptness level. This means that subtracting BE at abruptness level 5 from BE at abruptness level 4, $A_4 - A_5$, should yield a positive value. External consistency was measured as the proportion of significant comparisons that produced the hypothesized sign. The hypothesized response of a metric with a high external consistency changed little with factor level. A low external consistency indicated that the interaction was such that the response (sign) of the metric changed as factor level varied. Internal consistency summarized the degree to which significant comparisons were observed in a logical sequence. A metric is internally consistent if, when sensitive to a small difference in abruptness, it is also sensitive to larger differences in abruptness. Internal consistency was calculated as the ratio between the number of significant comparisons and the number of significant comparisons that would have been detected if the statistic was responding in a 100 percent consistent manner.

Statistic suitability ranking

Five properties were used to rank the patch and boundary statistics according to their ability to quantify abruptness. The properties were:
– main effect sensitivity to abruptness (S_{MEa});
– simple effect sensitivity to abruptness (S_{SE});
– external consistency (C_E);
– internal consistency (C_I); and
– main effect sensitivity to patchiness (S_{MEp}).

All statistic values were standardized using the maximum observed values across all statistics. The standardized scores for each property ranged from 0 to 1, with 1 representing the highest performance for a property. S_{MEp} was standardized inversely to the highest score, such that the highest value was assigned a zero and the lowest a one. For the others, the maximum statistic value was assigned a standardized score of one. Accordingly, the summary suitability scores had a possible range of 0 to 5 with 5 representing the best overall suitability.

Results and discussion

Simulations

Figure 2 shows one example of a simulated ecotone surface from each of the 25 abruptness-patchiness groups. Figure 3 illustrates the classified maps derived from the same surfaces. Table 2 lists descriptive statistics for the simulated ecotones, summarized by ecotone group. The average range and mean of values on the surfaces were similar between groups, and the surface mean values were very close to zero for all groups. The average standard deviations were similar within abruptness groups and variable between abruptness groups and within patchiness groups. Because we adjusted the standard deviations of the perturbation surfaces during the simulation, the differences in surface standard deviation between patchiness levels in the same abruptness group were effectively minimized. However, the differences in surface standard deviation between abruptness groups were unavoidable. The resulting surfaces had standard deviations that increased slightly with abruptness level. The sur-

Table 2. Descriptive statistics for the simulated ecotones, averaged by ecotone group. The ecotone values were in the range [−1,1].

		Range	Mean	Stdv	Moran's *I*
A_1	P_1	1.828	0.009	0.369	0.916
	P_2	1.777	0.001	0.369	0.916
	P_3	1.859	0.003	0.373	0.892
	P_4	1.816	0.000	0.365	0.877
	P_5	1.687	−0.001	0.361	0.811
A_2	P_1	1.848	0.002	0.419	0.942
	P_2	1.746	−0.004	0.408	0.938
	P_3	1.838	0.000	0.414	0.922
	P_4	1.774	0.001	0.406	0.907
	P_5	1.678	0.000	0.403	0.858
A_3	P_1	1.797	0.003	0.457	0.953
	P_2	1.787	0.000	0.449	0.949
	P_3	1.862	0.000	0.456	0.934
	P_4	1.781	−0.001	0.447	0.923
	P_5	1.713	0.001	0.444	0.881
A_4	P_1	1.886	−0.006	0.496	0.953
	P_2	1.827	−0.009	0.496	0.953
	P_3	1.929	−0.001	0.499	0.941
	P_4	1.848	0.000	0.493	0.933
	P_5	1.759	−0.003	0.490	0.898
A_5	P_1	1.851	0.004	0.518	0.956
	P_2	1.840	−0.002	0.516	0.955
	P_3	1.935	0.003	0.519	0.942
	P_4	1.878	0.003	0.511	0.935
	P_5	1.779	0.001	0.508	0.902

faces were sufficiently similar in terms of the numerical distribution of surface values that any observable differences among surfaces from different groups should be attributable solely to the spatial pattern of surface values.

Moran's I was sensitive to differences in both abruptness and patchiness, decreasing with increasing patchiness and increasing with increasing abruptness (Table 2). At each level of abruptness, differences in Moran's I between patchiness levels 1 and 2 were small, as were differences between abruptness levels 4 and 5 at each level of patchiness. The differences in spatial autocorrelation were not equal across incremental levels of patchiness or abruptness. Differences in Moran's I between patchiness levels increased with patchiness level, while differences between abruptness levels decreased with abruptness level. Non-linearity in the simulated differences between patchiness and abruptness levels therefore required a careful interpretation of statistic sensitivity.

Comparison of statistic sensitivities

Table 3 lists the results of the main effects analysis of the ANOVA. The F-ratios and Omega Squared values are given for each statistic, describing the patchiness and abruptness main effects and the interaction effects. All tests were significant at $p < 0.001$. It is immediately apparent that each patch- and boundary-based statistic was at least somewhat sensitive to the simulated differences in abruptness, to varying degrees of patchiness, and to interaction effects. Because interaction of factors was significant for all statistics (Table 3), significant main effects are not entirely conclusive of statistic behavior. The simple effects of each statistic were evaluated to provide a better description of statistic sensitivity at different factor levels. The Omega Squared values illustrating the sensitivity of the statistics to differences in abruptness at each level of patchiness (i.e., simple effects) are summarized in Table 4.

The sensitivity of patch statistics to abruptness improved consistently in patchier landscapes (Table 4). This is, at least partially, due to the sensitivity of the patch-based statistics to the number of patches on the landscape and the small number of patches present in our simulated landscapes. In the classified landscapes (Figure 3), landscapes with higher levels of patchiness had a greater number of patches and, therefore, provided more information on which patch-based statistics could distinguish abruptness levels. There is

Table 3. Main effect relationships between statistic values, factor levels (abruptness and patchiness), and factor interactions. ω^2 is standardized to allow comparison between statistics for a given factor (i.e., abruptness or patchiness). All F values are significant at $p < 0.001$. Statistics are listed in rank order for each source of variation.

Source of variance	Statistic	F	ω^2
Patch statistics			
Abruptness	AWMPFD	1983.536	0.815
	AWMSI	2023.419	0.806
	CONTAG	2537.143	0.790
	TE	2427.515	0.758
Patchiness	TE	202.863	0.063
	CONTAG	197.974	0.061
	AWMPFD	112.687	0.046
	AWMSI	114.468	0.045
Interaction	TE	65.916	0.081
	CONTAG	41.778	0.051
	AWMSI	16.505	0.025
	AWMPFD	7.604	0.011
Boundary Statistics			
Abruptness	DISP	2772.977	0.880
	CBE	1478.364	0.806
	N	826.595	0.710
	LMEAN	708.935	0.661
	LMIN	522.168	0.602
	BE	380.321	0.538
	LMAX	293.554	0.420
Patchiness	LMAX	70.049	0.101
	LMEAN	37.256	0.035
	LMIN	19.344	0.022
	CBE	33.260	0.018
	N	15.503	0.013
	BE	7.867	0.010
	DISP	28.801	0.009
Interaction	LMAX	6.069	0.029
	LMIN	4.216	0.015
	LMEAN	4.239	0.012
	DISP	10.096	0.012
	BE	2.712	0.010
	N	3.642	0.009
	CBE	3.880	0.006

Table 4. Sensitivity of statistics to abruptness for each level of patchiness (i.e., simple effects). Values are in units of ω^2. Maximum Omega squared values are in bold, minimum values are underlined.

Patch statistics				
	AWMPFD	AWMSI	CONTAG	TE
P_1	<u>0.397</u>	<u>0.366</u>	<u>0.387</u>	<u>0.363</u>
P_2	0.489	0.479	0.493	0.475
P_3	0.565	0.577	0.592	0.575
P_4	0.640	0.636	0.707	0.688
P_5	**0.711**	**0.736**	**0.821**	**0.800**

Boundary statistics							
	BE	DISP	LMAX	LMEAN	LMIN	N	CBE
P_1	0.209	0.629	<u>0.062</u>	0.308	0.299	0.364	0.501
P_2	0.207	<u>0.552</u>	0.094	**0.345**	**0.332**	**0.370**	0.479
P_3	**0.210**	0.623	0.199	0.329	0.234	**0.370**	0.458
P_4	<u>0.161</u>	0.670	0.236	<u>0.260</u>	<u>0.148</u>	<u>0.314</u>	<u>0.424</u>
P_5	0.194	**0.772**	**0.309**	0.331	0.254	0.338	**0.571**

no similar consistent relationship between patchiness level and the ability of the boundary-based statistics to distinguish levels of abruptness (Table 4).

The following sections describe the general behavior of the patch and boundary statistics, as identified in this analysis. The conclusions about the internal and external consistency of the statistics are based on the Bonferroni comparisons of statistic values at different levels of abruptness. Because of the amount of detail associated with those analyses, the specific results are not included here, but were reported by Bowersox (1999).

Patch-based statistics

The two patch shape statistics (AWMPFD and AWMSI) produced very similar results (Table 3). Their sensitivity to abruptness was the highest, and to patchiness the lowest, of all the patch-based statistics. The relationships of AWMPFD and AWMSI to patchiness and abruptness were externally consistent with the hypotheses. Each was directly related to patchiness and inversely related to abruptness. Also, AWMPFD and AWMSI were internally consistent. CONTAG and TE also produced comparable results (Table 3), but did not perform as well as abruptness measures. Both were at least moderately affected by sensitivity to patchiness.

CONTAG was inversely related to patchiness and directly related to abruptness. TE was directly related to patchiness and inversely related to abruptness. CONTAG did not detect differences between intermediate and high levels of abruptness at low levels of patchiness, but improved at higher levels of patchiness. TE did not detect differences among intermediate and high level abruptness at all patchiness levels except for patchiness level 3.

Boundary-based statistics

BE, CBE, DISP and N all exhibited sensitivity to abruptness as well as patchiness, but were much more sensitive to abruptness (Table 3). Each of these statistics responded to abruptness differences in a predictable and internally consistent manner. As hypothesized, BE, CBE, N and DISP decreased as abruptness increased. The interaction effects for BE, CBE, N and DISP were also the weakest of the boundary-based statistics. Abruptness sensitivity for both BE and N was fairly constant at patchiness levels 1, 2 and 3, dropped to a minimum at patchiness level 4, then increased slightly at patchiness level 5 (Table 4). Abruptness sensitivity of DISP was the opposite, exhibiting a trend of increasing abruptness sensitivity as patchiness increased. DISP had maximum abruptness sensitivity at patchiness level 5. CBE was also sensitive to differences in abruptness at every level of patchiness (Table 4). CBE interaction effects exhibited a pattern of increased CBE patchiness sensitivity as abruptness increased. Abruptness sensitivity for CBE decreased with successive patchiness level until patchiness level 5 where it greatly increased. The comparisons among the abruptness simple effects were externally and internally consistent for all four statistics.

LMAX, LMEAN and LMIN each had significant patchiness and abruptness main effects as well as significant interaction effects (Table 3). The interaction effects on LMAX were nearly twice as strong as the interaction effects on LMEAN and LMIN. The interaction effect for LMAX was such that abruptness sensitivity increased steadily as patchiness increased (Table 4). Maximum abruptness sensitivity for LMEAN and LMIN occurred at patchiness level 2, while the minimum occurred at patchiness level 4 and it fluctuated at the remaining patchiness levels. LMAX, LMEAN and LMIN performed as hypothesized for every abruptness comparison made; values of

Table 5. Patch- and surface-based statistics ranked according to abruptness suitability scores. S^a_{ME} is the relatively strength of the main effects of abruptness on the statistic value, S_{SE} is the simple effect of abruptness on the value, C_E is the external consistency of the statistic, C_I is the internal consistency, S^p_{ME} reflects the strength of the main effects of patchiness, and Score is the overall suitability score. Names of patch-based statistics are underlined.

Statistic	S^a_{ME}	S_{SE}	C_E	C_I	S^p_{ME}	Score
DISP	1.00	0.98	1.00	1.00	1.00	4.98
CBE	0.92	0.74	1.00	1.00	0.94	4.60
<u>AWMPFD</u>	0.93	0.84	1.00	1.00	0.78	4.55
<u>AWMSI</u>	0.92	0.83	1.00	0.98	0.78	4.51
<u>CONTAG</u>	0.90	0.89	1.00	1.00	0.69	4.48
<u>TE</u>	0.86	0.86	1.00	1.00	0.68	4.40
N	0.81	0.54	1.00	1.00	0.98	4.33
LMEAN	0.75	0.48	1.00	1.00	0.85	4.08
LMIN	0.68	0.39	1.00	1.00	0.92	3.99
BE	0.61	0.30	1.00	1.00	0.99	3.90
LMAX	0.48	0.26	1.00	0.95	0.45	3.14
Patch-based mean	0.71	0.66	0.93	0.99	0.60	3.89
Surface-based mean	0.67	0.48	0.95	0.96	0.82	3.88

LMAX, LMEAN and LMIN increased as abruptness increased.

Abruptness suitability rankings

Table 5 lists the suitability scores for each statistic, which are ordered by their overall rank as suitable abruptness measures, from highest to lowest. Standardized scores for main effects sensitivity to abruptness, simple effects sensitivity, external and internal consistency, and main effects sensitivity to patchiness were totaled to provide an overall score of suitability as abruptness statistics. The component score-values were all calculated relative to the highest score recorded for the property that was measured.

The patch-based statistics in order of their suitability as abruptness statistics were: AWMPFD, AWMSI, CONTAG, and TE. It is evident from this analysis that statistics that describe the shapes of patches, i.e., how simple or convoluted the patch shapes are, are reasonably good measures of ecotone abruptness. As ecotones become more gradual (i.e., less abrupt) at a given level of patchiness, the patches tend to get more convoluted and less compact. The patches at abrupt treelines, by contrast, tend to be compact because the transition from tree- cover to no-tree-cover occurs over a shorter distance. Because the contagion of the cover types (CONTAG) and the amount of edge between patches (TE) over an ecotone are sensitive to patchiness, these statistics are not as useful for detecting differences in abruptness. Observed differences in statistic values could be attributable to actual differences in patchiness, abruptness, or both.

In descending order, the most suitable surface-based statistics for quantifying abruptness were: DISP, CBE, N, LMEAN, LMIN, BE, LMAX. CBE and DISP were clearly superior because of both a strong sensitivity to the abruptness of the ecotone and a relative, but not complete, insensitivity to patchiness. We developed these two statistics specifically for the purpose of measuring abruptness and they performed as we had hypothesized. The dispersion of sites with a high rate of change in the variable surface (called boundary elements) about a mean location (DISP) was the superior statistic because of its strong sensitivity to abruptness and relatively weak sensitivity to patchiness.

Conclusions

We can use pattern statistics to understand process. For example, the relative importance of the role of biotic interactions in establishing the alpine treeline is not well understood. By comparing the abruptness of treelines generated from spatial models of treeline that include varying degrees of biotic interaction, we hope to be able to evaluate the role of these processes. However, abruptness is difficult to measure in an observational setting, e.g., using remote sensing. Abruptness, is a quality for which there is no specific statistic to measure it. We may be able to use existing landscape statistics to measure a property of interest, but we need to know something about their sensitivity to that characteristic, as well as the degree to which they measure other landscape properties. In rare cases it is useful to develop a new statistic to measure a new property of interest. In either case, simulation provides a means to quantitatively determine the information content with respect to desired landscape property (e.g., abruptness and patchiness).

Our analysis illustrates the importance of considering the effects of interacting landscape characteristics in an analysis of landscape statistics. To be interpretable in an observational setting, a statistic must be both sensitive to the property of interest and relatively insensitive to other properties. In particular, we show that attempts to measure abruptness of an ecotone can be confounded by the patchiness of the ecotone, rendering conclusions about abruptness more difficult to make. For this reason, it is important to select statistics that are least affected by interacting influences. Although we tested for one such influence, patchiness, simulations could be constrained to test for the influence of other pattern characteristics, like alternative non-random patterns of variation (e.g., periodic patterns).

We presented results that evaluated two approaches to quantifying landscape pattern. Patch-based statistics, especially AWMPFD and AWMSI, demonstrated ability to distinguish abruptness levels when landscape patchiness was high. This is true even though the nature of our simulations limited the power of the patch-based statistics. Whereas patch-based statistics require classification of images, boundary-based statistics extract pattern information from continuous variables based on the images, e.g., reflectance, vegetation indexes, or derived biophysical quanitities. Although boundary-based statistics have not previously been used for quantifying ecotone abruptness, they show some promise for this purpose. We presented two new statistics of pattern for the purpose of describing ecotone abruptness. These statistics, cumulative boundary elements (CBE) and boundary dispersion (DISP), were rated the best by our analysis for measuring abruptness, in terms of both their sensitivity to ecotone abruptness and their lack of sensitivity to patchiness.

Acknowledgement

This research was supported, in part, by a grant from the National Science Foundation (SBR-9709810) and the National Center for Geographic Information and Analysis. We thank Susan Maruca and Geoffrey Jacquez for the many fruitful discussions.

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