7
Multivariate Landscape Trajectory Analysis

An Example Using Simulation Modeling of American Marten Habitat Change under Four Timber Harvest Scenarios

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Abstract. Integrating temporal variability into spatial analyses is one of the abiding challenges in landscape ecology. In this chapter we use landscape trajectory analysis to assess changes in landscape patterns over time. Landscape trajectory analysis is an approach to quantify changes in landscape structure over time. There are three key concepts which underlie the approach—landscape structure, structure space, and location—and there are four useful measurements for analyzing landscape trajectories—displacement, velocity, acceleration, and divergence. We illustrate the approach with an analysis of American marten habitat under four timber harvest scenarios. We used the RMLands simulation model to project changes in forest composition and successional stage across a landscape in the Colorado Rockies under scenarios that varied cutting pattern (clumped or aggregated) and rotation length (200 or 300 years). Next, we used a multi-scale habitat capability model to predict American marten habitat at each time step. We then used FRAGSTATS to quantify 31 metrics describing the extent and pattern of marten habitat. We employed multi-temporal principal components analysis to describe the independent suite of major landscape structure components (i.e., the extent and pattern of marten habitat) as well as their trajectories of change under each disturbance scenario. We demonstrate that trajectory analysis in landscape structure space provides a rigorous, intuitive, and highly interpretable description of the interaction between disturbance, ecological process, spatial pattern, and temporal variation. For example, one can quantitatively understand the nature of the impact of each scenario on marten habitat by inspecting the route that each trajectory takes through landscape structure space. Threshold behavior is readily apparent as rapid changes in direction and rate of change in the landscape structure space. In addition, relative to initial conditions, the impact of each modeled disturbance scenario is readily calculated based on the degree of displacement of each scenario from the original extent and pattern of habitat. Furthermore, the relative similarity between scenarios in their impact on marten habitat is obtained by plotting and analyzing the divergence between the trajectories of the various scenarios through time.

7.1. Introduction

7.1.1. Patterns and Processes Through Space and Time

Temporal variability is a central attribute of ecological systems. Accurate description and conceptualization of ecological systems requires both quantification of spatial patterns and explicit consideration of their temporal dynamics. In a dynamic system, descriptions of current conditions are necessary precursors for understanding ecological relationships. However they are not sufficient. Understanding relationships between mechanisms and responses in ecological systems and predicting future changes likely to result from natural and anthropogenic disturbances requires that scientists integrate analysis of patterns and processes through both space and time.

7.1.2. Ecosystem and Landscape Dynamics: A Conceptual Framework

Ecological systems can be described as collections of state variables (measurable attributes that describe the "state" or condition of the system) depicting ecosystem structure and function at each location in a landscape at each moment in time. The description of the system is constrained by the resolution (i.e., lowest limit in space and in time at which each variable is resolved) and the extent (i.e., spatial and temporal domains over which the variables are measured) of the observations. The structure of the ecological system is described by patterns in each of the state variables across space and time. A key challenge facing landscape ecologists is simultaneously integrating ecological variability across locations in space with measurements of dynamics through time. It is relatively easy to describe the temporal trajectory of a single location through time, as it is to describe the static spatial structure of a landscape consisting of millions of pixels. It is more difficult conceptually and analytically to integrate the analysis of spatial structure across large extents and at fine grains with analysis of temporal variability.

Integrating analysis of spatial structure with that of temporal dynamics is fundamental to linking process to pattern. A landscape is a dynamic system. In quantitative landscape ecology, a landscape is represented by a model, typically defining the landscape as a mosaic of discrete patches. As a dynamic system, a landscape should be defined by its state and dynamics, where the state is given by a vector describing the condition of the landscape at a given moment, and dynamics result from changes in the state over time. The elements of the vector are state variables, elemental qualities describing attributes of the landscape (Horning and Randell, 1973). In landscape pattern analysis, these state variables are landscape metrics, which quantify different spatial properties of the landscape mosaic. These landscape metrics define the phase space, or all possible states of the system given the state variable set. In landscape pattern analysis, phase space is usually called landscape structure space; it is a space defined by all possible combinations of values that can be taken by the collection of landscape metrics describing the structure of the landscape.

The value of landscape variables will change over time as processes impact patterns in the landscape. Over continuous time, this results in a curve in landscape structure space. When measured over discrete time, this curve will appear as an ordered set of points in landscape structure space. The pathway described by these points we call a trajectory and its characteristics reflect the temporal dynamics of that landscape under the influence of disturbances and biotic interactions within that spatial and temporal domain.

In this chapter, we present an approach for integrating spatial and temporal analysis of landscape patterns using American marten habitat as an example. We focus on ways to (a) quantify the multivariate character of landscape structure; (b) measure its change over time; and (c) quantitatively compare the rates and patterns of landscape change among multiple landscapes over time.

7.1.3. Trajectory Analysis Approach

Landscape trajectory analysis is a quantitative approach for measuring differences among landscapes over time. There are three key concepts which underlie the approach: landscape structure, structure space, and location; and there are four useful measurements for analyzing landscape trajectories: displacement, velocity, acceleration, and divergence.

Landscape Structure

The first step in any spatial analysis is to define the landscape. In this chapter we limit our attention to landscapes represented by categorical raster maps, where the cell size specifies the spatial resolution of the data and the classification scheme depicts the cover classes. There are a number of limitations to categorical representations of continuously varying ecological attributes (McGarigal and Cushman, 2005); however, the vast majority of landscape ecological research today is based on categorical maps of landscape structure, hence our use here. Within this framework, a landscape is a map consisting of a mosaic of patches representing different cover types. There are three important attributes of this landscape: classification, resolution, and extent. Classification describes the number and kinds of cover types resolved in the map. Resolution specifies the minimum resolvable spatial unit, and is defined as minimum patch size or pixel size. Extent is the spatial domain of the landscape. Classification, resolution, and extent fundamentally influence patterns that are perceived and measured, and therefore must be defined appropriately with respect to the system and questions being addressed (McGarigal and Cushman, 2005).

The composition and configuration of the patch mosaic represented in categorical landscape maps can be described with landscape metrics (McGarigal and Marks, 1995). These metrics quantify a variety of attributes of patch size, shape, and distribution (McGarigal et al., 2002). There are many different metrics available to quantify the composition and configuration of landscape mosaics. It often becomes cumbersome and confusing to analyze dozens of metrics simultaneously. Many metrics measure similar attributes of landscape structure (McGarigal and

Marks, 1995; Gustafson, 1998; Jaeger, 2000; Li and Wu, 2004; Neel et al., 2004) and several efforts have been made to describe the multivariate relationships among large numbers of metrics (Riitters et al., 1995; McGarigal and McComb, 1995).

Landscape Structure Space

Landscape structure space is derived from a p-dimensional space, where each dimension represents a different landscape metric. It is usually necessary to standardize the landscape metrics to zero mean and unit variance, as landscape metrics often have different ranges and scales of measurement (McGarigal et al., 2002). We refer to this p-dimensional space as landscape metric space, denoting that the dimensions are defined by the individual landscape metrics (but in standardized form). Because many landscape metrics are partly redundant (Riitters et al., 1995) it is often preferable to obtain orthogonal combinations from an unconstrained ordination technique (McGarigal et al., 2000), such as principal components analysis (PCA) (e.g., McGarigal and McComb, 1995; Cushman and Wallin, 2000) or nonmetric multidimensional scaling (NMDS) (Kruskal, 1964; Clarke, 1993). In this manner, the p-dimensional space is reduced to an m-dimensional space, where hopefully $m \ll p$. We refer to this reduced m-dimensional space as landscape structure space, noting that the dimensions now represent composite structure gradients whose exact definitions will vary among data sets depending on the suite of landscape metrics measured and idiosyncrasies of the specific landscapes.

For our purposes, the choice of ordination technique used to derive the landscape structure space is not particularly relevant, as it will depend on the exact variance structure and other characteristics of the particular data set. For example, the appropriate technique will depend on whether is it reasonable to assume a linear relationship among variables—at least within the data space being represented. What is important here is recognizing that ordination techniques (albeit in different ways) seek to summarize redundancy among many variables, in this case landscape metrics, by combining them into a few new composite variables (e.g., principal components) that capture or explain the dominant gradients of variation in the full data set (McGarigal et al., 2000). Moreover, the derived composite variables are generally orthogonal; that is, they are completely independent of each other. Orthogonal axes insure that all dimensions of landscape structure space are independent, and facilitates quantitative interpretation of landscape trajectories.

Representing multivariate measurement of landscape structure as an m-dimensional landscape structure space greatly facilitates analysis when multiple metrics are measured simultaneously. The challenge of describing each landscape across all measured metrics is replaced by describing the relative locations and rates and directions of change in a much reduced landscape structure space. This makes for much more concise and meaningful analyses. Note, however, that the trajectory analysis described below can just as easily be conducted on the original p-dimensional landscape metric space, although the solution is not as concise. Ultimately, the choice of approach depends on how successfully the variance structure of the measured landscape metrics can be summarized by ordination. In the description that follows, we will presume the use of an ordination approach.

Location

Location is defined by the coordinates of the landscape on each axis of the landscape structure space. These coordinates are simply the values of the orthogonal axis scores (e.g., from PCA or NMDS). Location is defined by the position vector specifying the direction and distance of the landscape from the origin of the structure space. Vectors are represented as lowercase, non- italicized, non-bold letters. In simplest terms, the position vector describes the location of the landscape in the m-dimensional structure space. The position vector is most easily handled in component form, which decomposes its components along each axis of the structure space:

$$r_i = \mathrm{x}_{i1} + \mathrm{x}_{i2} + \cdots + \mathrm{x}_{im}$$

The coefficients x_{im} are the components of the position vector, defining the magnitude of displacement of the i^{th} landscape (r_i) from the origin along each of the m dimensions of the structure space. For example, consider a landscape r_i drawn from a large set of landscapes. This landscape has a unique landscape structure based on the computed values of many different landscape metrics. Suppose that PCA is used to summarize these landscape metrics into three orthogonal principal components representing the dominant independent landscape structure gradients across the entire set of landscapes: e.g., landscape contagion, diversity of patch types, and patch shape complexity. These principal components represent the axes of a three-dimensional landscape structure space. The focal landscape has a unique position or location along each of these principal component axes based on the computed values of the original metrics. The exact location along each axis is given by the corresponding principal component score. If, for example, the landscape happens to be more contagious than the average condition, it will have a positive score on the first axis. Furthermore, if the landscape happens to exhibit less diversity of patch types than the average condition, it will have a negative score on the second axis.

When one calculates the same standardized metrics for multiple landscapes, each landscape has a singular location in the landscape structure space. The matrix of landscape scores describes the relative locations of all sampled landscapes within the landscape structure space. We refer to this matrix as the location matrix; it contains a row for each landscape and a column for each landscape structure axis (e.g., principal component). Consequently, each row represents a position vector that gives the singular location of the corresponding landscape in the landscape structure space. Comparison of these locations is the basis for quantifying differences in structure among landscapes.

Multivariate analysis of landscape structure at single moments in time is ideal for quantifying relationships among landscapes at a given time, but is not capable of addressing multi-temporal phenomena. A key adaptation of the location matrix allows the direct inclusion of temporal patterns in the landscape structure space. In the basic location matrix, each landscape is a single row. The adaptation for multi-temporal analysis is to assign a separate row for each landscape at each date. For example, suppose that we measure landscape r_i at five equally spaced dates. This results in a matrix now with five rows, one landscape at each of the five dates, and

TABLE 7.1. Example of a multi-temporal matrix, where columns represent landscape metrics measured, and rows represent each landscape at each time.*

Landscape * Date	Metric 1	Metric 2	Metric m
L1D1	5	7	...
L1D2	6	6	...
L1D3	8	7	...
L1D4	12	9	...
L1D5	16	12	...

*Thus, row 1 contains the landscape metrics measured for landscape 1 in time 1, and row 5 contains the metrics measured on this landscape in time 5.

columns for each derived landscape structure axis (Table 7.1). Plotting the location of landscape ri in this space at each time produces a trajectory (Fig. 7.1). It is the characteristics of this kind of trajectory, and its relationships with trajectories of other landscapes that are the focus of landscape trajectory analysis. This kind of multi-temporal analysis of landscapes appears to be quite rare in landscape ecology, although there are a few examples (e.g., Cushman and Wallin, 2000; Nonaka and Spies, 2005).

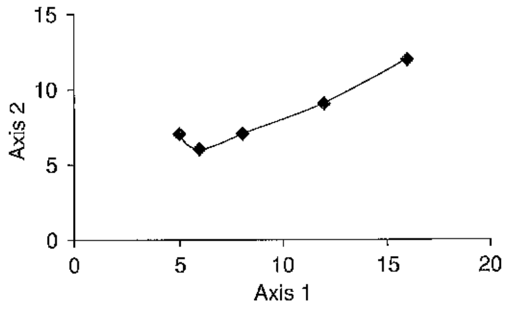

FIGURE 7.1. Example of a landscape trajectory; the path of one landscape in a two-dimensional landscape structure space across five sampling times. The dimensions of the space represent orthogonal landscape structure gradients derived by applying ordination to the full suite of measured landscape metrics.

Displacement

One of the simplest measurements of a landscape trajectory is the displacement of the landscape at any time period from initial conditions. Displacement is defined as the Euclidean distance between the location of the landscape at any time $j = t$ and its initial or starting location at $j = 0$:

$$\overline{\mathrm{d}_i} = \sqrt{\sum_{k=1}^{m} (x_{ijk} - x_0)^2}$$

where x_{ijk} is the score for landscape i (1...n) at time j (0, t) on axis k (1...m). Thus, displacement is simply the Euclidean distance between two points in m-dimensional landscape structure space.

Alternatively, displacement can also be expressed in component form:

$$\overline{d_i} = \Delta x_{i1} + \Delta x_{i2} + \cdots + \Delta x_{im}$$

where Δx_{ik} is the difference in scores between time $j = t$ and 0 for landscape i (1...n) on axis k (1...m). In this form, displacement is defined as the change in the landscape structure space along each dimension. This form facilitates interpretation because displacement can be described directly in relation to the particular aspects of landscape structure represented by each dimension.

Velocity

Velocity is a vector quantity consisting of both rate and direction of change in the landscape trajectory:

$$\overline{v_i} = \Delta r_i / \Delta t$$

where Δr_i is the change in position vector for the i^{th} landscape and Δt is the interval under consideration.

Velocity can also be expressed in component form:

$$\overline{v_i} = (\Delta x_{i1} + \Delta x_{i2} + \cdots + \Delta x_{im}) / \Delta t$$

where Δx_{ik} is the difference in scores for landscape i (1...n) on axis k (1...m) for that interval. In this form, velocity is defined as the rate of change along each dimension of the landscape structure space. As with displacement, this form facilitates interpretation because velocity can be described in relation to the particular aspects of landscape structure represented by each dimension.

Acceleration

In trajectory analysis, acceleration measures the rate and direction in the landscape structure space in which the velocity of a landscape is changing. Acceleration is also a vector quantity, with both magnitude and direction:

$$\overline{a_i} = \Delta v_i / \Delta t$$

where Δv_i is the change in velocity vector for the i^{th} landscape and Δt is the interval under consideration.

Acceleration can also be expressed in component form:

$$\overline{a_i} = (\Delta x_{i1} + \Delta x_{i2} + \cdots + \Delta x_{im}) / \Delta t^2$$

In this form, acceleration is defined as the rate of change in velocity along each dimension of the landscape structure space. As with the other trajectory measures, this form facilitates interpretation because acceleration can be described in relation to the particular aspects of landscape structure represented by each dimension.

Divergence

Comparing the trajectories of multiple landscapes, or of the same landscape under different scenarios, provides a means to quantify differences between trajectories. Divergence is defined as the Euclidean distance between the location of different landscapes at the same point in time:

$$\overline{g_j} = \sqrt{\sum_{k=1}^{m} (x_{ajk} - x_{bjk})^2}$$

where x_{ijk} is the score for landscape i (a,b) at time j (0...t) on axis k (1...m). Like displacement, this is simply the Pythagorean theorem applied to m dimensions, the difference being that here the distance is between two different trajectories at the same point in time, instead of the distance a single trajectory has moved away from the starting point after any time period.

Alternatively, divergence can also be expressed in component form:

$$\overline{g_j} = \Delta x_{j1} + \Delta x_{j2} + \cdots + \Delta x_{jm}$$

where Δx_{jk} is the difference in scores between any two landscapes at time j (0...t) on axis k (1...m). In this form, divergence is defined as the difference in the landscape structure space along each dimension.

7.2. Demonstration and Application

In this section, we provide an example of landscape trajectory analysis. The example is based on simulating landscape change and resulting changes in American marten (*Martes americana*) habitat in a 40,000 ha landscape in the San Juan Mountains of Colorado under four different timber harvest scenarios. The study area is described in greater detail elsewhere (Blair, 1996; McGarigal et al., 2001; Romme et al., 2002).

7.2.1. Methods

Landscape Simulation

For our purpose, we classified the landscape at a spatial resolution of 25 m into a variety of well-established cover types and seral stages, which provided a useful model of landscape structure sufficient for assessing marten habitat. We used the RMLands simulation model (Fig. 7.2) (http://www.umass.edu/landeco/research/rmlands/rmlands.html) to simulate four different timber harvest scenarios representing the combinations of a two-way factorial of cutting pattern (dispersed or aggregated clearcutting) and rotation length (200- or 300-year rotation). In all scenarios, harvesting was restricted to certain cover types and seral stages. Under dispersed cutting, 4–18-ha harvest units were maximally dispersed in a staggered-setting fashion; whereas, under aggregated cutting, harvest units were

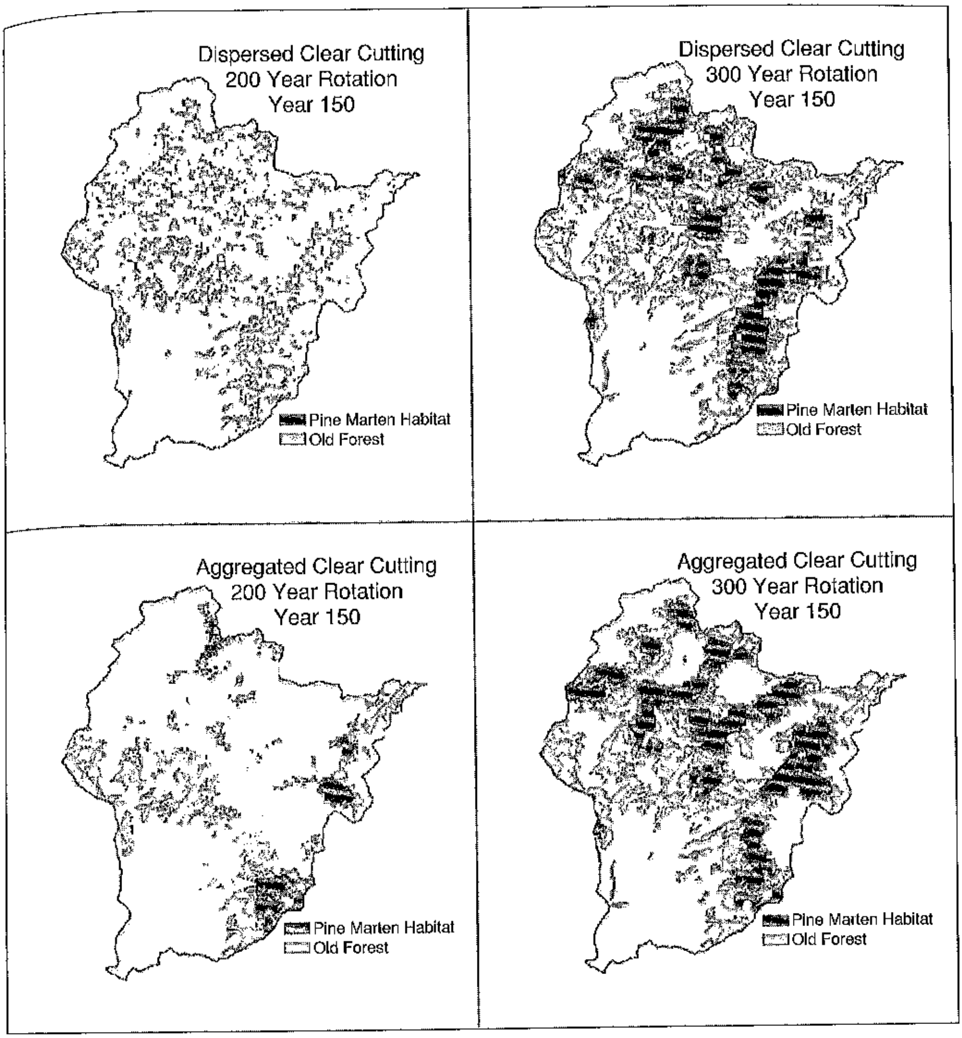

FIGURE 7.2. The four simulated timber harvest scenarios compose a combination of two levels of cutting pattern (aggregated and dispersed), and two-levels of rotation length (200 and 300 years). Shown here are the configurations of American marten habitat (and "old forest") after 150 years of a single simulation.

clumped into larger, contiguous blocks. Under short- and long-rotation scenarios, the intensity of timber harvest (i.e., total area harvested per time step) was adjusted accordingly. The model operates with a 10-year time step and produces an output of landscape condition (i.e., distribution of cover types and seral stages) at each step. Each simulation consisted of a 200–300-year period of disturbance and succession, depending on the rotation period of the scenario, and was replicated ten times. Additional details of the model parameterization are beyond the scope of this chapter and are not essential to our purpose. Under each scenario, disturbances and succession were implemented as stochastic processes in an attempt to mimic real-world patterns of disturbance and succession. Nevertheless, we made a number of simplifying assumptions (e.g., clearcutting as the only disturbance) to better illustrate habitat fragmentation differences among scenarios.

American Marten Habitat

We assessed marten habitat capability at each time step from each replicate run under each scenario based on the output from the landscape simulation. Habitat capability was defined as the ability of a location and its surrounding neighborhood to provide conditions important to survival and reproduction (sensu McComb et al., 2002) We applied a spatially-explicit, multi-scale marten habitat capability model (HCM) to assign a habitat capability index (HCI) value to each grid cell. The HCM was based on semi-quantitative information on marten habitat-associations, spatial attributes of marten habitat derived from local and regional syntheses of habitat-use studies, and expert opinion. In addition, the HCM was reviewed by several wildlife biologists with expertise on marten (Crist, 2002).

Although the details of the HCI model are not presented here, each cell was assigned a value between 0 (low value) and 1 (high value) based on the local composition (e.g., cover type, seral stage) and context (e.g., distance from edge) of each grid cell and the amount and spatial configuration (i.e., fragmentation) of suitable local habitat within a window scaled to the average home range size of the species (250 ha). Thus, each cell was given a habitat capability score that indicated its likelihood of supporting a pine marten. For our purpose, we classified HCI scores into two classes representing habitat (HCI $\geq .7$) and non-habitat (HCI $< .7$). Here, we are interested in analyzing trajectories of change in the extent and fragmentation of capable habitat under the different timber harvest scenarios.

Landscape Trajectory Analysis

We used FRAGSTATS (McGarigal et al., 2002) to compute 31 landscape metrics (Table 7.2) describing the area and configuration of marten habitat at each time step for each replicate run under each scenario. Because of partial redundancies among landscape metrics, we used PCA to transform the 31-dimension landscape metric space into a set of four uncorrelated gradients of landscape structure. There is some debate as to the most appropriate way of combining multiple landscape gradients into orthogonal axes, as there are frequently non-linear relationships among the constituent metrics (Neel et al., 2004). Some researchers have advocated using NMDS because it replaces the linearity assumption with the apparently less severe assumption of monotonicity. However, many metrics have known non-monotonic relationships (such as Edge Density to Class Area). In our own work, we have found that PCA analysis produced more interpretable gradients than NMDS, and that these gradients were qualitatively identical to those produced when the data were corrected for non-linear relationships. This may have been the result of sampling over relatively short landscape structure gradients where the problems of non-linearity are less severe. In the case considered here, we found PCA to produce meaningful axes consistent with our intuitive expectations. PCA was conducted

TABLE 7.2. Landscape metrics included in the analysis.*,[a]

	Acronym	Metric name
1	AI	Aggregation Index
2	AREA_AM	Area-Weighted Mean Patch Size
3	AREA_CV	Patch Size Coefficient of Variation
4	CAI_AM	Area-Weighted Mean Core Area Index
5	CAI_CV	Core Area Index Coefficient of Variation
6	CLUMPY	Clumpiness Index
7	COHESION	Patch Cohesion Index
8	CONNECT	Connectance Index
9	CONTIG_AM	Area-Weighted Mean Contiguity Index
10	CONTIG_CV	Contiguity Index Coefficient of Variation
11	CORE_AM	Area-Weighted Mean Core Area
12	CORE_CV	Core Area Coefficient of Variation
13	CPLAND	Core Area Percent of Landscape
14	DCAD	Disjunct Core Area Density
15	DIVISION	Landscape Division Index
16	ED	Edge Density
17	ENN_AM	Area-Weighted Mean Euclidean Nearest Neighbor Distance
18	ENN_CV	Euclidean Nearest Neighbor Coefficient of Variation
19	FRAC_AM	Area-Weighted Mean Fractal Dimension
20	FRAC_CV	Fractal Dimension Coefficient of Variation
21	GYRATE_AM	Area-Weighted Mean Radius of Gyration (Correlation Length)
22	GYRATE_CV	Radius of Gyration Coefficient of Variatoin
23	LPI	Largest Patch Index
24	NLSI	Normalized Landscape Shape Index
25	PD	Patch Density
26	PLAND	Class Percentage of Landscape
27	PROX_AM	Area-Weighted Mean Proximity Index
28	PROX_CV	Proximity Index Coefficient of Variation
29	SHAPE_AM	Area-Weighted Mean Shape Index
30	SHAPE_CV	Shape Index Coefficient of Variation
31	SPLIT	Splitting Index

*All metrics are class-level metrics describing the spatial properties of the mosaic of American marten habitat patches.

[a]Please refer to the FRAGSTATS website (www.umass.edu/landeco/research/fragstats/fragstats.html) for information on the definition and calculation of these metrics.

on the correlation matrix and included all time steps for all replicate runs under all scenarios. Thus, the landscape structure space encompassed the complete range of realized landscape structures. To facilitate trajectory analysis, we averaged over all runs (replicates) for each PCA factor score at each time step for each scenario. This provided a single value or score on each landscape structure axis (principal component) at each time step for each scenario.

Based on the multi-temporal location matrix, we computed the displacement, divergence, velocity, and acceleration of each scenario across the 200- or 300-year simulation period. For the purposes here, we limited the trajectory analysis to the component form of each measurement (i.e., where the trajectory is evaluated separately for each dimension). In addition, to facilitate illustration we restricted the trajectory analysis to the first 180 years of each simulation and the first two dimensions of the landscape structure space. Analysis was limited to the first 180 years because under one of the scenarios predicted marten habitat was entirely eliminated after year 180 making PCA results undefined. Plotting the trajectory of landscape change in the first two dimensions helps visualize the rates and patterns of change among the four scenarios with regard to the measured landscape metrics.

7.2.2. Results

Multi-Temporal Prinicipal Components Analysis

Nearly 80% of the variance among the 31 landscape metrics was explained by the first four axes (Table 7.3). We interpreted the axes based on the factor pattern (McGarigal et al., 2000; Table 7.3) as follows:

- Axis 1 is a gradient in marten *habitat extent*; landscapes characterized by large, extensive (i.e., far-reaching) and geometrically complex patches of habitat, in which a single patch may dominate the distribution, lie on one end of the gradient, while landscapes with little or no habitat lie on the opposite end.

TABLE 7.3. Multi-temporal principal components analysis of American marten habitat area and configuration under four simulated timber harvest scenarios in a 40,000-ha landscape in Colorado*

Axis	Eigenvalue (cumulative % variance)	Landscape metric	Factor loading
Axis 1	15.5 (49.7%)	AREA_AM	0.96
		LPI	0.96
		CORE_AM	0.95
		GYRATE_AM	0.95
		SHAPE_AM	0.95
		CPLAND	0.91
		SHAPE_CV	0.90
		PLAND	0.90
		FRAC_AM	0.88
		ED	0.80
		GYRATE_CV	0.78
Axis 2	3.93 (62.3%)	PD	0.93
		DCAD	0.90
Axis 3	3.36 (73.2%)	CLUMPY	0.95
		AI	0.93
		CONTIG_AM	0.92
		COHESION	0.87
		CAI_AM	0.83
Axis 4	1.89 (79.3%)	CAI_CV	0.88
		CONTIG_CV	0.76

*Eigenvalues represent the variance associated with each axis (i.e., variance in principal component scores on that axis). Cumulative % variance is the cumulative percentage of the total variance in the data set explained by the first 1–4 axes. Factor loadings are the correlation coefficients between the landscape metrics and the principal axes, after varimax rotation. Only loadings greater than 0.7 are shown.

- Axis 2 is a gradient in marten *habitat subdivision*; landscapes characterized by many disjunct patches of habitat lie on one end of the gradient, while landscapes with comparatively few patches lie on the opposite end. Given that this axis is orthogonal to axis 1, we can interpret this axis as a gradient in habitat configuration independent of habitat extent. In other words, landscapes on the positive end of the gradient possess more habitat patches compared to other landscapes with the same habitat extent, and conversely, landscapes on the negative end of the gradient possess fewer habitat patches compared to other landscapes with the same habitat extent.
- Axis 3 is a gradient in marten *habitat aggregation*; landscapes characterized by clumpy distributions of habitat lie on one end of the gradient, while landscapes with disaggregated distributions lie on the opposite end. Again, given orthogonality among axes, we can interpret this axis as a gradient of clumpiness independent of habitat extent.
- Axis 4 is a gradient in *variability of patch size and compaction*; landscapes characterized by high variability in habitat patch size and shape lie on one end of the gradient, while landscapes with relatively homogenous patches sizes and shapes lie on the opposite end. Again, we can interpret this axis as one of patch variability independent of overall habitat extent.

There were clear differences among the four scenarios in their trajectories of landscape structure (Fig. 7.3). While the overall patterns of change in marten

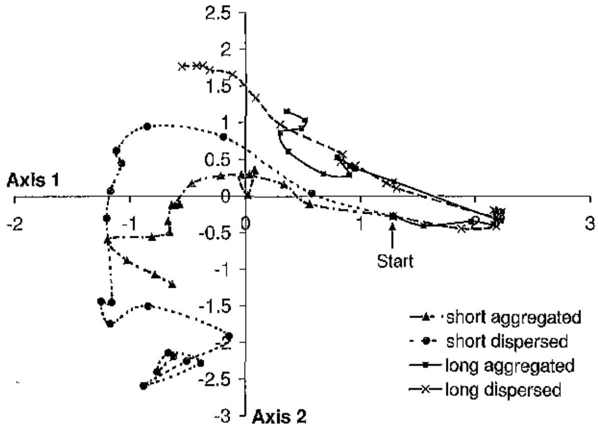

FIGURE 7.3. Landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here are trajectories in a two-dimensional landscape structure space defined by the first two axes of multi-temporal principal components analysis. Axis 1 is a multivariate gradient dominated by area of the landscape occupied by predicted marten habitat. As you move from right to left the predicted area of marten habitat decreases. Axis 2 is a multivariate gradient dominated by the density of patches of predicted marten habitat. As you move from top to bottom the density of patches of marten habitat decreases. Thus, the lower left quadrant, where both of the short cutting rotation scenarios end, is an area of landscape structure space represented by low area and low density of habitat patches.

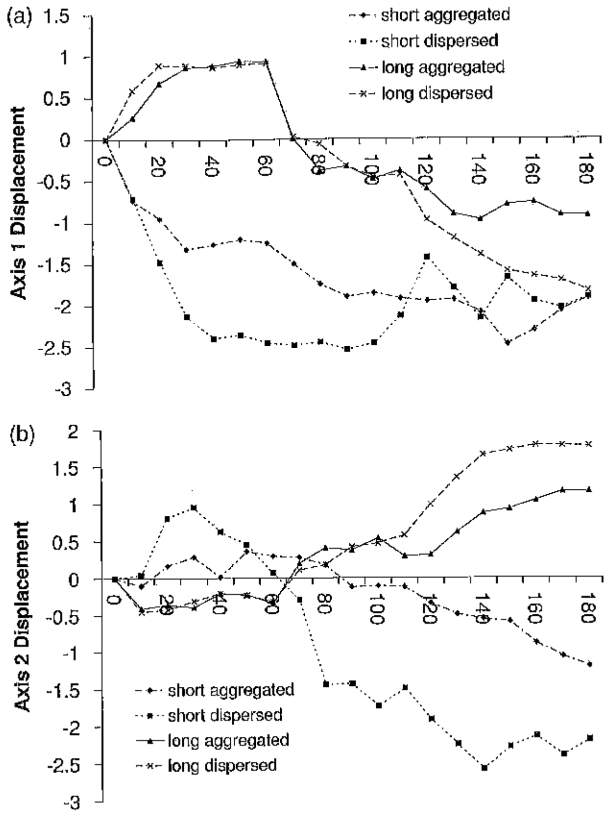

FIGURE 7.4. Displacement of landscape trajectories from initial conditions in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is displacement along axis 1 (a), representing the magnitude of change in habitat extent, and displacement along axis 2 (b), representing the magnitude of change in habitat patch density. Positive displacement indicates a net increase along the axis, while a negative displacement indicates a net decrease. In this example, the two short-rotation scenarios drop farther and faster on the first axis than the two long-rotation scenarios, indicating that the short-rotation scenarios result in greater habitat loss; although, note that the long rotation dispersed scenario ultimately achieves the same total negative displacement. Overall, the long rotation aggregated cutting scenario results in the smallest reduction in the area of the landscape occupied by marten habitat.

habitat are evident in Figure 7.3, the differences are more thoroughly examined by considering their displacement, divergence, velocity, and acceleration, as follows:

Displacement

Displacement (the Euclidean distance between the location of the landscape and its origin at any moment in time) of the trajectories illustrates the magnitude and nature of marten habitat change under each scenario (Fig. 7.4). Both 200-year rotation scenarios move rapidly toward the negative on axis 1, indicating a rapid decrease in the extent of marten habitat as forest is harvested (Fig. 7.4a). Both of these scenarios initially increase on axis 2, then decrease (Fig. 7.4b). Axis 2 is a patch density gradient and the initial increase is a result of fragmentation of marten habitat into disjuct patches. The decrease that follows reflects the elimination of habitat fragments as harvesting continues. The two 300-year rotation scenarios, in contrast, initially move toward the positive end of axis 1, indicating short-term increase in marten habitat. This initial increase is due to a rather large proportion of the landscape existing in mid-seral stages at the start of the simulation and the rate of in-growth to late-seral forest temporarily exceeding the harvest rate (Fig. 7.4a). However, after approximately 60 years these two scenarios both move strongly negatively on axis 1, indicating reduction in the extent of marten habitat. On axis 2 these two scenarios show a directional increase in patch density throughout the simulation period (Fig. 7.4b). This indicates that while habitat area is being reduced and fragmented in the 300-year rotation scenarios, the remaining fragments are not being eliminated and are accumulating at increasing densities.

Divergence

Divergence of the trajectories (the Euclidean distance between the location of different landscapes at the same point in time) illustrates differences among scenarios at any time in terms of the magnitude and nature of their impacts on marten habitat (Fig. 7.5). The 200- and 300-year rotation scenarios, regardless of cutting pattern, diverge rapidly on axis 1 over the first 40 years, reaching a peak in divergence at 60 years (Fig. 7.5a). This indicates large differences in how the short and long rotations impact the amount of marten habitat over the first half-century of harvest. The two 200-year rotation scenarios differ substantially from each other in the rate and extent to which they result in reductions of marten habitat. The divergence between these two scenarios rises to a peak at 40 years and begins to decrease after 60 years. This indicates that under a 200-year rotation, cutting pattern substantially interacts with rotation length such that habitat area is reduced substantially faster in the dispersed cutting scenario, but that eventually both cutting patterns result in similar levels of habitat loss. The initial divergence results from the nature of the habitat model, which predicts that old forest near edges, which is substantially greater under the dispersed cutting pattern, will have reduced habitat capacity. Conversely, the two 300-year rotation scenarios diverge very little from each other over the first 110 years. However, after 110 years we see some divergence, indicating that cutting pattern does influence habitat amount in the longer rotation, but that its influence appears relatively late in the simulation period and to a lesser degree than in the shorter rotations. As the simulation period approaches 200 years, the divergence among most scenarios on axis 1 decreases, indicating a convergence in landscape structure among scenarios to a condition with low levels of marten habitat area. The exception is the 300-year aggregated cutting scenario. The combination of relatively low rate of habitat loss and low level of habitat fragmentation in this scenario result in substantially less total habitat loss than occurs in the other

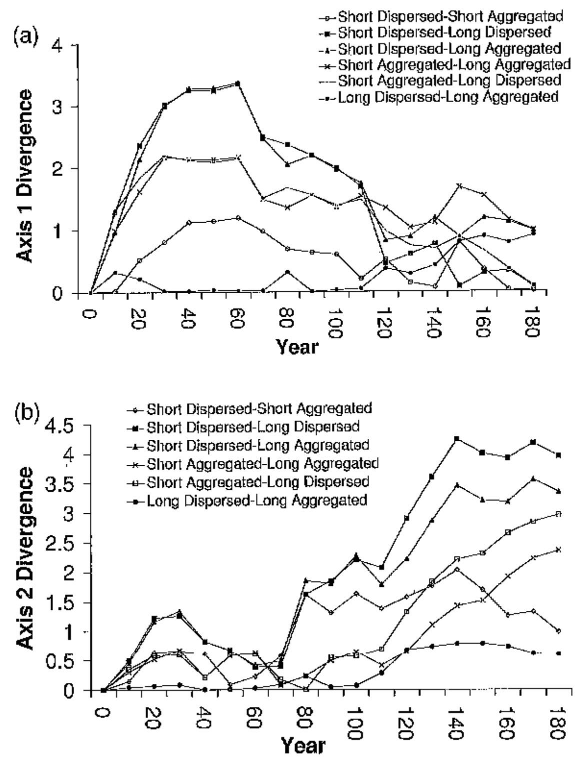

FIGURE 7.5. Divergence of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is divergence along axis 1 (a), representing the magnitude of change in habitat extent, and divergence along axis 2 (b), representing the magnitude of change in habitat patch density. Divergence measures the Euclidean distance between each pair of scenarios at each time step. Scenarios that have a large divergence differ greatly in the attribute of landscape structured measured on that axis. For example, the short dispersed and long aggregated scenarios diverge rapidly and relatively greatly along axis 1, and then slowly converge toward the end of the simulation period.

three scenarios, as illustrated by its final location on axis 1 relative to the other scenarios in Figure 7.3.

The trajectories of divergence along axis 2 are substantially different from those on axis 1 (Fig. 7.5b). In contrast to axis 1, divergence among scenarios on axis 2 shows a bimodal pattern of both short-term and long-term divergence. Initially, the 300-year rotation scenarios increase slowly on axis 2, while the 200 year scenarios remain relatively constant (Fig. 7.3), leading to the short-term pattern of divergence. From year 40 to 70 divergence among scenarios on axis 2 decreases as the 200-year rotation scenarios result in increasing patch density. After year 70 there is a rapid divergence among scenarios, as the two 200-year rotation scenarios experience rapidly decreasing patch density as the remaining fragments of marten habitat are eliminated.

Velocity

Velocity is a measure of the rate and direction of change in marten habitat under each scenario (Fig. 7.6). For illustration, we focus only on the 200-year rotation, dispersed-cutting scenario. Under this scenario, there is an initial rapid decrease in the area of marten habitat, as indicated by the large negative velocity on axis 1 over years 10–40 (Fig. 7.6a). Simultaneously, there is a substantial increase in rate and direction of change of marten habitat along axis 2, which reflects the increase in patch density as well-connected, large patches of habitat are broken into smaller and more isolated fragments (Fig. 7.6b). The combination of these two velocities provides a strong quantitative picture of the simultaneous habitat loss and fragmentation that is occurring in the landscape over the first 50 years of the simulation. From year 50 to100 there is a substantially different pattern of

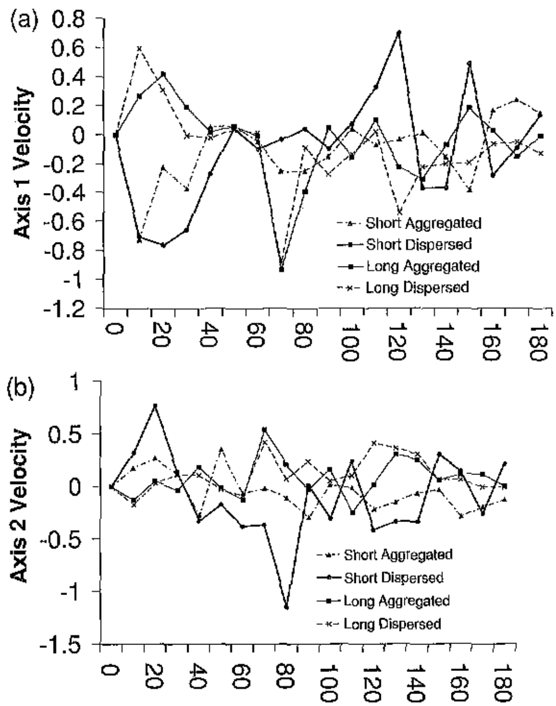

FIGURE 7.6. Velocity of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40,000-ha landscape in Colorado. Shown here is velocity along axis 1(a), representing the magnitude of change in habitat extent, and velocity along axis 2 (b), representing the magnitude of change in habitat patch density. As an example, the 200-year rotation, dispersed-cutting scenario shows a large negative velocity along axis 1 over the first 50 years of the simulation period, indicating a rapid decrease in the extent of marten habitat during this period. Along axis 2, this scenario shows an initial positive velocity corresponding to increasing patch density as marten habitat is being fragmented, followed by a period of negative velocity corresponding to the rapid reduction in patch density as remaining patches of habitat are lost to clear-cutting.

velocity along the two axes, with virtually zero velocity on axis 1 and negative velocity on axis 2 reaching a peak at year 80. This pattern of velocity indicates a phase in which the amount of habitat has equilibrated at a low percent cover while patch density is rapidly decreasing as small habitat fragments are eliminated. From year 100 to year 180 there are large shifts in velocity from positive to negative on both axes, gradually attenuating toward equilibrium. This third period reflects an approach to a dynamic equilibrium of habitat area and configuration, in which there is very low habitat area and very few habitat fragments.

Acceleration

Acceleration is a measure of the rate and direction of the change in velocity across the length of the simulation (Fig. 7.7). The acceleration at each time period in

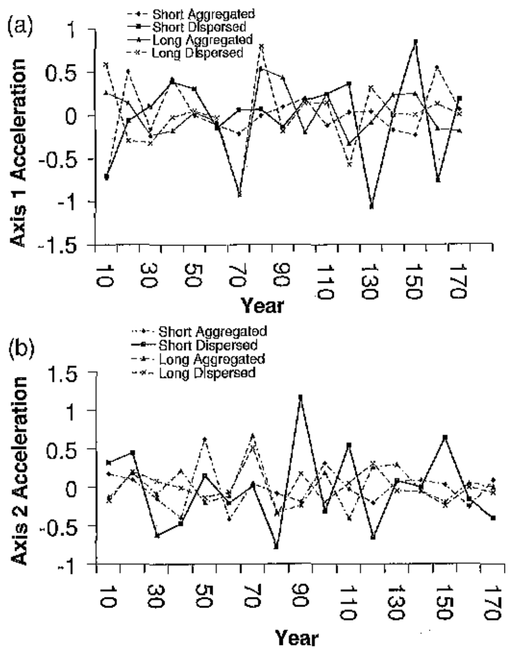

FIGURE 7.7. Acceleration of landscape trajectories in American marten habitat under four simulated timber harvest scenarios (see text for details) in a 40, 000-ha landscape in Colorado. Shown here is acceleration along axis 1 (a), representing the magnitude of change in habitat extent, and acceleration along axis 2 (b), representing the magnitude of change in habitat patch density. As an example, the 200-year rotation, dispersed-cutting scenario shows an initial negative acceleration along axis 1, indicating increasing rate of habitat loss, followed by a period of positive acceleration, corresponding to a slowing of habitat loss as marten habitat is reduced to very low area. Along axis 2, the initial positive acceleration reflects initial increase in the rate of fragmentation of marten habitat, and the following period of negative acceleration corresponds to a reduction in patch density as remaining habitat is eliminated.

Figure 7.7 is the slope of the line segment between the previous and current time period in Figure 7.6. For illustration purposes, we will again focus only on the 200-year rotation, dispersed-cutting scenario. Under this scenario, there is initial rapid negative acceleration on axis 1, and positive acceleration on axis 2 in the first phase of landscape change in which habitat is being rapidly reduced in area and broken into fragments. The direction of acceleration reverses on both axes from year 30 to 50, indicating the transition into the second phase of the trajectory in which habitat area changes little and the patch density decreases rapidly. This reversal of acceleration is diagnostic and quantifies both the magnitude and direction of the change in landscape velocity.

7.3. Discussion

Trajectories of change in landscape structure space provide a direct means to integrate temporal variability into spatial analyses. In our example, trajectory analysis enabled us to quantitatively compare the predicted impacts of several alternative disturbance regimes on the extent and configuration of American marten habitat continuously through time, with respect to multiple dimensions of landscape structure. Our results showed substantial differences both in the rates and the patterns of habitat loss and fragmentation resulting from these different timber harvest scenarios. More specifically, trajectory analysis allowed us to assess the displacement, divergence, velocity, and acceleration of landscape change in marten habitat under these scenarios.

Comparing the *displacement* of each scenario from inital conditions over time provided a means to evaluate the nature and extent of change from the original state. Computing the *divergence* among scenarios over time provided an objective measure of the relative differences among scenarios in their impacts on marten habitat area and fragmentation. In our example, we compared displacement and divergence with respect to habitat amount and habitat patch density, as reflected by the first two axes of a multi-temporal principal components analysis. The temporal patterns of displacement and divergence among scenarios revealed some interesting findings. First, cutting pattern may have little consequence on marten habitat area over the long term if the cutting intensity is high enough. Both short-rotation scenarios result in substantial and comparable habitat loss after 180 years, regardless of cutting pattern, as evidenced by similar displacement (Fig. 7.4a) and minimal divergence (Fig. 7.5a) on axis 1. Second, cutting pattern and harvest intensity may interact to affect marten habitat patterns. For example, in contrast to the short-rotation scenarios (as just noted), the magnitude of habitat loss under the long-rotation scenarios after 180 years depended strongly on the cutting pattern, as evidenced by their differences in displacement (Fig. 7.4a) and large divergence (Fig. 7.5a) on axis 1. Lastly, there may be substantial time lags in marten habitat response to changes in disturbance regimes, suggesting that short-term changes in habitat patterns could lead to erroneous conclusions about the long-term consequences of alternative disturbance regimes. For example, major displacement in habitat patch density (Fig. 7.4b) and divergence among scenarios (Fig. 7.5b) was not realized until at least 60–80 years of harvesting had elapsed. The most dramatic and potentially misleading time lags were evidenced as complete reversals in displacement direction after the initial several decades of harvesting (Fig. 7.4). Time lags of this nature demonstrate that landscapes may contain tremendous momentum that may take decades of active management to overcome.

With the measures of *displacement* and *divergence* in landscape structure space we have the means to quantify the impact of scenarios both with respect to initial conditions and relative to each other. These are the two comparisons most needed by landscape managers to provide information on the effects of land management alternatives. Also, quantifying *velocity* and *acceleration* through landscape structure space provides rigorous description of the rates and directions of changes in landscape structure. These measures facilitate quantitative comparison among scenarios and are critical to linking patterns of change to mechanistic drivers and in particular to revealing thresholds.

The topic of thresholds has received much interest in recent landscape ecology literature (Kareiva and Wennergren, 1995; With and Crist, 1995; Hill and Caswell, 1999; Jansson and Angelstam, 1999; Radford et al., 2005). A threshold is often defined in landscape ecology as a point where a measured phenomenon changes abruptly (Turner et al., 2001). There are three key parts of the definition: phenomena, change, and abruptness. The *phenomenon* may be a process or a pattern. The *change* can be in any measured variable that describes an attribute of the phenomenon. In practice one hopes to measure attributes that apply most directly to a causal relationship between pattern and process. Rigorous definition of a threshold will require careful consideration of the phenomenon, the attributes measured, and the criteria used to determine if a change in location or in velocity is sufficiently *abrupt* to be called a threshold. These are decisions which must be made by researchers on a case-by-case basis.

While there are no established methods for determining thresholds in landscape structure space, we suggest that thresholds could be defined using several different criteria. First, one could define thresholds based on a certain degree of observed change in landscape structure. The diagnostic characteristic in this definition is amount, or magnitude of *displacement* in landscape structure space. Second, one could define thresholds based on the rate and direction of landscape structure change. The diagnostic attribute in this definition is *velocity*. Peaks in velocity along any dimension of landscape structure space could define the location of a threshold because large velocities indicate rapid changes in landscape structure. In our example, significant peaks (or troughs) in velocity exist on the first two landscape structure axes for most scenarios at 70–80 years (Fig. 7.6), which coincides with the major changes in displacement and divergence among scenarios noted above. Third, one could define thresholds based on the *acceleration* of change in landscape structure space. As noted above, a key attribute of thresholds is abruptness. Abruptness in landscape trajectory analysis could be defined as a rapid change in the rate and direction of landscape change through structure space, which could be measured directly by acceleration. In our example, each scenario typically exhibited one or two disproportionately large peaks (or troughs) in acceleration which coincided with substantial changes in rate and direction of the trajectory (Fig. 7.7).

In conclusion, the trajectory analysis approach described here provides a powerful framework for integrating temporal variability into spatial analyses. Trajectory analysis is a flexible approach to quantify changes in location (displacement and divergence), velocity, and acceleration of landscapes in a multivariate landscape structure space. As such, trajectory analysis provides a rigorous, intuitive, and highly interpretable description of the interaction between disturbance, ecological process, spatial pattern and temporal variation.

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