Spring 2010

Modeling complex dynamics at alpine treeline ecotones

Yu Zeng
University of Iowa

Recommended Citation
Zeng, Yu. "Modeling complex dynamics at alpine treeline ecotones." PhD (Doctor of Philosophy) thesis, University of Iowa, 2010.
http://ir.uiowa.edu/etd/633.

MODELING COMPLEX DYNAMICS AT ALPINE TREELINE ECOTONES

by

Yu Zeng

An Abstract

A thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Geography
in the Graduate College of
The University of Iowa

May 2010

Thesis Supervisor: Professor George P. Malanson

ABSTRACT

Alpine treeline ecotones (ATE) are the transition zones between contiguous subalpine forest and open alpine tundra. Because of their transitional natures between different ecosystems in high mountain areas there are a variety of interactions between different species, between vegetation and environmental factors, and between ecological pattern and process. These interactions, or feedbacks, are often nonlinear and potentially make alpine treeline ecotones sensitive to environmental change, especially climate change. Feedbacks between pattern and process create a variety of distinctive yet sometime surprising alpine treeline patterns in three dimensions. These nonlinear interactions and resultant patterns are considered to be an example of spatial complexity, and in this study the research framework of complexity theory was adopted. Dynamic simulation of alpine treeline ecotones is used as the basic research method, and local nonlinear interactions, or more specifically positive feedbacks, are considered the key mechanism driving alpine treeline dynamics. A cellular simulation was created with tree/no-tree states that change as a function of probabilities of tree establishment and mortality, which are functions of the neighborhood and an underlying gradient; the former changes in space and time endogenously; the latter can change in space and time exogenously. Three research projects were conducted for this dissertation; they explore the endogenous and exogenous aspects of alpine treeline dynamics. First, the endogenous dynamics of alpine treeline ecotones were examined. Findings indicate that local positive feedbacks originated from interactions between trees can create fractal spatial dynamics in space and time and self-organization constrains the range of pattern-process relations. Second, the impacts of geomorphologic factors, which impose an exogenous spatial structure on alpine treeline dynamics, were investigated. The results show that there is a geomorphic limit to the endogenous fractal alpine treeline dynamics and self organization. Third, the impacts of climate change, which imposes an exogenous temporal structure on alpine treeline dynamics, were examined. In this case, the self-organized nature of alpine treeline dynamics are not significantly affected by external climate change and the use of alpine treeline ecotones as potential indicator of climate change is called into question. Results of this study suggest that further research using complexity theory is needed to improve our understanding of alpine treeline dynamics and their interactions with exogenous environmental factors.

Abstract Approved by:_______________________________________
Thesis Supervisor

____
Title and Department

____
Date

MODELING COMPLEX DYNAMICS AT ALPINE TREELINE ECOTONES

by

Yu Zeng

A thesis submitted in partial fulfillment
of the requirements for the Doctor of
Philosophy degree in Geography
in the Graduate College of
The University of Iowa

May 2010

Thesis Supervisor: Professor George P. Malanson

Graduate College
The University of Iowa
Iowa City, Iowa

CERTIFICATE OF APPROVAL

PH.D. THESIS

This is to certify that the Ph.D. thesis of

Yu Zeng

has been approved by the Examining Committee
for the thesis requirement for the Doctor of Philosophy
degree in Geography at the May 2010 graduation.

Thesis Committee: ___________________________________
George P. Malanson, Thesis Supervisor

____
Marc Armstrong

____
David Bennett

____
Marc Linderman

____
You-Kuan Zhang

ACKNOWLEDGMENTS

I thank my advisor George Malanson for his guidance, patience, support and encouragement throughout the whole process of doing this research and writing this dissertation. I thank my committee members Marc Armstrong, David Bennett, Marc Linderman and You-Kuan Zhang for their critical and constructive suggestions, support and encouragement for this dissertation. I thank my family, my wife Hongbo and my daughter Xiaomeng, for their support of and encouragement. This work was supported by NSF grant 0196547 to George P. Malanson.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1

INTRODUCTION

The major purpose of this thesis is to explore the endogenous and exogenous aspects of ecological dynamics at alpine treeline ecotones (ATE). The research aims to contribute to our understanding of the complex dynamics at alpine treeline ecotones as a result of endogenous nonlinear interactions between pattern and process alone and the exogenous impacts of geomorphic factors and climate change on these dynamics. By working within the framework of complexity theory this research also contributes to a theoretical advancement of landscape ecology and biogeography, and the methodology illustrates the application of the analytical methods of complexity theory to geographical research.

1.1 Background

Alpine treeline ecotones are the transition zones between contiguous subalpine forest and open alpine tundra. Other ecotones, such as the forest-grassland, boreal-deciduous forest, and mangrove-marsh ecotones, exist, and the major differences between alpine treeline ecotones and other ecotones are that alpine treeline ecotones: 1) are relatively narrow due to the rapid changes in environmental factors in alpine regions such as temperature, precipitation, soil, and nutrients; 2) have sharp physiographic and physiological contrasts between the subalpine trees and tundra species; 3) have extremely harsh environmental conditions in terms of resources; and 4) may display facilitation rather than competition for survival within species or physiognomic types. Further, because of these differences in transitions in ecosystems in high mountain areas, a variety of interactions occur between different species, between vegetation and environmental factors, and between ecological pattern and process(Malanson et al. 2001, 2007). These interactions, or feedbacks, are often nonlinear in nature and make alpine treeline ecotones sensitive to environmental change, especially climate change. Feedbacks between pattern and process create a variety of distinctive, yet sometime surprising, alpine treeline patterns, which can be defined as spatial complexity. Processes at alpine treeline ecotones are spatial in that the processes in one place can alter treeline patterns and thus influence the processes in other places. These changes in treeline patterns may indicate changes in the relationships between trees, and between trees and tundra species, which in turn cause changes in various processes. Spatial treeline patterns usually change gradually, but at certain points they can change into very different forms in a relatively short time. Another feature of these feedbacks between pattern and process is that they can propagate to influence patterns and processes in other places so that an initially local change can have effects across whole ecotones, which is a typical feature of cross-scale interaction (Jensen, 1998). Treeline patterns at alpine regions change through dispersed local positive feedbacks, as a result of which new large scale alpine treeline patterns can emerge. Study of these pattern-process interactions at various scales is the key to further understanding of changes of alpine treeline ecotones and global environmental change.

Alpine treelines have been an active research field because they represent classic ecotones (interface of two or more ecosystems) that may have sensitive responses to climate change (e.g., Holtmeier 2009). There are several hypotheses related to alpine treeline ecotones. Steven and Fox (1991) proposed size –related, growth-related and stature-related hypotheses, all of which consider tree size, growth, or stature as the limiting factors of alpine treeline formation. They emphasize the disadvantages and resource limitations associated with individual tree growth, rather than the pattern-process interaction at larger scales. Korner (1999) generalized five hypotheses: stress hypothesis, carbon balance hypothesis, growth limitation hypothesis, and reproduction hypothesis. He focused more on environmental constraints and impacts on tree growth. These hypotheses also focus on individual trees on a local level. In addition, they are more concerned with the ultimate causes of formation of alpine treelines than how alpine treeline ecotones evolve, i.e. how spatial patterns and processes interact to create the complex spatial patterns with or without exogenous factors. Although positive feedbacks have been suggested by previous researchers (Wilson and Agnew 1992), the questions of how these positive feedbacks work in alpine treeline ecotones and what system mechanisms at alpine treeline ecotones these positive feedbacks would produce, as well as how exogenous factors interact with the positive feedbacks to produce current patterns of alpine treeline ecotones, are still not explored (Malanson, 1999; Malanson et al. 2001; Korner, 1998; Malanson and Zeng, 2004).

In order to further understand these complex patterns, a new research perspective and framework with a holistic view and adequate analytical details is called for. Complexity theory has potential to meet the demands of this task, and questions raised above can be explored from this perspective. Changes in ecotones often are considered to result from complex interactions among different species and between species and physical environment of factors such as geomorphology, soil, climate, hydrology, or CO^2 (Cairns and Malanson, 1998; Malanson, 1999; Korner, 1998; Walsh et al. 2003). A key aspect in ecotone research is the integration of temporal and spatial aspects of landscapes to paint a holistic picture to explain landscape changes, rather than changes of individual trees at a local scale. Given the nonlinear nature of positive feedbacks, such integration based on a spatial complexity framework can provide a holistic view that is based on detailed analysis of temporal and spatial changes in landscapes.

Complexity theory is the study of complex phenomena or systems (Levin, 1999; Bak, Chen, and Wiesenfeld 1987; Prigogine and Stengers, 1984; Cowan, Pines, and Meltzer, 1994; Hilborn, 1994). This theory deals with why a variety of unexpected outcomes can emerge from a set of even very simple interactions and how to measure, describe and predict them. Complexity theory is actually an umbrella name for a collection of theories that consider nonlinear feedbacks or interactions among the entities as the key to understanding emerging properties such as new patterns and processes (Malanson et al. 2006). According to this theory, at certain points in the course of landscape change, landscape patterns can alter drastically into very different patterns due to the feedbacks between pattern and process. These types of points, called thresholds or critical points, play key roles in complexity theory. Identification of such points will help us to know when, why and how landscape patterns change drastically. However, under certain circumstances, entities and their spatial patterns can adjust their responses to each other’s changes to form and maintain some particular types of landscape patterns. Complexity theory has been applied by leading researchers in many disciplines such as ecology and economics as well as in geography. A special issue of *Science* was dedicated to the study of complex social and biophysical systems (2 April 1999, Vol 284, Issue 5411) and a special issue of the *Proceedings of the National Academy of Sciences* was published for computational simulation of complex systems (14 May 2002, Vol 99).

Parrish and Edelstein-Keshet (1999) studied complexity in animal aggregation; Werner (1999) discussed complex landform systems; Rind (1999) explored complexity in climate systems; Epstein (2002) did research on modeling civil violence; Bonabeau (2002) modeled a human-environment system; Macy and Flache (2002) studied social dilemmas. Other researchers using complexity theory for their modeling work include Carpenter et al. (1999) in lake ecosystem dynamics, as well as Sole and Manrubia (1995) in rainforest gap dynamics. Their work generated many new insights into complex phenomena.

The study of ecological complexity that is a characteristic of nonlinear interactions between spatial pattern and process is a frontier of spatial ecology (Levin, 1992; 1999; Tilman and Kareiva, 1997; Green et al. 2005; Murtaugh, 2007). Spatial patterns of species and environment, i.e. spatial heterogeneity, has a strong influence on ecological processes, and ecological processes, in turn, determine changes in spatial patterns of species and environment. Due to the increasing interest in studying ecological complexity, a new journal *Ecological Complexity* was launched in 2004. Research shows that the introduction of space in the ecological models will change species interactions and distributions and thus the dynamics of ecosystems (e.g., Durrett and Levin, 1994; Hassell et al. 1994; Cotterie 2005; Pascual and Guichard 2005; Virah-Sawmy et al. 2009). Since ecological processes usually are not linear and their interactions with spatial patterns are also nonlinear, spatial complexity is inherent in ecosystem dynamics; conversely, changes in spatial patterns can engender nonlinear relations. Studying and revealing such spatial complexity will greatly improve our understanding of ecosystem dynamics. So, complexity theory has the potential to be used for the interpretation of landscape changes or dynamics.

Biological species do not exist without biotic and abiotic environments, and study of the endogenous dynamics of ecological systems can only give us a partial understanding of them. Investigation of the interactions between the ecological systems and their environment beyond what can be bounded as endogenous can better shed light on their complex dynamics. This study considers both endogenous and exogenous aspects of an ecosystem. I investigate how endogenous mechanisms in ecological systems respond to external factors, and the degree of impacts of exogenous environmental factors on the ecological systems in question. I first investigate the endogenous dynamics of alpine treeline ecotones; then I incorporate geomorphic features as spatial heterogeneity and climate change as temporal heterogeneity into this study to examine their impacts on endogenous dynamics. Through these investigations, holistic explanations can be generated to advance our knowledge of alpine treeline dynamics.

There are three research projects proposed for this dissertation that center on exploring spatial complexity at alpine treeline ecotones based on local nonlinear interactions, i.e. positive feedbacks, as the key mechanism that drives alpine treeline dynamics. In the first project, I explore the endogenous dynamics of alpine treeline ecotones and identify fundamental characteristics, such as scaling property of treeline dynamics, and answer questions on how local positive feedbacks originate from interactions between trees and create observed spatial patterns. In the second project I examine the impact of geomorphologic factors on alpine treeline dynamics. More specifically, I add the impact of solifluction, which operates at the same spatial scale as the endogenous processes of tree establishment and growth. In the third project, I investigate the impact of climate change on alpine treeline dynamics. I look into both impacts of climate amelioration and deterioration, as defined from the individual plant perspective, and the timing of their initiation relative to changes in the spatial pattern. The latter two projects explore the limits of endogenous dynamics and compare the relative strengths of endogenous and exogenous factors.

1.2 Research Objective and Hypotheses

The main objective of this dissertation research is to study the spatial complexity, i.e. pattern-process interactions and the resultant patterns, at alpine treeline ecotones. There are three specific hypotheses to test in this study:

a. Endogenous alpine treeline dynamics exhibit self-organized complexity in time and space, which means that alpine treeline dynamics show temporal and spatial scaling exhibiting self-similarity.

b. Temporal and spatial scaling in alpine treeline dynamics will be maintained at ecotones with typical surface geomorphic patterns due to the nature of self-organization process in alpine treelines.

c. Temporal and spatial scaling in alpine treeline dynamics will break down when there is considerable climate change and thus exhibit the impact of climate change, given the prevailing assumption that climate change as a key environmental factor will impact alpine treeline.

1.3 Study Area

Although this research is a spatially explicit simulation of alpine treeline dynamics at hypothetical ecotones, the ecotones simulated are based on observational studies in Glacier National Park in northwestern Montana. This is a high mountain area with seven peaks with elevations greater than 3,000 meters above sea level. The major subalpine tree species are subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelmannii*), lodgepole pine (*Pinus contorta*), limber pine (*Pinus flexilis*), and whitebark pine (*Pinus albicaulis*) (Lesica 2002).

1.4 Research Framework and Model

The research framework is a landscape modeling of alpine treeline ecotones from the perspective of complexity theory. The major shortcomings of current landscape studies are 1) few take spatial complexity into account and thus they are unable to explain and predict the dramatic changes in landscape patterns, especially in landscape modeling (Evans et al. 2001; Parker & Meretsky, 2004); 2) most are still more interested in replicating spatial patterns than integrating the two sides of a coin – spatial and temporal aspects of landscapes, and thus make it difficult to explain landscape changes (Messina & Walsh, 2001; Malanson et al. 2001; Manson, 2005); and 3) even though some landscape models claimed to capture complexity, they actually did not adequately model and analyze the nonlinear feedbacks on landscapes (Kohler, 2000; Fonstad & Marcus, 2003). Importantly, most research was focused on aggregated complexity (Manson, 2001), which emphasizes the complicated aggregation of different components and their relations, rather than the complexity of complexity theory literature, i.e. the nonlinearity in across-scale interactions that are the key to the complex dynamics.

A very simple system, e.g. a sandpile model (Bak, Chen, and Wiesenfeld, 1987) or Iterative Map (May, 1976), can generate enormous complexity if the nonlinearity of interaction is strong. Therefore, I adopt a research framework based on complexity theory which focuses on capturing spatial complexity, the nonlinear feedbacks between pattern and process, and carry out three research projects to address these issues to improve our ability to study landscape changes. Spatial simulation of alpine treelines using simple models has been conducted by many researchers (Nobel, 1993; Cairns and Malanson, 1998; Malanson etal. 2001; Alftine and Malanson, 2004; Bader and Ruitjen, 2008). Only the work of Bader et al. (2008) has addressed complexity theory. The aim of this research is to understand the underlying dynamics of alpine treeline, not to replicate patterns observed on particular slopes. Thus it is informative to simplify the model. Representations of the environment, vegetation, and the processes that relate them are abstracted to the maximum degree. I argue that complexity can be analyzed most effectively in a model that assumes away complications. The exemplar is the work of Hagerstrand (1965), who built a model of the diffusion of an innovation based on a simple theoretical assumption of an exponential decline in contact and left out all the details of the actual landscape and the people on it.

Under this spatial complexity framework, spatial heterogeneity, nonlinearity, and across-scale interaction on landscapes will be primary considerations in model construction and analysis of results. The research methodology is based on dynamical modeling of alpine treeline ecotones. Analyzing and modeling how landscape structures emerge, evolve, and transform is the key to our understanding of landscape dynamics. In the dynamic simulation model, alpine treeline ecotones are represented in a 2-dimensional grid. The grid consists of individual cells whose states represent tundra or trees. The state of a cell is determined by two essential local ecological processes: tree establishment and mortality. These two processes are modeled as nonlinear positive feedbacks and are also influenced by neighborhood spatial pattern. The change of state of cells across the whole landscape captures the alpine treeline dynamics. With the further addition of external forces to the landscape, i.e. the geomorphologic and climatic factors, the exogenous impacts on alpine treeline dynamics are captured. Seed rain and germination are subsumed in establishment. The grid of cells represents a one-dimensional environmental gradient as a linear decrease (from 0.05 to 0.0) in establishment probability with elevation (rows of cells); this low probability reflects the extreme physical environment.

Feedbacks among neighboring trees modify establishment probability of tree in the focal cell positively and negatively. The positive feedback comes from facilitation among nearby trees through reduction of damaging environmental factors such as strong winter wind, cold night temperature, or improvement of environmental quality such as increasing water storage during the growing season and accumulating fallen foliage (Wilson and Agnew, 1992; Callaway, 1998; Callaway et al. 2002). The negative feedback can be created by a dense tree neighborhood where competition for environmental resources such as light, water, and nutrients dominates the interactions among trees or when shade lowers soil temperatures (e.g., Korner, 1998) but it is canceled out by positive feedback here given the fact that it is the strength of the latter that makes alpine treelines possible. I take into account of these feedbacks between trees that affect two basic ecological processes: tree establishment and mortality. The fundamental rationale is that the establishment of trees will positively improve local environment for future tree establishment and reduce tree mortality in nearby places, but in a nonlinear form. In this model, the additional (to the initial slope of probability above) probability of establishment of a tree on a tundra cell is described as a function that captures the combination of local positive feedback or facilitation and local negative feedback; the probability of establishment of a tree in the focal point initially increases with an increase of the number of trees in its neighborhood and then decreases after the number of trees occupy over half of its neighborhood; tree mortality is a function of tree age and the number of trees in its immediate neighborhood. If the tree age is in its young age, it is vulnerable to adverse environmental conditions and its mortality will decrease with the progression of its age and increase of the number of trees in its neighborhood.

To analyze the temporal evolution of the treeline landscape, especially the scaling property, a Fast Fourier Transform is applied to the simulated time series to calculate its power spectrum. Then, a standard linear regression model is used to find the scaling coefficients of spatial and temporal pattern series of the simulated ecotone. The regression coefficient of frequency to the power spectrum represents the power slope of this frequency distribution of power spectrum. The general straight trend of this regression line is interpreted in complexity research community as a smooth distribution of all frequencies or scales of the phenomenon in question. The value of the coefficient or power slope is not as meaningful as Bak first suggested (when he considered the value between 0.5 and 1.0 to be indicative of self-organized complexity; Bak, Chen, and Wiesenfeld, 1987). Rather, the values of power slope can go beyond this range to show different types of such self-organization which is defined as self-organized complexity (Turcotte and Rundle. 2002). A sudden spike of a particular frequency or a breakdown of this general straight line into two or more segments indicates the self-organization is not operating across all scales. In the current literature of complexity research, indicators or criteria of such self-organized complexity and its breakdowns are derived from visual inspection of such log-normalized power spectrum-frequency graphs and no quantified measures have been developed. The reason may be because of 1) the emphasis on the form, rather than the parameters, of functions that describe the fundamentally qualitative characteristics of the systems; and 2) the relatively early stage of this field.

Simulations based on this model will be run with the time step of one year which corresponds to the basic climatic annual cycle and biological growth cycle. All simulation runs start from a randomized treeline at the low altitude and move upslope. Though this model is modified for each project, the fundamental structure and internal ecological processes are kept the same.

1.5 Sensitivity Analysis

Sensitivity analysis is a major concern in dynamic simulation studies. Even though the models developed are properly parameterized through calibration and validation, the sensitivity of small disturbances to parameters in the models can cause serious problems in the reliability and robustness of model outputs. There are several limitations and difficulties of developing and using dynamic models to study alpine treeline ecotones. First, there is no actual observational data available that the treeline models can be calibrated and validated against, for the time scale of this type of simulations goes several hundreds or even thousands of years with a time step of one year. Second, because of the nonlinear interactions or feedbacks and stochasticity inherent and embedded in this type of complex model, the model results are usually particular realizations of many possible outcomes, which is also an advantage of using this type of model to help explore possible, alternative outcomes. In this study, sensitivity was handled by Monte Carlo type runs of the simulations to test the reliability and robustness of simulation results by seeding random number generators for different runs.

Only if the spatial and temporal patterns of alpine treeline dynamics stayed the same through many different runs were the results will be used for further analysis.

1.6 Significance and Intellectual Merit of This Study

This is pioneering research to study the dynamics of alpine treeline ecotones (ATE) under the research framework of complexity theory. The findings are the first to show the fractal nature of alpine treeline dynamics and to explain the endogenous fractal dynamics of alpine treeline ecotones and the impacts of exogenous environmental factors on these dynamics.

This thesis aims to contribute to the current state of knowledge in alpine treeline ecotones and geography in the following aspects:

1) Development of a new theory to explain alpine treeline dynamics in this research advances our understanding the spatiotemporal dynamics of alpine treeline ecotones.

2) Development of a new analytical method based on complexity theory in this research improves geographical analysis of spatial complex systems.

3) Individual projects in this research help illustrate the inherent spatial complexity in other geographic phenomena and how to develop new methods by applying complexity theory;

4) The examination of endogenous and exogenous impacts on alpine treeline ecotones contributes to biological responses of climate change research in a much larger climate change research community and has policy implications of how to make environmental policies of monitoring global climate change.

CHAPTER 2

ENDOGENOUS FRACTAL DYNAMICS AT ALPINE TREELINE ECOTONES

2.1 Introduction

Ecotones, the transition zones between adjacent ecosystems (Risser 1995), are central to our understanding of the relations between spatial pattern and ecological fluxes across landscapes. Ecotones are primarily characterized by changes in species composition, which reveals the limit for a species range, at least locally, and can indicate how a species relates to the environment and other species. Because of this limit, ecotones have been suggested to be sensitive indicators of global climate change (e.g., Hansen et al. 1988, Kupfer and Cairns 1996). Among ecotones, treelines are the most studied, and most treeline studies are of those where forest borders grassland or tundra (rather than forest-shrubland/wetland/other boundaries). The contrast in physiognomy has led to a number of hypotheses of treeline formation, location and pattern, but most lack the dynamics needed to explain how treelines are generated or evolve.

Current explanations of alpine treelines focus on the relations of individual plants to their abiotic environment (Stevens and Fox 1991, Cairns and Malanson 1997) or include feedbacks wherein individuals alter the environment at a local scale(e.g., Malanson 1997, Korner 1998, Smith et al. 2003). Positive feedbacks, wherein trees improve the environment for trees, have been hypothesized as the basis for sharp ecotones (Wilson and Agnew 1992) and facilitation among trees (i.e., trees grow better with tree neighbors) in alpine treeline environments has been suggested (Hattenschwiler and Smith 1999, Callaway et al. 2002). Feedbacks are not universal explanations of ecotones, however (Walker et al. 2003), and it remains unclear how feedbacks between pattern and process, a focal point of ecotone research (Wiens et al. 1985, Gosz 1993), can explain the dynamics of ecotone position and spatial pattern at an appropriate scale that can shed light on internal mechanisms. More generally, Levin (1992) called for understanding of patterns and their underlying mechanisms across scales and suggested that no single natural scale provides such understanding. To develop insights into ecotone dynamics we use theoretical simulations of alpine treeline ecotones to explain how local feedbacks between pattern and process can cross scales to create ecotone dynamics on landscapes. Our objective is to examine general relations between pattern and process, not to explain the dynamics of a particular place.

We use the alpine treeline ecotone as a model system because it exhibits a variety of spatial patterns and the role of feedbacks, while not well quantified, is well established; e.g., Callaway (1998) reported facilitative effects at exposed treeline sites resulting in aggregated patterns with higher growth rates. Patterns, which include abrupt change from trees to tundra, linear hedges, and moving patches of variable size and shape (Marr 1977, Holtmeier and Broll 1992, Allen and Walsh 1996) may be independent of the pre-existing physical environment (Malanson et al. 2001, 2002), and are often attributed to endogenous interactions of vegetation, wind, and snow instead (e.g., Daly and Shankman 1985, Walker et al. 1993, 2001, Hattenschwiler and Smith 1999, Germino and Smith 2002, Smith et al. 2003).

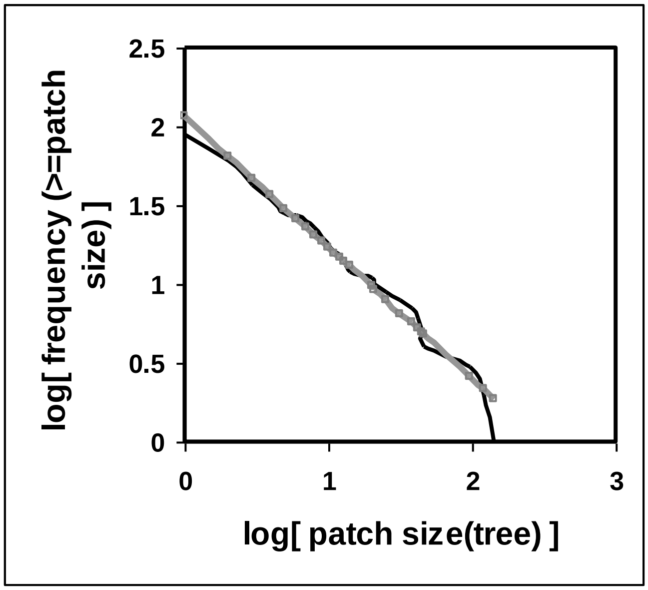
Endogenous factors include both negative and positive feedbacks. The primary negative feedback is shading and cooler soil temperatures that would inhibit tree growth by limiting the formation of tissue even if carbon is sufficient (Korner 1998, Hoch and

Korner 2003). Positive feedbacks arise from structural protection from wind and intense radiation and from higher canopy temperatures due to lower albedo (Tranquillini 1979, Smith et al. 2003). The trapping of snow by larger plants is regarded as a key feedback (Hiemstra et al. 2002, Alftine and Malanson 2004). The role of snow changes across the ecotone, however (Hessl and Baker 1997, Callaway et al. 1998, Moir et al. 1999); with patches of meadow in forest, more snow may inhibit seedling establishment (e.g., Billings 1969, Rochefort and Peterson, 1996), while at more wind-swept sites snow held by vegetation may provide an important source of water (Lloyd 1997) or may increase nutrient availability by maintaining higher winter soil temperatures (see Sturm et al. 2001 for the Arctic). We will focus on the advance of trees into exposed tundra as an example of the leading edge of an ecotone.

2.2 Rationale

Alpine treeline in Glacier National Park (GNP) advanced into tundra in the 19th century (Bekker 2002). We analyzed a 1999 airborne multi-spectral remote sensing image with 1-m spatial resolution for Lee Ridge, GNP, at the leading edge of a recent (1950-1980) treeline advance (Alftine et al. 2003). It was classified as tree or tundra (Figure 2.1a). Patch sizes have a power law distribution with an exponent of 0.83 (Figure 2.1b), which shows a fractal spatial structure (a power-law distribution is self-similar) and is suggestive of a spatial process with a fractal temporal structure (Wooton 2001, Pascual et al. 2002). The low value of exponent means there are few small patches of trees, and we expect single trees to have higher mortality due to the harsh alpine environment (Callaway 1998, Callaway et al. 2002). This empirical information suggests a modeling and analytical methodology based in complexity theory (e.g., Sole et al. 1999).

a



b

Figure 2.1. Observed alpine treeline landscape and spatial structure.

a. Classified ADAR image of a treeline ecotone in Glacier National Park, MT (by Department of Geography, University of North Carolina at Chapel Hill);
b. Corresponding cumulative frequency distribution of patch sizes in a. and its regression line.

Complexity theory, an attempt to understand emergence, or how simple processes can combine to produce holistic systems (Phillips, 2004), may help advance our understanding of ecotone processes and patterns (Malanson 1999). A related indicator, phase change, has been observed and modeled for treelines bordering grasslands (Milne et al. 1996, Loehle et al. 1996, Li 2002). Self-organized complexity is a general umbrella for work that addresses commonly observed power-law distributions (Turcotte and Rundle 2002). Although self-organization has been defined in many ways (Phillips 1999), we follow systems dynamics usage to mean that although a system has a number of spatial and temporal degrees of freedom (the term 'spatially extended dynamic system' is used), its dynamics can be simplified because they generate order, especially a fractal structure such as power-law distributions of important variables; i.e., the degrees of freedom can be reduced to an attractor, usually of low dimension, without external tuning (Haken, 1975; Bak et al., 1988). Self organizing complexity does not necessarily include evolution to criticality (e.g., Bak et al. 1988, Fonstad and Marcus 2003).

Sole and Manrubia (1995) and Wootton (2001) used empirically calibrated cellular automata (CA) to show how landscape ecological patterns arise from local scale processes, and they analyzed power law distributions of gaps (in tropical rainforest and in mussel patterns, respectively) across their landscapes (a CA is a spatially explicit simulation in which cells have states that are determined in large part by the states of their neighbors (e.g., Wolfram, 1984). In geography, similar dynamic simulations incorporating nonlinear interaction have been used, mainly in urban systems and landscape studies (Allen, 1982; Straussfogel, 1991; Phipps, 1989; Sheppard, 1985), which showed complex system dynamics but did not examine the across-scale dynamics and the scaling relations underlying the phenomena. We take this approach further. We construct a CA using two essential ecological processes driving alpine treeline advance: tree establishment and mortality. We capture the endogenous interaction between pattern and process in a local neighborhood with the assumption that interaction among trees beyond their local neighborhood is insignificant, and use it to simulate alpine treeline advance. We use landscape indicators to describe the treeline process and spatial pattern and analyze the dynamics at different scales through Fourier analysis and quantify the pattern-process dynamics using power law distributions which reveal the underlying scaling relations of treeline advance across a landscape. Using the model, we examine how nonlinear feedbacks across scales drive dynamics across the landscape. Finally, we develop an ecological narrative of how variable spatial patterns might be generated by a simple model.

2.3 Methods

We examined spatial and temporal structures using a CA of treeline. Noble (1993) similarly modeled treeline, but did not address dynamics or process-pattern relations. The cells change between two states, tundra and tree (the latter includes krummholz here), and these changes capture the dynamics of establishment and mortality. Seed rain and germination are subsumed in establishment. The grid of cells represents an alpine treeline landscape in a mountain slope with a linear environmental quality gradient. The CA model was run on a 100 × 1050 lattice representing a slope in the long dimension wherein the cells are nominally 1 m. All simulation runs started from a random distribution of trees in the lowest two rows, from which trees establish upslope. The initial condition of establishment probability is a slope from 0.05 to 0.0 over the bottom 300 rows of the lattice (nominally an ecotone of 300 m width). This 100 × 300 window moves upslope 1 cell every iteration, leaving lower cells with a base probability of 0.05. By computing the active ecotone within a large area we eliminated the exogenous effect of topography and simulate unrestricted advance that would occur with a slow continuous amelioration of climate starting at time 0.

Feedbacks among neighboring trees modify establishment probability of a tree in the focal cell positively and negatively. The positive feedback comes from facilitation among nearby trees through a reduction of damaging environmental factors such as strong winter wind, cold night temperature, or improvement of environmental quality such as increasing water storage during growing season and accumulating fallen foliage (Wilson and Agnew 1992, Callaway 1998, Callaway et al 2002). The negative feedback can be created by a dense tree neighborhood where competition for environmental resources such as light, water and nutrients dominates the interactions among trees or when shade lowers soil temperatures (e.g., Korner 1998). The probability of establishment of a tree on a tundra cell is described as a function that captures the positive neighborhood feedback or facilitation and negative neighborhood feedback (Figure 2.2a):

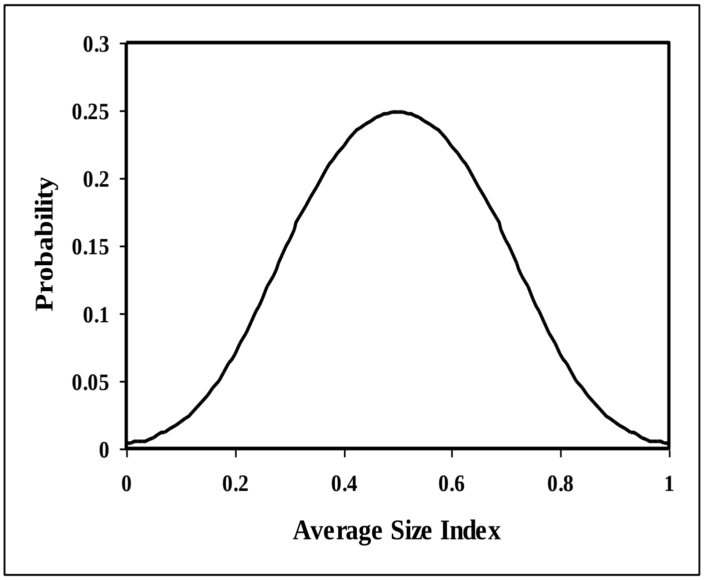
$$Pe = \frac{\alpha}{1 + \beta e^{-r(x - x^2)}} \tag{1}$$

where x is the average size index of the local neighborhood which is the percentage of tree-occupied cells in a tree neighborhood; this average size index represents the density of the tree neighborhood. The positive feedback or facilitation exists when tree neighborhood is sparse and negative feedback appears when trees are densely located in the neighborhood. α is a coefficient to adjust the magnitude of establishment probability and thus the strength of positive and negative feedbacks in establishment process and takes 0.5; ß is a coefficient and takes 150 here; γ is a coefficient and takes 20; and the local neighborhood size is 5 × 5.

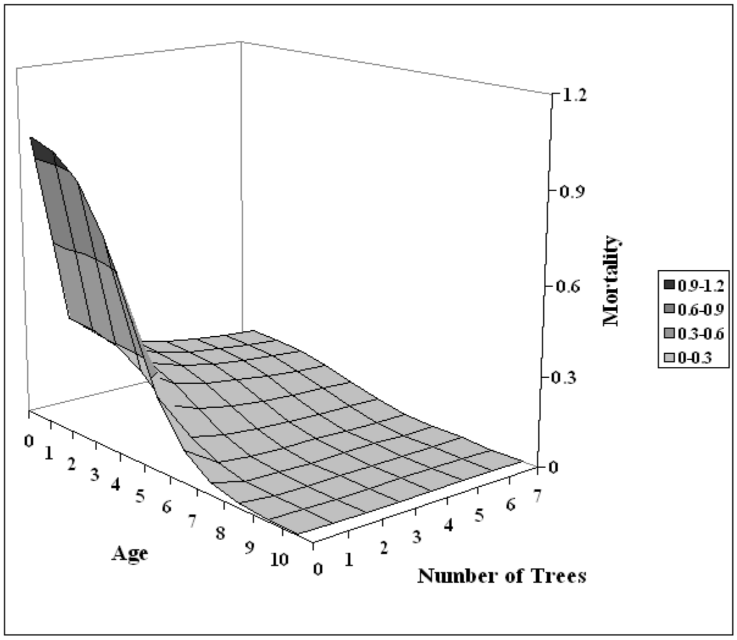
After establishment, the trees endure a harsh physical environment each year, and the mortality is especially high when the trees are very young. The protection from immediate neighboring trees becomes a very important factor for survival of young trees. In this simulation, tree mortality is a function of tree age and the number of trees in its immediate neighborhood. Trees usually take 5 to 10 years to firmly establish in alpine regions; if the tree age is less than or equal to 6 years, the probability of mortality is:

$$Pm = \frac{1}{C\sqrt{n}}\left(1 - \frac{1}{1+\lambda e^{-Z}}\right) \qquad (2)$$

where *Z* is the age of the tree, which reduces the mortality with growth of the tree; λ is a coefficient; here it takes 50. If the tree age is greater than 6 years, mortality is 0.02; when there is no tree in the neighborhood, Pm is equal to $1-\frac{1}{1+\lambda e^{-Z}}$. Figure 2.2b shows the decline of mortality with the tree growth used in this model, i.e. the second part of the equation (2). *C* is a parameter to adjust the strength of positive feedback in mortality, here it takes 3.0; *n* is the number of tree cells in the immediate neighborhood (3 × 3) (seedlings are protected only by the immediate neighboring trees). All the values of coefficients are the results from calibration through trial runs of the model against the observed alpine treeline landscape pattern.



a



b

Figure 2.2. Tree establishment and mortality functions

a. Tree establishment probability function
b. Tree mortality function.

Every run simulates 747 annual iterations (landscape of 1050 lines minus the moving ecotone size of 300 and the 2 lines of initial random treelines plus 1); cell states and tree ages are updated every iteration. The first 200 iterations are discarded to reduce the effects of initialization, for we initiate the simulation on a random landscape and let the landscape evolve into a relative stable stage in terms of its extent and growth rate that resembles the observed alpine treeline. We calculated means for 12 repetitions; we used a small number because the variance was very low, which suggests reliability of simulation results.

To analyze the temporal evolution of the treeline landscape, especially the scaling property, a Fast Fourier Transform is applied to the simulated time series to calculate the power spectrum of the time series. For a function of *f(t)*, its Fourier transform is defined as

$$F(\omega) = \int_{-\infty}^{\infty} f(t)e^{-i\omega t}\ dt \qquad (3)$$

and the corresponding inverse Fourier transform is defined as

$$f(t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} F(\omega)e^{i\omega t}\ d\omega \qquad (4)$$

where *i* is the imaginary unity number; t is the time; ω is the range of angular frequencies.

When the Fourier transform is used for discrete series, the discrete Fourier transform (DFT) is defined as

$$F(k\Delta f) = \sum_{n=0}^{N-1} f(n\Delta t)e^{-i(2\omega k\,\Delta f)(n\Delta t)} \quad k = 0, 1, 2, \ldots, N-1 \qquad (5)$$

where *N* is the number of discrete samples taken; T is the total sampling time; Δt is time increment between samples, Δt = *T/N*. Here we used a Fast Fourier Transformation (FFT), which is a discrete Fourier Transformation and requires the number of sampling points be a power of 2, and we chose 512 iterations.

After the FFT, we used regression analysis of the power spectrum obtained from the FFT to examine the scaling properties of alpine treeline movement and spatial patterns. A linear regression model is used to find the relationship of log-normalized frequency and the power spectrum of the system dynamics using the least-square principle.

$$Log(Y) = \alpha + \beta Log(X) \qquad (6)$$

where Y is the power spectrum of the time series; X is the frequency of the time series; α is the intercept of the regression line and ß is the coefficient or scaling exponent. Power spectrum and frequency refer to the system time series. The standard way of determining the scaling exponent of the '1/f' type noise is:

$$F(S) = S^{-\tau} \qquad (7)$$

F is the frequency of patch size and S is the patch size. τ is the scaling/critical exponent between them. If linear, it indicates that a power law relationship exists, and larger patches will persist longer in the landscape before being merged into continuous forest, which may indicate self-organization of trees at the landscape level.

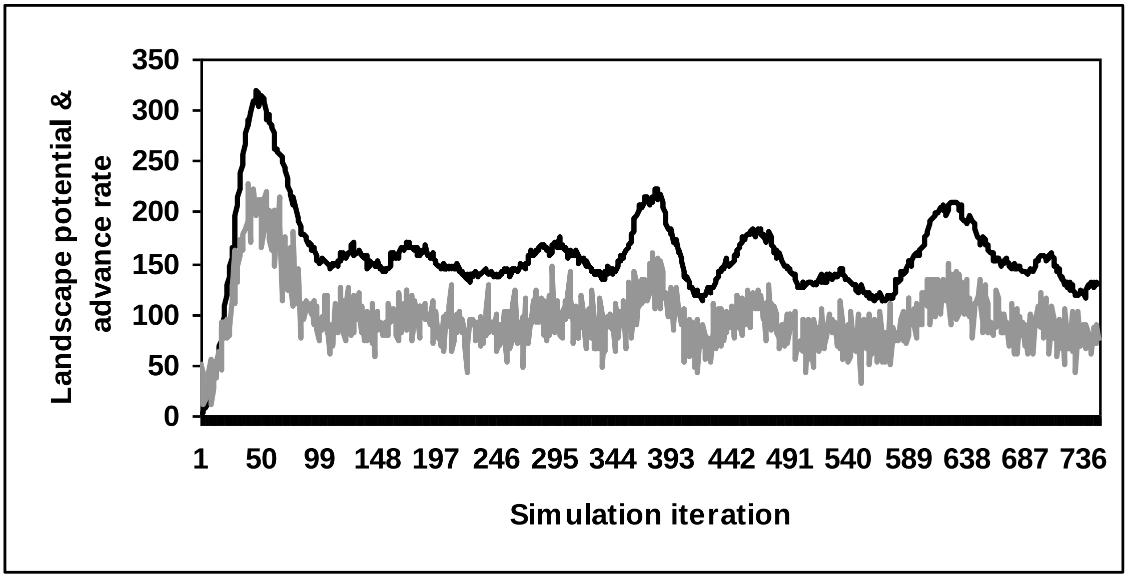
We deliberately excluded the exogenous effects of climatic variability and topographic heterogeneity, because the purpose of this study is to reveal the endogenous dynamics which may shed light on the internal mechanism driving the alpine treeline landscape. Additional research can examine the effect that exogenous factors, such as climate and topological heterogeneity, would exert. The model is not calibrated to produce specific patterns, but is for theoretical exploration. The coefficient values were chosen only to keep the rate of advance of the ecotone on the order of 1 m/yr - i.e., within the moving window. Sensitivity analyses show the results are robust with different coefficient values and different window sizes (3×3, 5×5, 7×7, 9×9), except that an extreme left skew of equation 1 produces no fractal spatial pattern. We carried out 12 simulation runs and analyzed the statistics. The statistics of the simulation results show a very small standard deviation.

2.4 Analysis and Results

2.4.1 Fractal Analysis of Dynamics

We examined treeline advance dynamics in terms of its spatial process and pattern. We calculated two landscape scale indicators to investigate the spatial process of treeline advance. Landscape potential is the sum of the establishment probabilities of all unoccupied cells; this represents the cumulative effects of all trees on the slope; advance rate is the net gain of tree cells in every iteration. These indicators shows fluctuations around long term means of 159.9 (mean standard deviation of 1.44) and 97.2 (mean standard deviation of 0.59), respectively, at a variety of scales (e.g., Figure 2.3a). The dynamics of landscape potential and advance rate are similar (Pearson correlation = 0.8438; $p<0.001$) except the latter has higher frequency noise. We applied Fourier analysis to the time series of landscape potential for 512 iterations. The power spectrum is obtained by squaring the amplitude spectrum calculated from the Fast Fourier Transform. The power law exponent is calculated by regressing the log-normalized power spectrum on log-normalized frequency. The power spectrum of landscape potential reveals a temporal fractal scaling at a landscape scale with a mean critical exponent of 2.02 (standard deviation of 0.037). The result of Fourier analysis of landscape potential in one simulation is graphed in Figure 2.3b. The regression result matches very well with the power spectrum and indicates there is a clear scaling property in the treeline advance process and treeline advance process is fractal. This suggests that treeline advance involves all scales of processes. The changes of landscape potential display no characteristic scale, which means tree establishment and mortality processes across the landscape fluctuates in a scale-free way. Then we analyzed the evolution of spatial patterns across space. We use the characteristic exponent of the frequency distribution of patch sizes in every iteration to represent spatial structure (Turcotte 1990) and its time series. This distribution is also a distribution characterized by the power law. So, we calculated the power law distribution of the patch sizes across the landscape for every iteration and use it to represent the spatial structure of treeline landscape as we did for the remote sensing image. In this way, we construct a time series of this value to represent the evolution of spatial structure of the treeline landscape. The statistics of all simulation runs show that the mean of this critical or characteristic exponent of the power law distribution is 0.697 with a small standard deviation 0.005. This indicates the consistency of the results from different simulation runs. Its power spectrum also displays temporal fractal scaling and the mean critical exponent of all simulation runs is

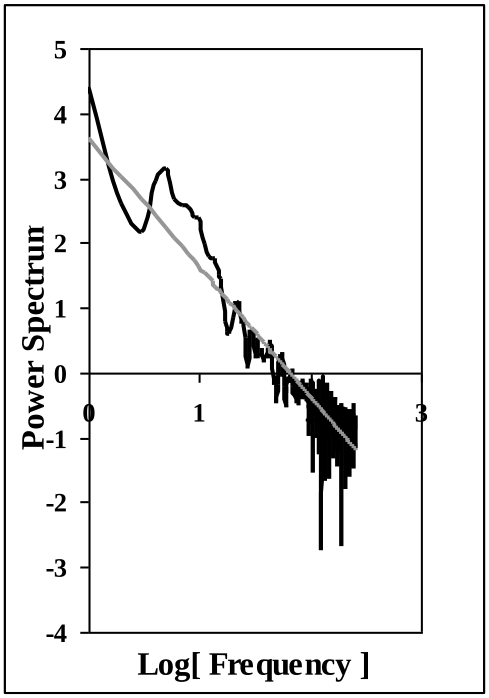
1.54 with a standard deviation 0.179 (e.g., Figure 2.3c). These results suggest that the temporal evolution of treeline spatial pattern is fractal (fractal dynamics, *sensu* Sole and Manrubia 1995). So, the spatial structure of the treeline landscape exhibits a temporal fluctuation with various fractal spatial patterns. These temporal fractal patterns for landscape potential and patch size distribution are characteristic of scale-invariance, which suggests long-term temporal and spatial correlation across the treeline landscape.



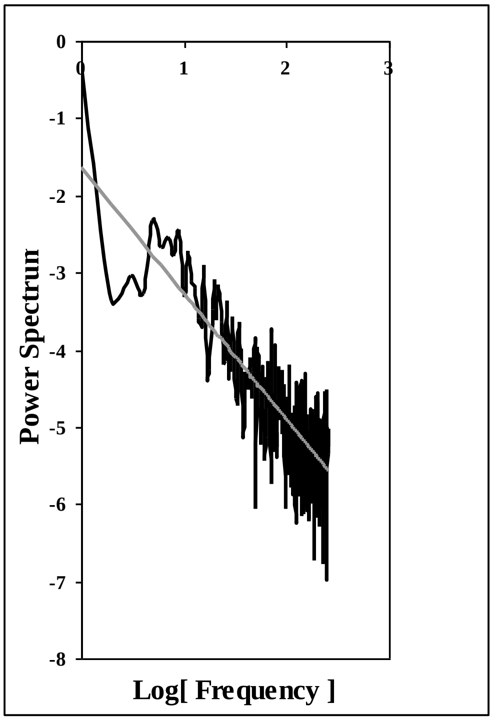
a

Figure 2.3. Dynamics of the cellular automaton treeline model.

a. Landscape Potential and Advance Rate starting from a random treeline structure. Upper line, time series of landscape potential; lower line, time series of advance rate. b. Power spectrum of landscape potential and it's regression line. c. Power spectrum of the exponent of the frequency distribution of patch size and its regression line. d. Time series of landscape potential and spatial structure evolution (After 200 transients are discarded); black, time series of landscape potential; gray, time series of exponent of power law distribution of patch size; their values are normalized to [0.0, 1.0].

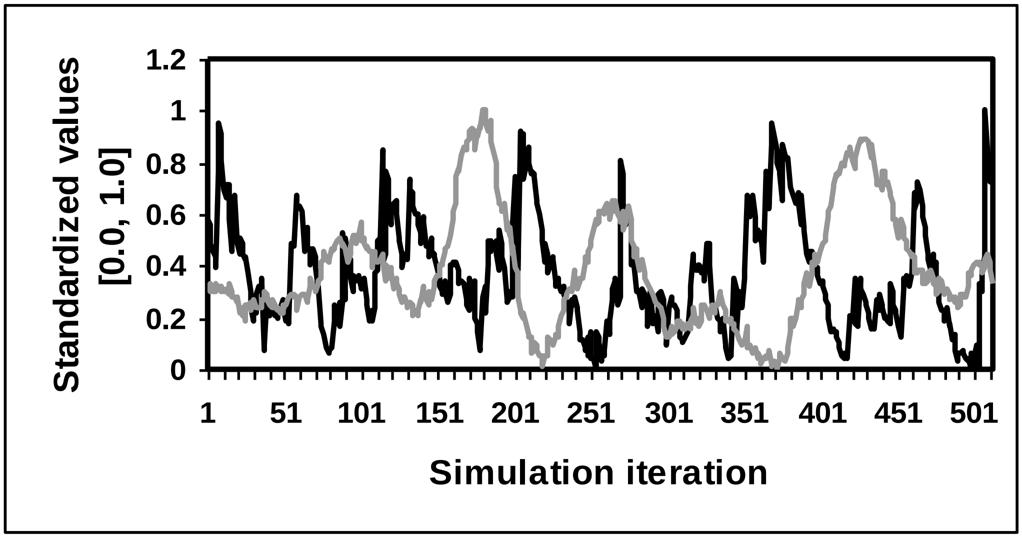


b



c

Figure 2.3 continued



d

Figure 2.3 continued

2.4.2 Correlation Analysis of Dynamics

In order to search for the underlying mechanisms for such fractal scaling, we analyzed the relation between the time series of landscape potential and that of the exponent of frequency distribution of patch size (Figure 2.3d). The exponent of frequency distribution of patch size is negatively correlated with landscape potential (Pearson correlation = -0.3443; $p<0.001$). When we lagged landscape potential by 5 years with respect to the exponent of the frequency distribution of patch size, the coefficient reaches -0.4186, suggesting that spatial structure may change ahead of landscape potential and exert a positive impact on it. Lower exponents represent the existence of large tree patches; this state, which has a higher fractal dimension, corresponds to higher potential for treeline advance (Figure 2.4a, b). At these times more tundra cells are on the edge of, but not surrounded by, forest, and so are most likely to change. The high fractal dimension of the treeline landscape may be an indicator of the vulnerability of tundra to invading trees, which may be instrumental to raise the landscape potential and thus helps trees to advance into tundra. The rules in our model only specify the nonlinear positive and negative feedbacks between pattern and process at a local scale, but these local interactions create significant correlation between pattern and process (fractal pattern and potential or advance rate) at a landscape level. This linear correlation emerges from the dispersed, localized interactions. Furthermore, large fluctuations show that the ecotone varies between high and low fractal patterns (inverse to the exponent of the power law slope) (Figure 2.3d). These large fluctuations signal a significant change of state of treeline advance similar to the second order phase transition, and thus make an important impact on landscape potential and advance rates.

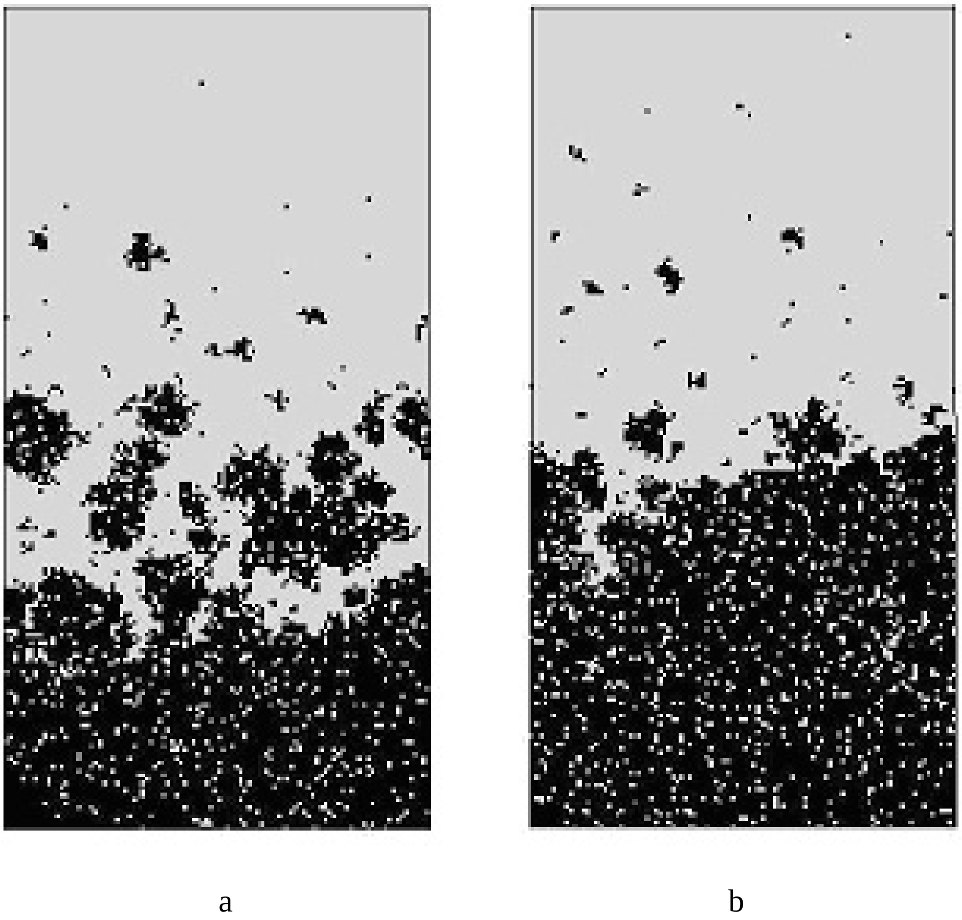


Figure 2.4. Snap shots of two distinct fractal states and evolution of spatial structure. Grey area represents tundra; black area represents alpine trees. a. Snapshot of high fractal state (iteration 414 in Figure 2.2 d); b. Snapshot of low fractal state (iteration 213 in Figure 2.2 d).

2.5 Discussion

2.5.1 A Complexity Narrative Explanation

Our simple model demonstrates that local endogenous, nonlinear interactions (the effects of trees on neighboring cells) can produce landscape-scale order. Landscape dynamics (rates of advance) are fractal (i.e., they have a power-law distribution and so are self-similar), and the spatial patterns (size distribution of patches) are also fractal. The local interactions create long-term, landscape scale linear correlations (between advance and potential). These results suggest that multi-scale pattern-process interaction is the key to treeline advance and the self-organizing behaviors exhibited in this system. Based on analyses of the dynamics and similarities between the simulations and a range of observed spatial patterns (e.g., Allen and Walsh 1996), we could conclude that the endogenous dynamics of alpine treeline are a process of self-organized complexity (Turcotte and Rundle 2002). Rather than stopping at this point and hypothesizing a process alone, we go on to identify a pattern-process mechanism.

We see feedbacks between pattern and process at multiple scales as the explanation. When new tree patches form or existing patches expand, localized pattern-process interactions are established across the landscape. Smith et al. (2003) explained how the spatial pattern of trees determines the distribution of environmental resources and stresses. The pattern increases biotic and abiotic environmental heterogeneity; resource-rich sites ameliorate the harsh alpine conditions and facilitate tree establishment and reduce mortality. These interactions cause fluctuations at small and medium scales at most times; trees affect their immediate neighborhood through relatively simple, although nonlinear effects. As the number of trees increases, large patches develop, the open space between them and between the patches and the contiguous forest becomes small, and negative feedback (i.e., cooler soil temperatures) reduces the effect of positive feedback. Occasionally, the interactions coherently create connectivity at the landscape scale in a synchronized coalescence of patches. When large patches merge into each other and/or into contiguous forest, a second-order phase transition (i.e., the transition is smooth rather than dramatic) between high and low fractal states is triggered to produce large changes across the landscape, which collapse the spatial variability of the environment (through feedbacks, not through exogenous forces) and extend connectivity of trees across the landscape.

These endogenous fractal dynamics can be explained in three hierarchical scales. At the local scale, interaction between pattern and process in individual tree establishment and mortality drive the dynamics. At the landscape scale, treeline advance exhibits a fractal dynamic characterizing spatial and temporal fractal scaling properties. Between them is a middle scale of patch dynamics, best captured by the inverse cascade model (Turcotte et al. 1999) that connects the local and global scales through the growth and coalescence of tree patches. Using a forest fire CA (a percolation model in which sites are removed by spreading fires), Turcotte et al. (1999) introduced the inverse cascade model, in which trees coalesced in patches to form a fractal landscape. The inverse cascade builds clusters of trees that are eventually destroyed by coalescence. The result is a 1/f-type power-law distribution of clusters. The processes provide a better explanation of the dynamics for percolation models that exhibit self-organized criticality, and the criticality is not constrained to a small region. These conclusions might apply to other cases where endogenous processes have been used to explain non-random patterns of vegetation (e.g., Watts 1947, Billings 1969, Valentin et al. 1999, Rietkerk et al. 2002).

That a significant linear correlation between landscape pattern and process emerges from dispersed, nonlinear, localized interactions may explain why many seemingly linear relations are found in a complex world with so many nonlinear processes. Perhaps linear correlations at a large scale do not necessarily indicate linearity in ecosystems, but instead indicate an emergent property as a result of collective nonlinear interactions at smaller scales as suggested by Levin (1992, 1999). Thus, a limited predictive power can emerge in a spatially extended nonlinear dynamic system through cross scale self-organization.

2.5.2 Implications for Ecotones as Indicators of Climatic Change

Our results show that a variety of spatial patterns and advance rates are generated without variable external forcing. The exogenous forces of continued climatic variability and underlying topographic and soil variability would complicate the endogenous dynamics. By focusing on the latter, we are able to examine the emergent properties that theoretically should be common to ecotones. On one hand, this suggests that a relatively large change in ecotone position at one period does not necessarily indicate a correspondingly large climatic change. An ecotone may be far from equilibrium, and its change (or lack thereof; cf. Butler et al. 1994, Klasner and Fagre 2002) at any one time may only exhibit the nonlinearity in its advance driven by endogenous dynamics; as suggested by Payette et al. (1989) for Arctic treeline, the spatial pattern when climate begins to change may affect how an ecotone will respond. So, the conventional monitoring measures based on advance rates (e.g., Hughes 2000, Walther et al. 2002) are questionable indicators in active ecotones without careful examination. On the other hand, sudden changes in an ecotones temporal and spatial fractal scaling properties may indicate response to abnormal external forcing. In theory, scaling properties, such as a power law slope, might be considered as potential indicators of responses to climatic change, but we still must acknowledge that topographic and climatic variability may overwhelm any such signal at some ecotones.

CHAPTER 3

GEOMORPHOLOGICAL LIMITS TO SELF-ORGANIZATION OF ALPINE FOREST-TUNDRA ECOTONE VEGETATION

3.1 Introduction

The interactions of geomorphology and ecology are keen in mountain environments because the climatic gradients that often control patterns of vegetation, while spatially compressed, may be superseded by the even greater spatial heterogeneity of landforms and the higher energy of geomorphic processes. One ecological pattern that has traditionally been associated strongly with a temperature gradient is the alpine forest-tundra ecotone (ATE) (Holtmeier 2003). This transition zone from contiguous forest cover to open alpine tundra is the elevational limit to the growth of tree forms and tree species and encompasses the range from upright trees to small patches of prostrate krummholz. While temperature is certainly important (e.g., Bunn et al. 2005), soil moisture has been shown also to be important at least locally in determining this spatial limit (Cairns and Malanson 1998, Lloyd and Graumlich 1997). Thus, it has been hypothesized that the ATE might be a sensitive indicator of climate change if the limit is tightly coupled to climate variables (di Castri et al. 1988, Kupfer and Cairns 1996). Holtmeier (2005) cited topography as a determinant of this coupling, and, as with other potential responses to climate change (cf. Malanson 1993), the soil and geomorphic surface must also be amenable for the growth of the new plants if a change is to occur.

At small spatial scales, such as 10^{-1} meters, in which small vegetation can have dominant presence, alpine vegetation such as tundra has an impact on soil texture and geomorphic features (e.g., Haugland 2006) that would create a feedback loop. The existence of vegetation changes the energy and water balance at those micro sites, which modifies the freezing and thawing cycles and micro-scale weathering processes. At a larger spatial scale corresponding to alpine trees, however, the influence of vegetation on geomorphic features takes a much longer time to become significant. In this study, alpine trees are the primary objects and the influence on geomorphic features becomes hard to model in this case, given the temporal scale of the advance of treeline.

While feedbacks between the vegetation and landforms certainly exist in this environment, our focus is on the complexity engendered by feedbacks within the vegetation. Endogenous factors are likely to be important in ecosystems (Jonzen et al., 2002) as in other systems with memory (Sornette and Helmstetter 2003). Sprugel (1976) described the interaction of endogenous and exogenous factors in fir waves, which have been suggested as an interaction for ATEs (Malanson 1997). Conversely, the Arctic tree-tundra boundary seems to be a single state system that converges to a single position and pattern at continental scale for a given climate (Levis et al. 1999).

Self organization of patterns of vegetation and geomorphology is a developing theme in environmental science (e.g., Phillips 2001, 2006, Stallins 2006). Such linkages have been proposed for systems as diverse as dune complexes on barrier island (Stallins and Parker 2003, Stallins 2006), ridge and slough patterns in the Everglades (Wu et al., 2006), boreal peatlands (Hilbert et al., 2000, Nungesser 2003), and arid zone shrublands (Rietkerk et al., 2002). In all cases the spur to this theme is structured spatial patterns (e.g., Ludwig et al. 1999, Stallins 2001).

At ATEs we expect that geomorphic pattern will affect local scale ecological processes, but that ecological feedback, which allows local processes to extend across patch and landscape scales, will dominate the dynamics. First, geomorphic processes create heterogeneity at the scale of seedling establishment. Because seedling establishment is the fundamental process of an advancing ATE, this scale of heterogeneity could alter the rates and spatial patterns in an ecotone. Second, however, static simulations indicate that spatial patterns at landscape scale are qualitatively different from the patterns of underlying geomorphology (Walsh et al., 2003). We extend a simple cellular automaton simulation of an advancing ATE to incorporate geomorphology. The addition of geomorphology allows us to examine how endogenous self-organized dynamics are changed by the exogenous template of – as viewed here – underlying geomorphology.

We hypothesize that self-organization will be maintained qualitatively up to, but not beyond, a threshold in geomorphic structure. We examine the hypothesis that feedbacks create patterns of vegetation that do not correspond to the pattern of geomorphology. We go beyond this hypothesis to examine how geomorphology can affect dynamics beyond the range of what we observe.

3.2 Background

ATEs provide a good model system for examining the effects of nonlinearity in dynamics caused by positive feedback (Malanson 1999). Feedbacks have been hypothesized to be a central component of treelines in general (Wilson and Agnew 1992) and ATEs in particular (Alftine et al., 2003, Holtmeier 2003, Smith et al., 2003, Alftine and Malanson 2004). Even skeptics find that positive feedbacks must be examined (Wiegand et al., 2006). The essential positive feedback is that the presence of trees, dwarf trees, or krummholz changes the nearby environment so that it is more hospitable for the establishment and growth of tree-species (Callaway et al., 2002). The factors affected are primarily climatological and hydrological: tree canopies have lower albedo and higher temperatures, and they reduce wind, slow transpiration, and accumulate more snow. Thus, ATEs with different canopies might respond differently to climatic change. The positive feedbacks at the ATE are essentially spatial: pattern at the ATE is often related to the interaction of vegetation, wind, and snow (e.g., Marr 1977, Daly and Shankman 1985, Holtmeier and Broll 1992, Hattenschwiler and Smith 1999, Hiemstra et al., 2002, Germino et al., 2002, Smith et al., 2003). Moreover, countervailing negative feedbacks exist because too much snow can shorten the growing season (e.g., Billings 1969, Rochefort and Peterson, 1996) and the shade from canopies and will reduce soil temperatures, which certainly reduces the tree development of trees (e.g., Korner 1998, Hoch and Korner 2003, Korner and Paulsen 2004).

We include the positive and negative feedbacks in a simple cellular automaton with two states: tree and tundra. Zeng and Malanson (2006) assumed a bell-shaped positive feedback to the probability of conversion of tundra to tree that peaked when half of the neighboring cells is occupied by trees. This form captured the effects of positive feedback in a nonlinear form where negative feedback would arise with increase of nearby trees and cancel out the positive feedback when a tundra cell was completely surrounded by tree cells. This simulation produced a wide range of patterns, as seen at ATEs and fractal temporal fluctuations. They developed a narrative explanation that individual establishment events lead to an acceleration of advance as positive feedback propagates across the landscape to affect a wider number of possible establishment sites, but that this change leads to a coalescence of patches that in turn decreases the probable sites for the establishment of trees and slows the potential advance of trees. They concluded that the dynamics of ATE landscapes are self-organizing wherein linear relations between spatial pattern and the rate of advance emerge at a landscape scale from nonlinear interactions at a local scale.

These simulations were implemented on a plane that varied in only one dimension, representing a completely homogeneous slope that varies only in elevation. First, we know that such a representation is only useful for trying to understand some of treeline dynamics in the abstract; Second, we can see how topography, soils, and geomorphic processes interact with patterns of vegetation in ATEs. We want to explore how still simple representations affect this type of simulation and what we can additionally learn about the potential dynamics of ATEs.

Geology, topography, and soils will make a homogeneous plane heterogeneous by altering the substrate on which seeds must land and penetrate during germination and in altering the soils into which the plants must root and from which they garner nutrients and water (cf. Kruckberg 2002). Several examples illustrate such heterogeneity.

First, a primary control of the ATE in some environments is the underlying geology. In the White Mountains of California, ancient bristlecone pines (*Pinus longaeva*) only grow on soils derived from Reed dolomite (Sharp and Glazner, 1997). Those soils are alkaline and deficient in a variety of nutrients, but the bristlecone pine is able to tolerate such conditions, whereas competing ATE plants, such as sagebrush, cannot. On soils on adjacent outcrops of Deep Spring and Campito formation sandstones, bristlecone seedlings are out-competed by those of sagebrush, and virtually no bristlecone pines grow there (Sharp and Glazner, 1997, p. 223). Modeling of ATE advance of bristlecone pines must, therefore, incorporate the pattern of the Reed dolomite geology base, or the effort is futile.

Second, the slope per se is a limit for the ATEs. In many areas trees grow tall and dense up to the base of cliffs and in individual crannies on the cliff face, but no ATE, as usually conceived, occurs (e.g., Holtmeier 2003). But in addition to this limitation, the amount of area that is within the potential climate range between the upper and lower elevations of the ATE depends on slope angle. In the Medicine Bow Mountains, Libby Flats is an extensive area with a low slope angle that falls within the ecotone, and here an extensive array of tree islands with three-dimensional shapes trained by wind and snow provides an exemplar of such interactions because of the areal extent of the landscape (Hiemstra et al. 2002). Elsewhere, ATEs are rather narrow where the slopes are steep and the spatial patterns and the effects on wind and snow are necessarily simplified. We do not consider slope aspect because we are seeking generality that would apply at any one aspect but not across a slope on which aspect changes. We also do not consider slope shape here.

Third, assuming that the underlying bedrock allows for the development of soils that can be utilized by tree seedlings, geomorphic processes come into play. Solifluction, for example, varies dramatically in spatial scale throughout the American west. Here, we focus on common stair-step like patterns that have stony flat treads and vegetated sloping risers. In locations such as the Colorado Front Range (Bowman and Seastedt, 2001), for example, individual solifluction risers may be meters high with corresponding treads that are several meters across (Figure 3.1). The same geomorphic processes in Glacier National Park (GNP), Montana, however, have created treads and risers that are measured in centimeters rather than meters (Figure 3.2) (Butler and Malanson, 1989; Walsh et al., 2003b; Butler et al., 2004; Resler et al., 2005). Large-scale relict stone polygons also characterize broad upland areas in the granitic Colorado Front Range (Caine, 2001), but are virtually absent in the sedimentary rocks and surficial deposits of the northern Rockies of GNP. The Colorado relict polygons present raised centers comprised primarily of finer-grained material that provide starkly different conditions for seedling establishment and successful growth than do the adjacent coarse, well-drained polygon “gutters”.

Figure 3.1. Representative solifluction treads and risers, with krummholz islands, on Niwot Ridge, Colorado Front Range.

Figure 3.2. Representative solifluction treads and risers, Glacier National Park, Montana.

Turf exfoliation is ‘‘a denudation process active in periglacial areas which destroys a continuous ground vegetation cover by removing the soil exposed along small terrace fronts’’ (Pérez, 1992, p. 82)., *i.e.* at the base of solifluction terrace risers (Butler *et al.*, 2004). From the perspective of a tree seedling, the flat surfaces of terrace treads provide harsh, dry, wind-swept environments susceptible to deep freezing and frost heaving. Such environments are inimical to seedling survival. Dense turf mats along riser fronts pose equally difficult problems from the perspective of penetration into the underlying soil. If, however, a seedling lands upon a site with a spatial scale of 10^{-1} meter where turf exfoliation has occurred (Figure 3.3), it may encounter a location where the exposed soil is less compacted and may be penetrated (Butler et al., 2004). The riser provides microclimatic protection from the harsh winds sweeping across the surface (*sensu* Resler et al., 2005). In such locations, tree seedlings have some potential for successful establishment and subsequent survival.

Figure 3.3. Seedling established at a site of turf exfoliation.

Fourth, the soil and substrate can be further modified as zoogeomorphic agents, such as gophers, create widespread burrow systems with corresponding spoil mounds at and above the ATE in many areas in the west (Butler, 1995), and in some cases may be the primary force of soil erosion in the ATE (Thorn, 1978; Armstrong et al., 2001; Seastedt, 2001). The effects of these surface disturbances on seedling establishment at or above the current ATE has not been sufficiently examined; on the one hand, pedoturbation by animals distributes fine-grained sediment across the surface in quantities sufficient for tree seedling establishment, but these sites, when actively occupied by gophers or other animals, may be disrupted sufficiently frequently so as to preclude seedling establishment because of the unstable substrate. The indurated soil in so-called “gopher eskers” may also be too dense for easy penetration and successful seedling establishment.

3.3 Rationale

We use a modified version of the cellular automaton (CA) simulation created by Zeng and Malanson (2006) as a starting point. To incorporate geomorphology as an exogenous template on which the ecological dynamics play out, we alter the underlying surface that determines the probability of a cell changing from tundra to tree or vice versa; this is termed ‘site-quality’ from the perspective of a tree. The original model took an essentially isotropic plane, based on field indicators (Malanson et al., 2002), and modified it to create a gradient in probability in one direction only as on a smooth slope where elevation was the only factor. Here, we add alternating horizontal strips of increased or decreased site-quality that might mimic an effect of solifluction treads and risers. Walsh et al. (2003) included a similar test in their report by adding stripes as columns to the static model discussed by Malanson et al. (2001). In the static situation the stripes had a small effect that could not be interpreted in terms of observed vegetation patterns except to note that the latter were more irregular than those simulated. We explore the effect on the dynamics of trees advancing into tundra. Additionally, we go beyond the width of solifluction patterns actually observed to investigate the changes in dynamics in hypothetical situations. If the ATE is considered as a complex ecological system, exogenous factors may have the potential to change its dynamics at certain critical points. In this research, we change the width of strips to see under what conditions geomorphologic features can make a significant impact on the complexity of the ATE. The results, though hypothetical in this case, can help us illustrate how exogenous geomorphologic forces interact with complex ecosystem dynamics and at what critical points they can break down the scaling properties in the dynamics of the ATEs.

3.4 Methods

3.4.1 Cellular automaton (CA)

We examined spatial and temporal structures using a CA model of the ATE. This CA model simulates the dynamics of an ATE advance. This model was run on a rectangular lattice which represents a mountain slope and consists of a number of cells. The cells change between two states, tundra and tree (the latter includes krummholz here), and these changes capture the dynamics of establishment and mortality. Seed rain and germination are subsumed in establishment. The grid of cells represents an ATE on a mountain slope with a linear environmental quality gradient. The CA model was run from bottom to top on a 100 × 1050 lattice representing a slope in the long dimension wherein the cells are nominally 1 meter square. All simulation runs started from a random distribution of trees in the lowest two rows, from which trees establish upslope. The initial condition of establishment probability is a slope from 0.05 to 0.0 over the bottom 300 rows of the lattice (nominally an ecotone of 300 m width). This 100 × 300 window starts from lower cells with a base probability of 0.05. For every iteration, an ecotone bottom line is determined. We assumed an initial condition with 85% trees in the bottom 5 rows of the lattice. Then, the 100 × 300 window is applied to this new ecotone bottom line to run the establishment and mortality processes. When the top of the window reaches the top of the lattice, the simulation stops and writes output. Cell states and tree ages are updated every iteration which represents one calendar year; this representation is based on rates observed in the Rocky Mountains (Hattenschwiler and Smith, 1999; Germino et al., 2002). The first 200 iterations are discarded to reduce the effects of initialization.

The additional (to the initial slope of probability above) probability of establishment (P_e) of a tree on a tundra cell is described as a function that captures the combination of local positive feedback or facilitation and local negative feedback:

$$Pe = \frac{\alpha}{1 + \beta e^{-r(x - x^2)}} \tag{1}$$

where x is the average size index of the local neighborhood which is the percentage of tree-occupied cells in a tree neighborhood; this average size index represents the density of the tree neighborhood. Positive feedback or facilitation exists when tree neighborhood is sparse and negative feedback appears when trees are densely located in the neighborhood; α is a coefficient to adjust the magnitude of establishment probability and, thus, the strength of positive and negative feedbacks in establishment process and takes 0.5; ß is a coefficient and its value is150; γ is a coefficient and takes 20; and the local neighborhood size is 5 × 5.

After establishment, the trees are subject to stress and damage each year, and the mortality is especially high when the trees are very young. The protection by immediate neighboring trees becomes an important factor for survival of young trees. In this simulation, tree mortality is a function of tree age and the number of trees in its immediate neighborhood. Trees usually take 5 to 10 years to firmly establish in alpine regions; if the tree age is less than or equal to 6 years; the probability of mortality (P_m) is:

$$P_m = \frac{1}{C\sqrt{n}}\left(1 - \frac{1}{1+\lambda e^{-z}}\right) \qquad (2)$$

where *Z* is the age of the tree, which reduces the mortality with growth of the tree; λ is a coefficient which adjusts the strength of the age effect; here its value is 50. If the tree age is greater than 6 years, mortality is 0.02; if no tree exists in the neighborhood, Pm is equal to 1. *C* is a parameter to adjust the strength of positive feedback in mortality, here it takes 3.0; *n* is the number of tree cells in the immediate neighborhood (3 × 3) (seedlings are protected only by the immediate neighboring trees);

To analyze the temporal evolution of the treeline landscape, especially the scaling property, a Fast Fourier Transform is applied to the simulated time series to calculate the power spectrum of the time series. For a function of *f(t)*, its Fourier transform is defined as

$$F(\omega) = \int_{-\infty}^{\infty} f(t)e^{-i\omega t}\ dt \qquad (3)$$

and the corresponding inverse Fourier transform is defined as

$$f(t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} F(\omega)e^{i\omega t}\ d\omega \qquad (4)$$

where *i* is the imaginary unity number; t is the time; ω is the range of angular frequencies.

When the Fourier transform is used for discrete series, the discrete Fourier transform (DFT) is defined as

$$F(k\Delta f) = \sum_{n=0}^{N-1} f(n\Delta t)e^{-i(2\omega k\,\Delta f)(n\Delta t)} \quad k = 0, 1, 2, \ldots, N\text{-}1 \qquad (5)$$

where *N* is the number of discrete samples taken; T is the total sampling time; Δ t is time increment between samples, Δ t = *T/N*. Here we used a Fast Fourier Transformation (FFT), which is a discrete Fourier Transformation and requires the number of sampling points be a power of 2, and we chose 512 iterations.

3.4.2 Analyses

Because the trends in resultant time series of spatial pattern of simulation are detected as the result of an enlarging ecotone along the slope, we applied Detrended Fluctuation Analysis (Peng et al, 1995) to the time series of spatial pattern. Detrended Fluctuation Analysis uses regression to subtract trends to obtain a time series for Fourier Analysis.

To analyze the temporal evolution of the ATE, especially the scaling property, a Fast Fourier Transform (FFT) was applied to each simulated time series to calculate its power spectrum. We used regression analysis of the log-normalized frequency and power spectrum obtained from FFT to examine the scaling properties:

$$Log(Y) = \alpha + \beta Log(X) \qquad (3)$$

where Y is the power spectrum of the time series; X is the frequency of the time series; α is the intercept of the regression line and ß is the coefficient or scaling exponent. Power spectrum and frequency refer to the system time series. The standard way of determining the scaling exponent of the *'1/f'* type noise is:

$$F(S) = S^{-\tau} \qquad (4)$$

F is the frequency of patch size and S is the patch size. τ is the scaling/critical exponent between them. If linear, it indicates that a power law relationship exists, and larger patches will persist longer in the landscape before being merged into continuous forest, which may indicate self-organization of trees at the landscape level. After these analyses, we looked for critical points or thresholds where the dynamics of ATE change. The *p*-values of regression coefficients, i.e. the power law slopes, are all less than 0.0001 as shown in the Appendix.

3.4.3 Experimental design

We designed a series of experiments to examine the effect of the underlying geomorphic landscape on ATE dynamics. Through these experiments, the spatial and temporal characteristics of ATE dynamics will be analyzed and the complexity associated with the geomorphological factors will be revealed.

We focus on examining the effect of a highly structured geomorphic landscape on the dynamics of ATE by constructing the alternate strips on the slope that represent the solifluction. This can be observed on mountain slopes in Glacier National Park. We change the width of the strips to simulate the ATE advance and compare the results with the original, normal landscape with no strip used as a baseline. The widths of strips on landscapes are 1, 5, 10, 15, 20, 25, 30, 35, 40, 45, and 50 cells. The simulations are run on landscapes with strips of various widths and the results are compared with the result from simulation without strips. We analyze all the temporal and spatial results to investigate how geomorphologic features influence the dynamics of ATE.

3.5 Results

We ran the simulations on a number of landscapes with different geomorphological features and examined the spatial dynamics of the advance of ATE and the relationship between the advance of ATE and underlying geomorphological features. The baseline simulation is the simulation on a normal landscape with gradually declining site quality without any strips. The advance dynamics of ATE are semi-validated by comparing them with the observed average new tree establishment, ecotone length, and spatial pattern in Glacier National Park, USA. By the term of “semi-validated”, we mean that we just compare with current ATE data, not historic time series, because there is no reliable long time series of tree advance available. The baseline run shows a progressive advance of ATE from low altitude, with relatively high site quality, to the top of the landscape, with very low site quality. The range or length of the ATE gradually increases with the ATE advancing into the higher elevation region while tree establishment probability in the ecotone fluctuates through time. The mean rate of tree establishment generated in the upper slope (from iteration 800 to 1200) is 2.6 per iteration/year and the mean length of the ecotone is 86 cells.

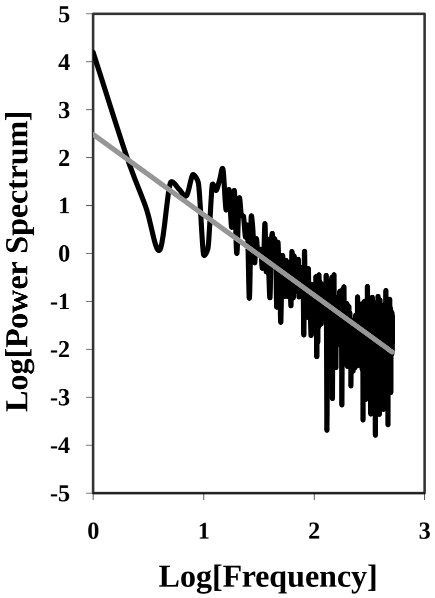
3.5.1 Dynamics of the ATE Advance

We have generated outputs at every iteration of the simulation for the number of new trees, landscape potential, ecotone length and ecotone position. The number of new trees and landscape potential are computed for the ecotone at each iteration. Landscape potential is the sum of the probability of tree establishment over the ecotone and can be considered similar to the energy in a physical system. Because trees are distributed over this potential surface using a random number generator, the number of new trees displays a strong influence of randomness which contaminates the advance dynamics and, thus, we decided not to use this variable for further analysis, and instead use the time series of landscape potential. The simulations show that geomorphological impact on the advance dynamics of the ATE is not significant until the width of strips reaches around 10 cells wide. The raw time series of landscape potential and its Fourier Analysis indicate the consistent power law distribution of the potential of tree establishment in the landscape dynamics with no strips, with 1-cell, and with strips of 5 cells wide (Figure 3.4 a, b, c) with scaling exponents of 1.68, 1.69, and 1.6, respectively. From the landscapes with the alteration of strips of 10 cells and greater, the impact of geomorphological features becomes significant as shown in the graph as a spike considerably higher than the nearby frequencies. At these widths the signals of geomorphological features enter the dynamics of the advance of the ATE (Figure 3.4 d, e, f, g, h, i) and become its dominate cycle in (Table 3.1). Advances of trees into tundra occurs in adjacent pairs of strips. When the trees fill one pair of strips of alternating site quality (normal sites and solifluction sites), a new round of tree establishment in another pair of such strips starts. This is different from the continuous tree establishment in a slope without strips. All the dominate cycles from

Fourier Analysis of the simulation results are consistently corresponding to the width of strips on the landscapes. For example, the simulation on landscape with strip width of 20 cells would generate a striped pattern of the treeline landscape with treelines of 20-cell width cells alternating with tundra of the same width, which is consistent with the dominant cycle of 39.38 which is close to 40, we obtained from Fourier Analysis.

Strip Width	10	15	20	25	30	35	40	45	50
Dominate Cycle	19.69	30.12	39.38	48.76	60.23	68.27	78.77	85.33	93.09

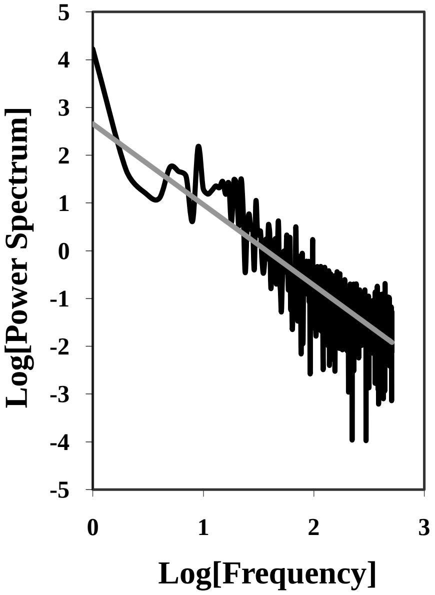
Table 3.1. Dominate Cycles in the Dynamics of Establishing the ATE on Landscapes with Different Strip Widths



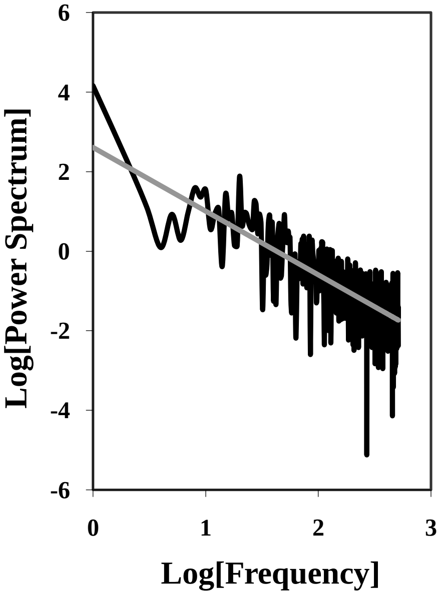
a

Figure 3.4 Power spectrum of tree advance dynamics on landscape (black line) with regression where there is a scaling property (gray line).

a. no strip.
b. 1-cell strip.
c. 5-cell strip.
d. 10-cell strip.
e. 15-cell strip.
f. 20-cell strip.
g. 25-cell strip.
h. 35-cell strip.
i. 45-cell strip.

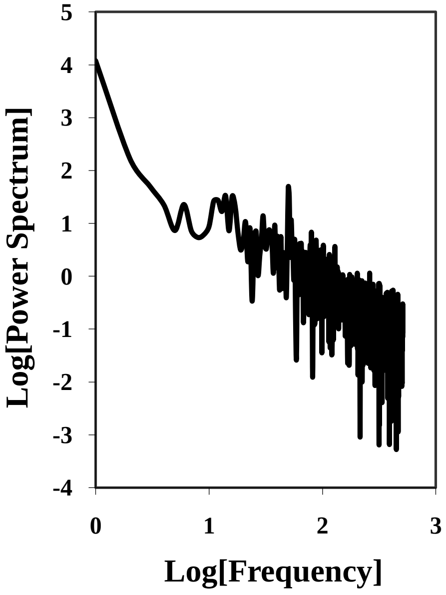


b

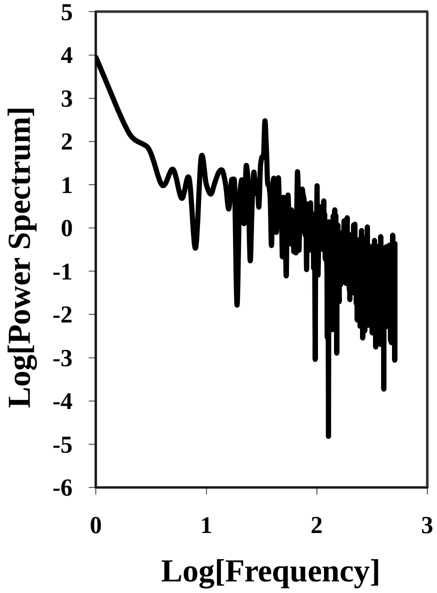


c

Figure 3.4 continued

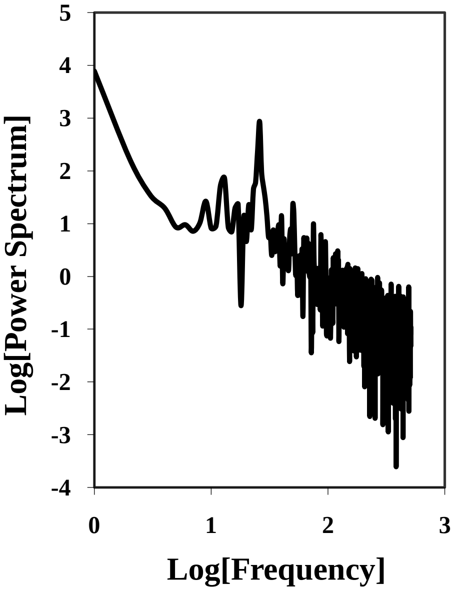


d

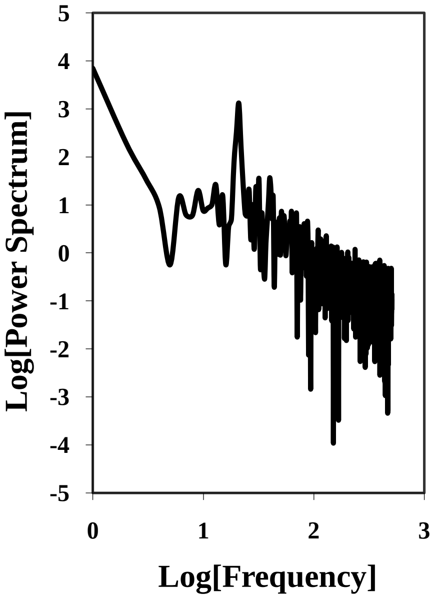


e

Figure 3.4 continued

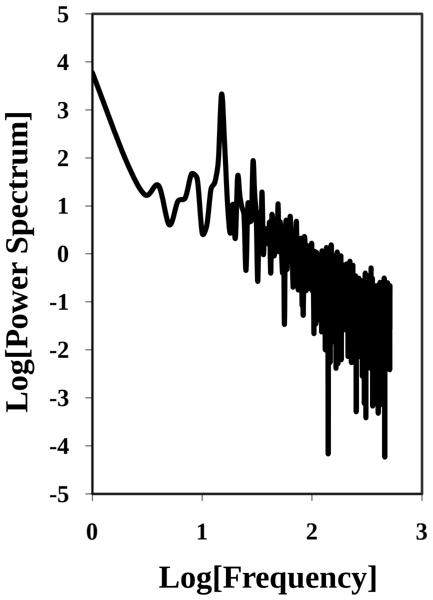


f

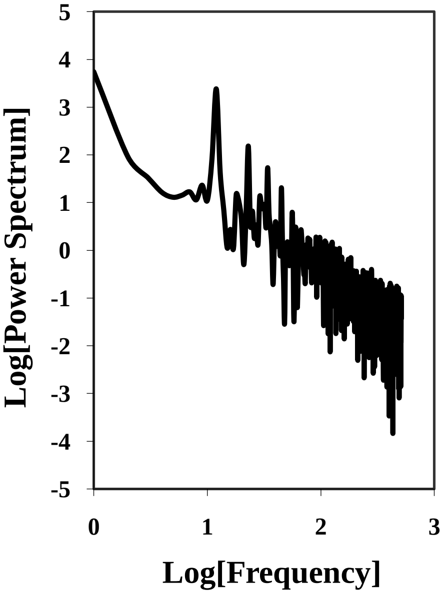


g

Figure 3.4 continued



h



i

Figure 3.4 continued

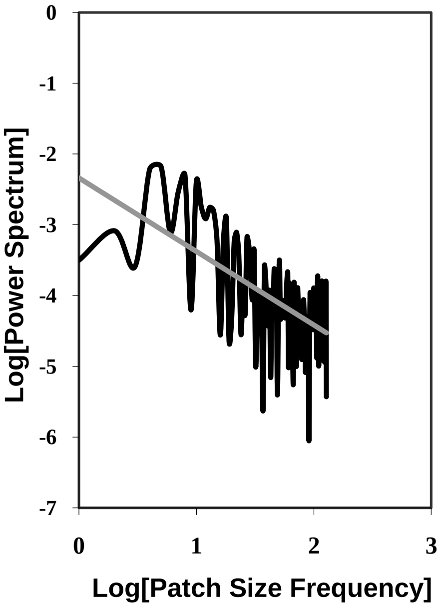
These results indicate that landscapes with strips of a few cells wide would not interfere with the nature of self-organized complexity in the dynamics of advancing the ATE. A threshold exists, however, in the relationship between the dynamics of establishing the ATE and the underlying geomorphic strips. Once the strip width reaches 10 cells wide, the scaling characteristic in the dynamics of establishing the ATE are lost and replaced by a dominate scale that is dictated by the geomorphology. The Figures 3.4a-k show that a clear scaling property exists in the log-log plot of tree establishment time series from the simulations on landscapes with no strips and 5-cell strips, while clear spikes, centered on frequencies of 1.71 and 1.53 respectively, exist in the power spectrums of time series on landscapes with 10-cell and 15-cell strips. This demonstrates that strips of 10-cell width have the potential to break down the scaling property of the dynamics of establishing the ATE and disturb the endogenous self-organized complexity.

3.5.2 Dynamics of spatial pattern

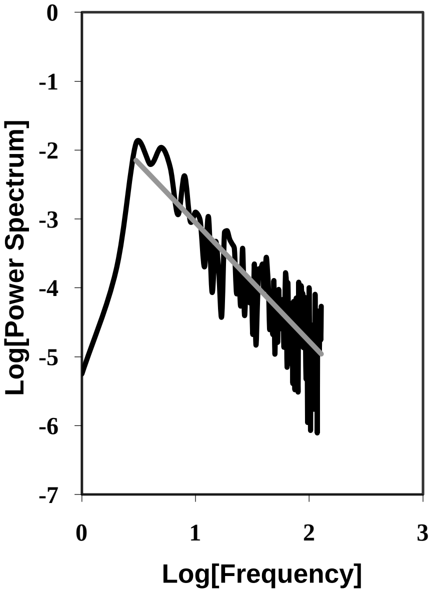
Spatially, we produced the time series of spatial patterns in the process of the advance of the ATE. We computed the spatial pattern for every iteration as the power law slope of patch sizes and analyzed the temporal change of the exponents of the power law slope. Research in ecology, physics, geomorphology, and other fields show that the power law distribution is a very useful description of spatial patterns in complex systems and landscapes. The analysis of its change through time can integrate the spatial and temporal aspects of complex systems and provide useful insights into landscape complexity.

As the ATE advances up the slope its ecotone length or range changes. Therefore its spatial patterns demonstrate a trend with time in their mean and variance. To analyze the temporal distribution of spatial pattern in terms of a power law distribution, we applied Detrended Fluctuation Analysis (Peng et al, 1995) before doing Fourier Analysis. The basic procedure in detrended analysis is to use regression models to detect the trend of the mean and variance and then subtract the trends from the raw time series. In addition, we also noted a power law distribution of the change in the spatial pattern of the ATE along the slope. This suggests another trend in the change of spatial pattern along the slope. It would be interesting to see how this change happens on different geomorphic landscapes or, in other words, if and how geomorphological features dictate these changes and if a critical point exists at which a phase transition which means a different landscape pattern, occurs in the spatial pattern. Therefore, we applied Fourier Analysis on different segments of the time series of the exponents of the power law distribution along the slope with different strip widths, and compared them.

The temporal change of the spatial pattern of the advance of the ATE on landscape with no strip does not show a clear scaling property. This might be because of the nature of the changing ecotone length in its advancing process. Close examination of every segment of the time series, however, reveals that the scaling property starts to appear around iteration 600 (400 plus 200 discarded transient iterations). The scaling property stretches from frequency 0.6 to more than 2.0 (Figure 3.5).



a

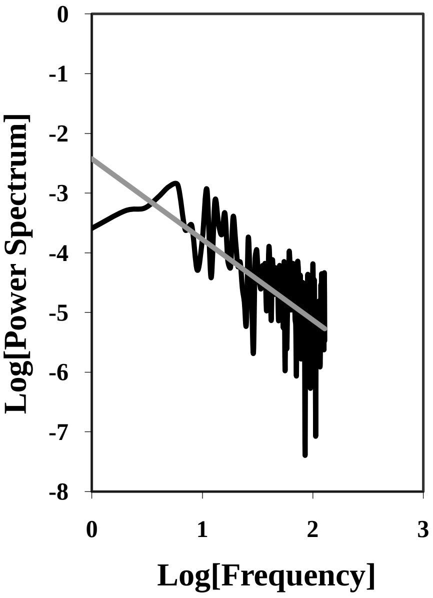


b

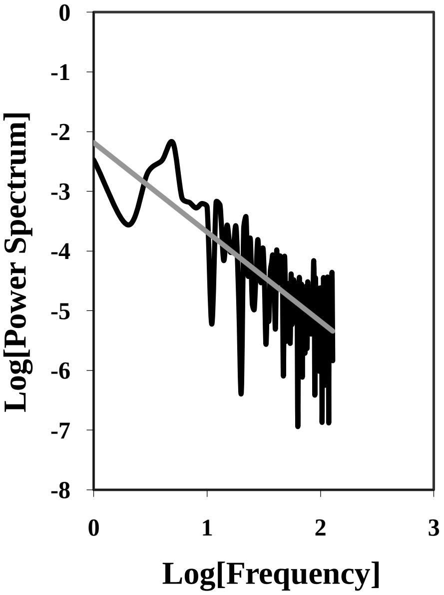
Figure 3.5 Power spectrum on segments of spatial pattern dynamics of landscape with no strips (black line) with regression where there is a scaling property (gray line).

a. 600 – 855 Iterations.
b. 1000-1255 Iterations

For the spatial pattern of landscapes with 5-cell strips, the scaling property is not as clear as that in a landscape with no strips. A few frequencies in the low part of the power spectrum deviate downward from the linear pattern. But the basic linear pattern in the log-log plot of power spectrum is still maintained without a frequency spike in the power spectrum (Figure 3.6). Geomorphological features, like strips, do have an impact on the scaling property of the spatial patterns on landscape, though the impact does not distort the basic shape of the scaling property.



a

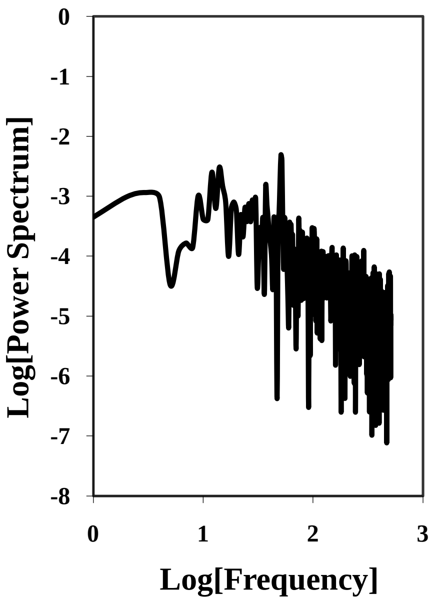


b

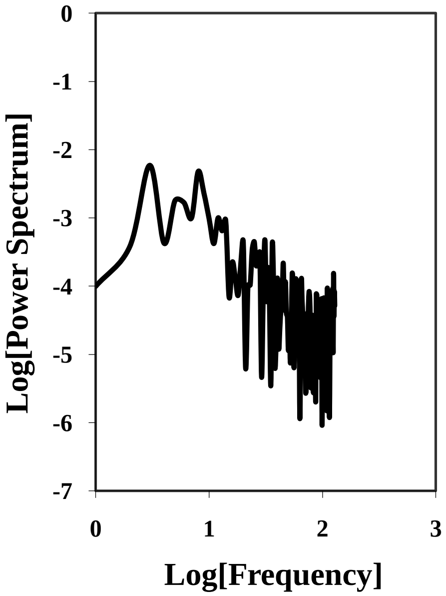
Figure 3.6 Power spectrum on segments of spatial pattern dynamics of landscape with strips of 5-cell width (black line) with regression where there is a scaling property (gray line).

a. 600 – 855 Iterations
b. 1000-1255 Iterations

In the case of temporal change of spatial pattern on a landscape with 10-cell strips, the scaling property can be maintained after iteration 900 (700 + 200 transients). Although we expected a spike or cycle of near 20 in this power spectrum in the overall spatial pattern dynamics, the results show that, After the first 256 iterations, the expected spike or cycle did not appear (Figure 3.7). For the Fourier analysis of almost the whole time series (N = 1024), however, a spike at a cycle of 10 does show up clearly. This indicates where the geomorphological impact on the dynamics of the ATE becomes significant.



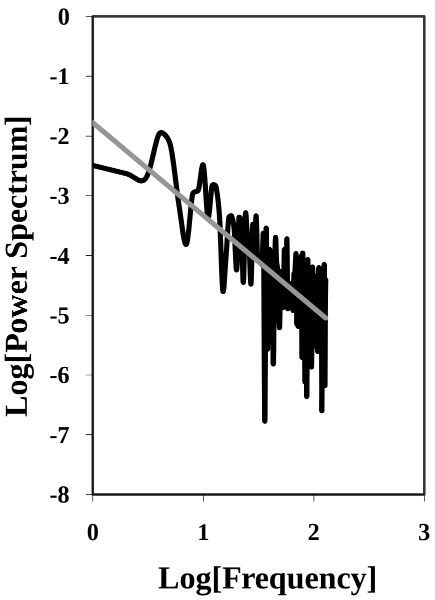
a



b

Figure 3.7 Power spectrum on segments of spatial pattern dynamics of landscape with strips of 10-cell width (black line) with regression where there is a scaling property (gray line).

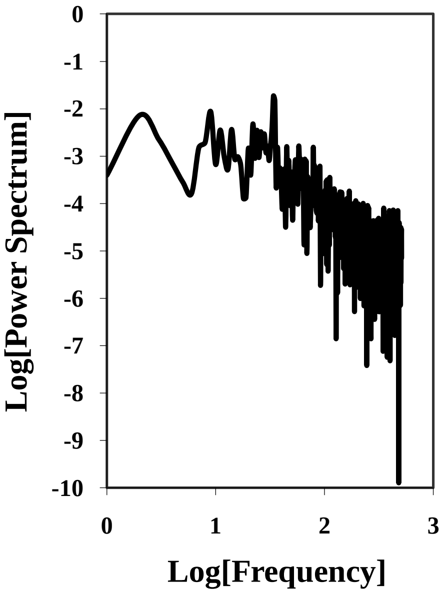
a. 200-1223 iterations
b. 600 – 855 Iterations
c. 900-1155 Iterations



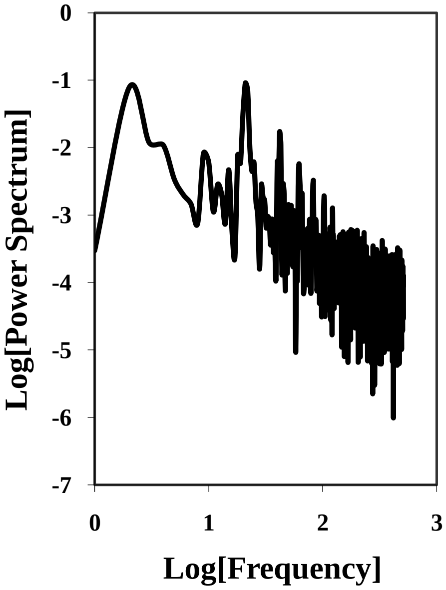
c

Figure 3.7 continued

In the case of landscapes with 15-, 20-, 25-, 30-, 35-, 40-, 45- and 50-cell strips, the spike of expected cycles of 30, 40, 50, 60, 70, 80, 90, and 100, respectively, show up in the power spectrum of the whole time series. (Figure 3.8). In these landscapes with longer strips, the signals of geomorphological features persistently appear in the power spectrum of the time series of spatial patterns. The 10-cell strip seems to appear as a threshold in the dynamics of tree advances and spatial patterns. This should not be considered as a coincidence when we consider the interactions between pattern and process in this model. This suggests a synchronous-like interactive nature of spatial pattern and process in a spatially complex system. We will continue to explore this coupling feature of this system in the following section.

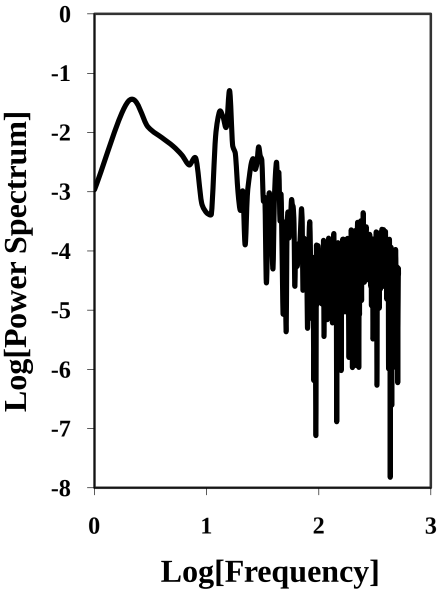


a

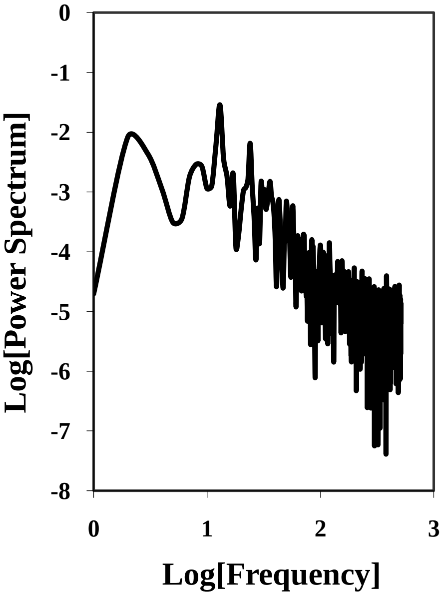


b

Figure 3.8 Power spectrum of spatial pattern dynamics of landscape with wider strips.
a.15-cell strip.
b. 25-cell strip.
c. 35-cell strip.
d. 45-cell strip.



c



d

Figure 3.8 continued

3.5.3 Coupling of the advance of the ATE with geomorphological features

To analyze how the advances of the ATE couple with geomorphological features and how spatial pattern and process interact, we conducted a correlation analysis of the dynamics of establishing trees and the evolution of the spatial patterns of the ATE. We computed the correlation between these two time series for every different strip width and found that correlation changes with strip width (Figure 3.9).

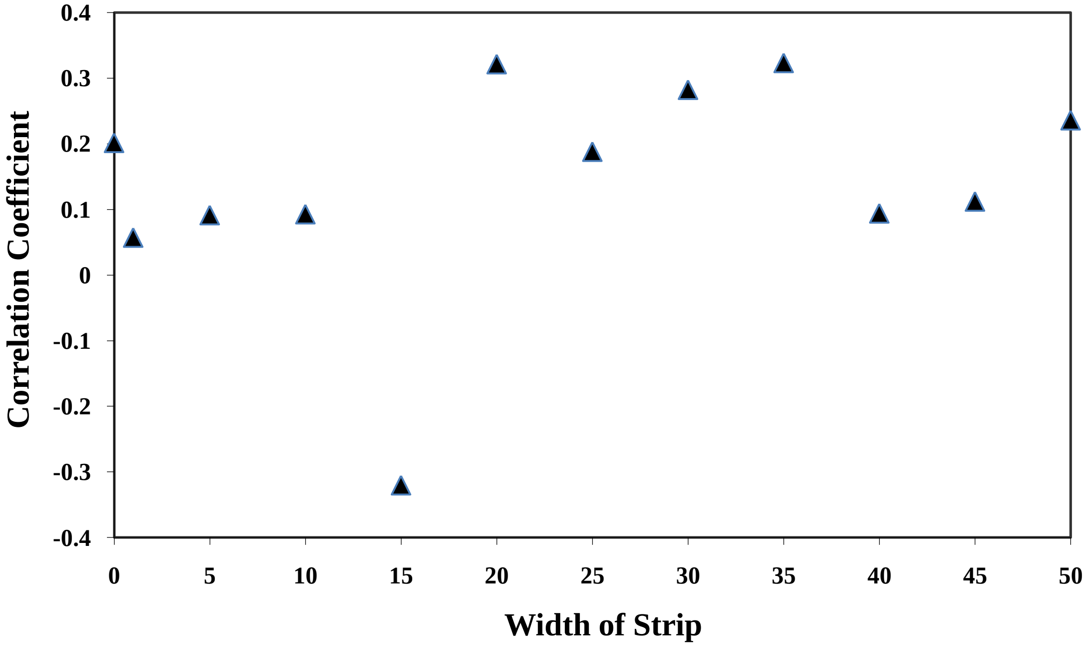


Figure 3.9 Correlation with change in strip width.

The correlations show a positive relationship between the establishment of trees and the exponent of the power law distribution (a spatial pattern metric), except for the correlation on the landscape with 15-cell wide strips. The higher exponents represent the more dispersed ATEs, so that the higher establishment of tree corresponds to higher dispersed distribution of tree patches in the ATE, which is consistent with the theory that more heterogeneous alpine tree patches provide more positive feedback and sites for the establishment of trees (Zeng and Malanson 2006). On the landscape without strips a positive correlation of 0.2013 ($p<0.001$) occurs. When we do a lagged correlation with spatial pattern five years ahead of the potential of tree establishment, the correlation coefficient improves to 0.2133. This suggests that the change in spatial pattern may lead the potential for tree establishment and facilitate it, which is consistent with the previous results (Zeng & Malanson, 2006). But in the case of 5-cell and 10-cell strips, this positive correlation deteriorates because of the interference of strips on the landscape. Then, the general positive relationship surprisingly breaks down at the 15-cell strips. The reason for this is still not understood. Another finding is that the correlation strengthens with the increase of strip width later or further upslope. One explanation for this is that existing strips of trees provide additional edges for tree establishment ahead of and behind the tree strips. In addition, a collapse of spatial pattern, i.e. the loss of small tree patches, happens somewhere along the slope once the strip width is larger than 15 cells wide and the location of collapse moves upslope with increase of strip width. (Figure 3.10). Figure 3.10 also shows the cyclic advance of treelines on a landscape with strip width of 30 cells and indicates the dominate impact of underlying strips on the landscape on treeline advance. Finally, the change of landscape potential representing the process of establishing trees usually leads to the change of spatial pattern before a collapse. This may occur because the dominant geomorphological influence becomes weaker and weaker on the upper slope where the site quality difference becomes less significant.

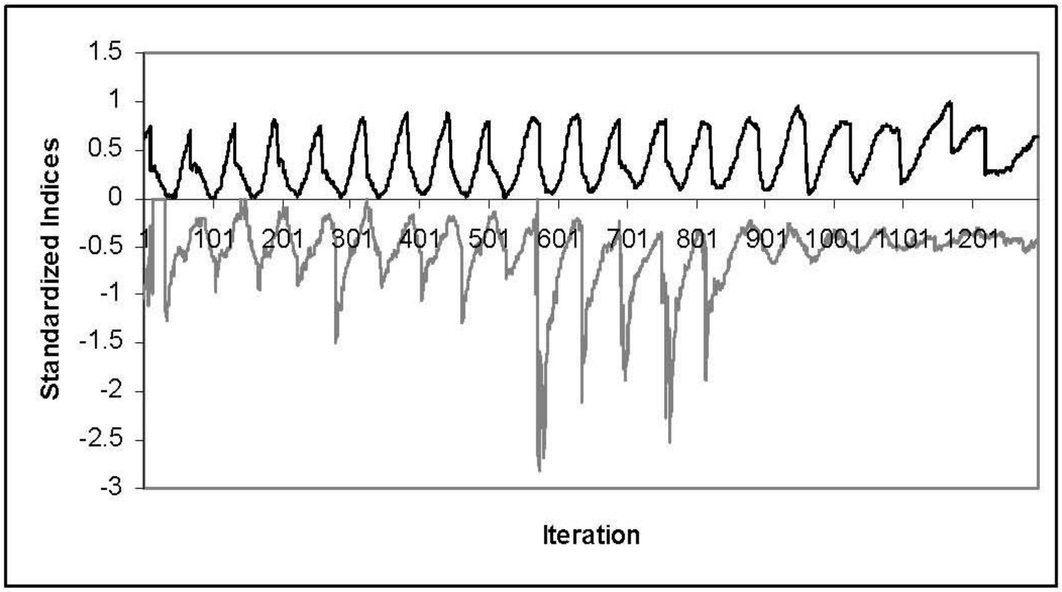


Figure 3.10 Temporal change of tree advance (black line) and spatial pattern (gray line) on landscape with strip width of 30 cells.

3.6 Conclusion

We have presented a portion of what could be examined with this model. Additional work could address other aspects of pattern variation that could be induced by geomorphology, especially the overall amount of area (or number of cells) within which pattern could develop as on slopes of different extent for a given range of elevation. This paper results in three observations that expand on our previous work:

1) The advance of the ATE shows robust dynamics and maintains its internal self-organized complexity on a landscape with geomorphological pattern below a threshold, i.e. 10 cell width in this case.
2) Once geomorphological patterning reaches a certain level, however, it does exert its influence on the dynamics of the ATE. Signals from the geomorphological features can gradually enter the dynamics of the ATE and, at some points, break down the scaling properties and change the spatial patterns of the vegetation significantly.
3) Geomorphological signals can also break down the interaction between spatial process and spatial pattern.

More specifically, the impact of geomorphological features starts to influence the dynamics of spatial pattern on the landscapes with 10-cell strips. Thus, the 10-cell width in strip should be regarded as a critical point which breaks down the scaling property of the pattern of the advance of the ATE. This threshold may be related to the fact that the size of the neighborhood within which we are modeling feedback is 5X5. Second, the impact of geomorphic pattern on the dynamics of spatial patterns of the ATE becomes longer with the increase of the width of strips. In other words, geomorphic impact shifts to the upper slope with the increasing strip width. Finally, starting from 30-cell strips, the geomorphic impact dominates the dynamics of spatial patterns and becomes the dominate cycle. In general, this disruption of vegetation self-organization is what we would expect as we increase the strength of an exogenous signal in any system. Here, we see that the strength needed in terms of spatial geomorphological pattern is beyond any that we observe on a given slope, but may not actually reach the scale of pattern that we see among slopes in areas with strong lithological control.

A tighter coupling of vegetation and geomorphology at the actual spatial scale of the small terraces observed here probably does occur above the treeline ecotone in alpine tundra. There, the small size of the individual plants matches the small size of the terraces and the temporal scales of the dynamics are probably similar as well (cf. Haugland and Beatty 2005). These relations could affect the initial spatial pattern of tree establishment – because turf exfoliation only occurs where a *Dryas*-armored terrace front occurs; the exfoliation exposes fines for the seedlings; but no exfoliation or exposure would occur unless the *Dryas* had been present "armoring" the front and then being eroded – but not long-term dynamics. We would expect the dynamics and complexity to be more similar to that observed for other environments where tighter scale coupling creates biogeomorphology as opposed to uncoupled dynamics (e.g., Valentin et al., 1999; Rietkerk et al., 2002). It is possible that geomorphic factors at the scale of trees could affect dynamics in response to climate change in the ribbon forest conditions reported by Butler et al. (2003), but the future temporal scale is as yet unknown. The time since initial occupation by trees since the Little Ice Age is too short for all but initial dynamics to be observed.

CHAPTER 4

MODELING IMPACTS OF CLIMATE CHANGE ON ALPINE TREELINE DYNAMICS

4.1 Introduction

Climate change has been suggested to have significant impacts on mountain ecosystems, especially those in the high mountain regions (Diaz et al., 2003). The impacts include changes in mean temperature, length of growing season, snow depth, fire regimes, and frost duration (Beniston, 2003). Studies show that climate change may be more rapid than the migration capacity of mountain forests (Beniston, 2003). Alpine treelines, as a unique ecological system which exist in the boundary zone between tundra and subalpine tree communities, may be exceptionally sensitive to climate change, because climate is one of the most important factors in maintaining a limit for trees (Korner, 1998; Holtmeier, 2003, 2009; Kupfer and Cairns, 1996; Malanson, 2001; Malanson et al., 2007). The suggested impacts of climate warming include significant shift of alpine treelines and change in their advance rate and spatial patterns. If this rationale is correct, change in their advance rate and spatial patterns should correlate with changes in climate factors such as temperature and precipitation.

Investigation of the responses of vegetation to climate change is an active research area. However, the studies of climate change impact on alpine treelines have mixed or conflicting results. Alpine treeline positions may not be sensitive to climate change (Korner, 1998) or respond with a long lag time (Davis, 1989). The time lag of response may depend on the relationship between strength of positive feedbacks and rate of climate change (Malanson, 2001). Tree-ring chronological studies in Alaskan treelines shows positive and negative tree growth responses to climate warming (Wilmking et al, 2004). Camarero and Gutierrez (2004) found a negative relationship between alpine treeline advance and March temperature variability in the Pyrenees. Bunn et al. (2005) reported that the response of tree rings to the interaction of temperature and precipitation depended on topographic setting. A simulation study of the impact of climate change on tropical alpine treeline ecotones suggests that the rate and extent of tropical alpine treelines are limited or slowed by internal positive feedbacks (Bader et al, 2008), which means the response of tropical alpine treelines to climate change may not be as discernable as expected.

Central to the problem is complexity. The responses of vegetation, including alpine treelines, can be complex, since ecosystems are complex systems themselves, as our previous research indicates (Malanson, 1999; 2001; Zeng and Malanson, 2006; Zeng et al, 2007). The major factor that complicates the responses is the nonlinear interactions or positive feedbacks among individual plants. In the case of alpine treelines, nonlinearity is exhibited in the processes of tree establishment and mortality and the interaction between trees and between each tree and its immediate abiotic environment, such as factors of microclimate, geomorphology, soil and hydrology. For example, the relationship between krummholz radial growth and temperature variation is nonlinear and the same climate conditions that facilitate seedling establishment can also be unfavorable to tree redial growth (Daniels and Veblen, 2004). Positive feedbacks arise from structural protection from wind and intense radiation and from higher canopy temperatures due to lower albedo (Tranquillini 1979; Smith et al. 2003). The trapping of snow by larger plants is regarded as a key feedback (Hiemstra, et al, 2002; Smith et al. 2003; Alftine and Malanson 2004). The role of snow changes across ecotones, however, depending on the many factors such as the timing (i.e. spring or summer seasons) and snow depth (Hessl and Baker 1997; Callaway et al. 2002; Moir, et al, 1999) With patches of meadow in forest, more snow may inhibit seedling establishment (e.g., Billings 1969; Rochefort and Peterson 1996), while at more windswept sites snow held by vegetation may either provide an important source of water (Lloyd and Graumlich, 1997) or may increase nutrient availability by maintaining higher winter soil temperatures (Sturm et al. 2001). Therefore, it is possible that the internal mechanisms of ecosystems, e.g. alpine treelines, may complicate responses to climate change. Another complicating factor is that there seems to be a lack of consensus of what kind of climate factors should be considered to accurately represent climatic factors for alpine treelines in the models (Korner, 1998; Korner and Paulsen, 2004; Hoch and Korner, 2009). The role of climatic factors and representation of their impacts can also be complicated, since different combinations of climatic factors may have different impacts on alpine treelines. Though alpine treelines were suggested to be a potential indicator of climate change (Kupfer and Cairns, 1996), we still lack a fundamental understanding of how treeline vegetation responds to climate change.

In this research, we use a cellular automaton with positive feedbacks for an alpine treeline model to examine the impact of climate change on the self-organizing behaviors of alpine treeline econtones. Zeng and Malanson (2006) simulated endogenous processes on as simple a representation of an alpine treeline ecotone as possible, and Zeng et al. (2007) extended this model by adding exogenous spatial patterns as would be created by geomorphic proceses. Here we examine climate change as a temporal exogenous factor in this alpine treeline model. We use the same alpine treeline model with a modified mountain slope representing climate change. We represent climate change scenarios by modifying the site quality – from the perspective of establishment and growth probabilities – of a spatially smooth mountain slope because of the complicated roles of different climate factors and thus the difficulty in representing them. The basic scenarios considered are extended gradual change and short abrupt change under warming and cooling scenarios. We hypothesize that temporal and spatial scaling in alpine treeline dynamics will be break down to indicate the impact of climate change, which means the scaling property of treeline dynamics would not hold..

4.2 Method

The research methodology is based on the dynamic modeling of alpine treeline ecotones. Analyzing and modeling how landscape structures emerge, evolve, and transform is the key to our understanding of landscape dynamics. In the dynamic simulation model, alpine treeline ecotones are represented in a 2-dimensional grid. The grid consists of individual cells whose states represent tundra or trees. The state of a cell is determined by two essential local ecological processes: tree establishment and mortality. These two processes are modeled as nonlinear positive feedbacks and are also influenced by neighborhood spatial pattern. The change of state of cells across the whole landscape captures the dynamics. With the further addition of external forces to the landscape, i.e. the geomorphologic and climatic factors, exogenous impacts on alpine treeline dynamics can be included; here we change climate. Seed rain and germination are subsumed in establishment. The grid of cells represents a one-dimensional environmental gradient as a linear decrease (from 0.05 to 0.0) in establishment probability with elevation (rows of cells).

Feedbacks among neighboring trees modify establishment probability of tree in the focal cell positively and negatively. The positive feedback comes from facilitation among nearby trees through reduction of damaging environmental factors such as strong winter wind, cold night temperature, or improvement of environmental quality such as increasing water storage during the growing season and accumulating fallen foliage (Wilson and Agnew, 1992; Callaway, 1998; Callaway et al., 2002). The negative feedback can be created by a dense tree neighborhood where competition for environmental resources such as light, water, and nutrients dominates the interactions among trees or when shade lowers soil temperatures (e.g., Korner, 1998) but it is canceled out by positive feedback here. The additional (to the initial slope of probability above) probability of establishment of a tree on a tundra cell is described as a function that captures the combination of local positive feedback or facilitation and local negative feedback

$$P_e = \frac{\alpha}{1 + \beta e^{\left[-\gamma\left(x - x^2\right)\right]}} \qquad (1)$$

x is the average size index of the local neighborhood in number of cells in terms of percentage of average patch site; α is a coefficient to adjust the magnitude of establishment probability and thus the strength of positive and negative feedbacks in establishment process and takes 0.5; β is a coefficient and takes 150 here; γ is a coefficient and takes 20; and the local neighborhood size is 5×5.

Tree mortality is a function of tree age and the number of trees in its immediate neighborhood (22). If the tree age is less than or equal to 6 years,

$$P_m = \frac{1}{C\sqrt{n}}\left(1 - \frac{1}{1+\lambda e^{-z}}\right) \qquad (2)$$

λ is a coefficient; here it takes 50. If the tree age is greater than 6 years, mortality is 0.02; C is a parameter to adjust the strength of positive feedback in mortality, here it takes 3.0; n is the number of tree cells in the immediate neighborhood (3×3); z is the age of the tree.

To analyze the temporal evolution of the treeline landscape, especially the scaling property, a Fast Fourier Transform is applied to the simulated time series to calculate the power spectrum of the time series. For a function of *f(t)*, its Fourier transform is defined as

$$F(\omega) = \int_{-\infty}^{\infty} f(t)e^{-i\omega t}\ dt \qquad (3)$$

and the corresponding inverse Fourier transform is defined as

$$f(t) = \frac{1}{2\pi}\int_{-\infty}^{\infty} F(\omega)e^{i\omega t}\ d\omega \qquad (4)$$

where *i* is the imaginary unity number; t is the time; ω is the range of angular frequencies.

When the Fourier transform is used for discrete series, the discrete Fourier transform (DFT) is defined as

$$F(k\Delta f) = \sum_{n=0}^{N-1} f(n\Delta t)e^{-i(2\omega k\,\Delta f)(n\Delta t)} \quad k = 0, 1, 2, \ldots, N\text{-}1 \qquad (5)$$

where N is the number of discrete samples taken; T is the total sampling time; Δt is time increment between samples, $\Delta t = T/N$. Here we used a Fast Fourier Transformation (FFT), which is a discrete Fourier Transformation and requires the number of sampling points be a power of 2, and we chose 512 iterations.

After the FFT, we used regression analysis of the power spectrum obtained from the FFT to examine the scaling properties of alpine treeline movement and spatial patterns. A linear regression model is used to find the relationship of log-normalized frequency and the power spectrum of the system dynamics using the least-square principle.

$$Log(Y) = \alpha + \beta Log(X) \qquad (6)$$

where Y is the power spectrum of the time series; X is the frequency of the time series; α is the intercept of the regression line and ß is the coefficient or scaling exponent. Power spectrum and frequency refer to the system time series. The standard way of determining the scaling exponent of the '1/f' type noise is:

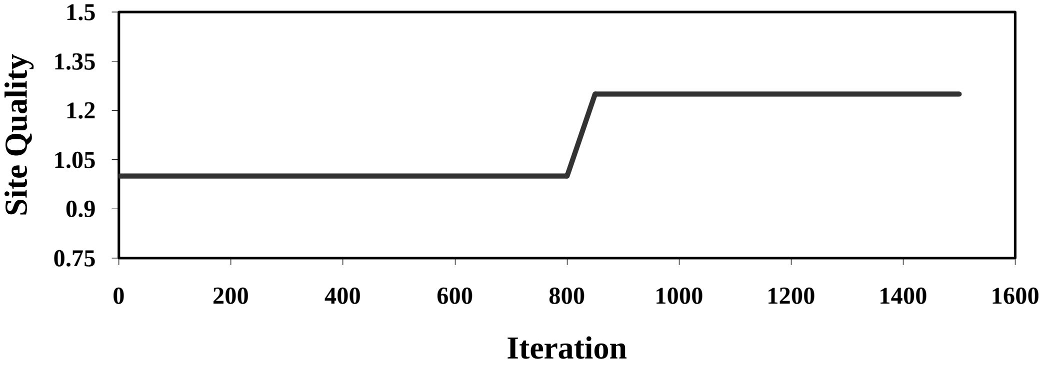
$$F(S) = S^{-\tau} \qquad (7)$$

F is the frequency of patch size and S is the patch size. τ is the scaling/critical exponent between them. If linear, it indicates that a power law relationship exists, and larger patches will persist longer in the landscape before being merged into continuous forest, which may indicate self-organization of trees at the landscape level. The p-values of regression coefficients, i.e. the power law slopes, are all less than 0.0001 as shown in the Appendix.

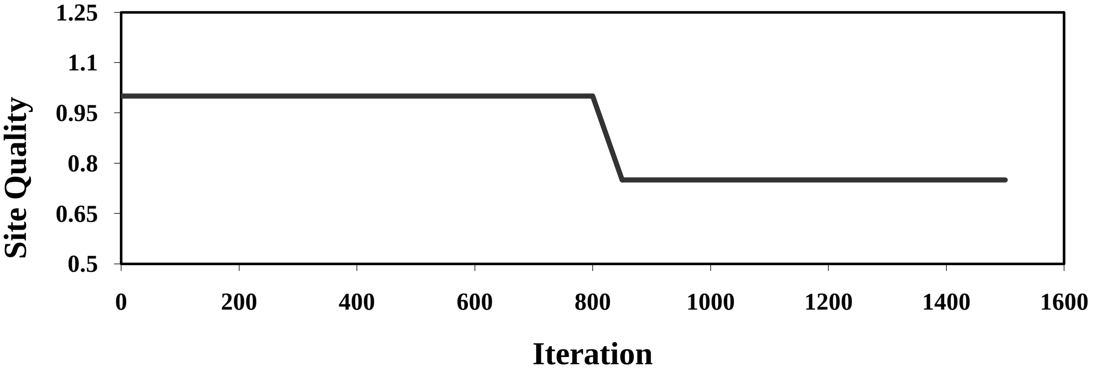
All simulation runs start from a randomized treeline at the low altitude and move upslope. Though this model is modified for each project, the fundamental structure and internal ecological processes are kept the same.

Because this research is focused on exploring spatial complexity in alpine treeline ecotones through testing hypotheses, it is a theoretical modeling practice. Though the observed spatial patterns of treeline patches are used for adjusting the parameters of this model to produce the results consistent with observations in Glacier National Park, MT, conventional calibration and validation are not carried out for this model. Actually, few models in current complexity research community use conventional calibrated and validated model and there is always a problem of this in modeling complexity (Epstein, 1999; Parker et al., 2003). In addition, there is still no historical data of alpine treeline time series of hundreds of years for calibration and validation at this site. So, this research is theory oriented and not fully calibrated and validated. This lack does not impede the theoretical exploration of alpine treeline phenomena.

The experimental design is based on a methodological framework of control and comparison. The first set of experiments serves as a control. In the control runs, climate change effect is disabled, and the simulation is run on an alpine slope as described in the methods section. The second set of experiments is climate amelioration which includes two types of scenarios: small, rapid climate amelioration over a short period and large, slow, but extended climate amelioration. The last set of experiments is climate deterioration which include two types of scenarios: small, rapid, short and large, slow, extended climate deterioration at the same rate. The rapid amelioration (Figure 4.1a) is represented by increasing the site quality by 25% in 50 years (from year 800 to year 849) within the 1,500 simulation years. Similarly, the rapid deterioration (Figure 4.1b) is represented by decreasing the site quality by 25% in 50 years (from year 800 to year 849) within the 1,500 simulation years. The extended amelioration (Figure 4.1c) is represented by increasing the site quality by a factor of 2 linearly over 400 years, starting from year 600, and the gradual deterioration (4. 1 d) is represented by dividing the site quality by 2, linearly, from years 600 to 1000.



a



b

Figure 4.1. Experiment Design.
a. small, rapid climate amelioration
b. small, rapid climate deterioration
c. large, gradual climate amelioration
d. large, gradual climate deterioration

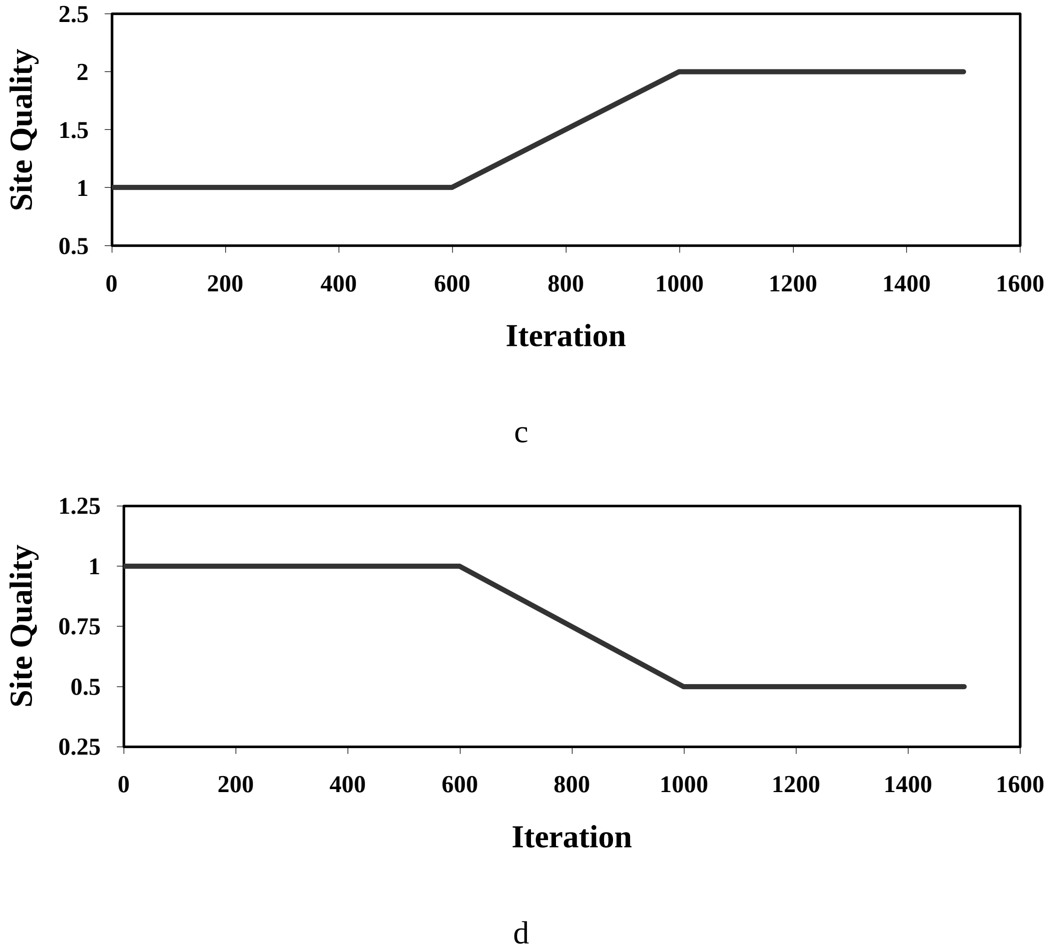


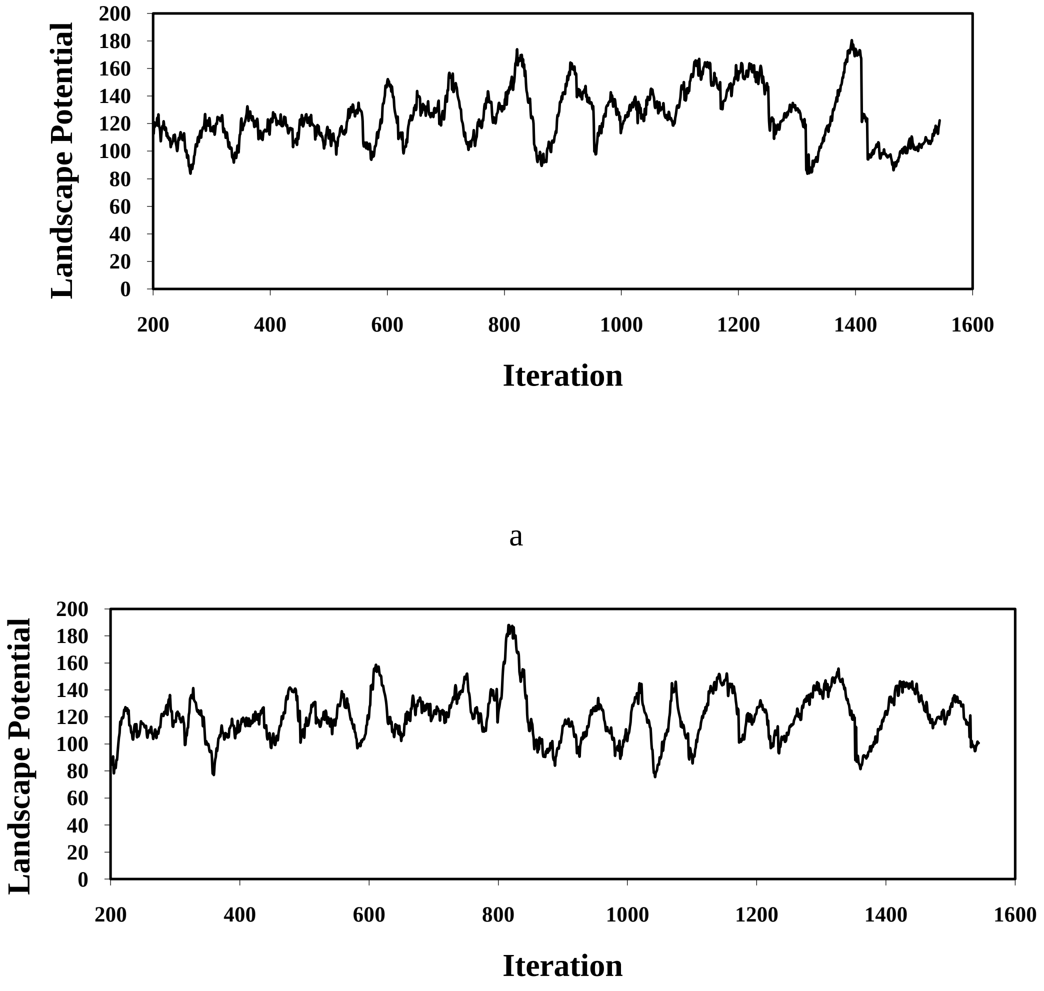
Figure 4.1 continued

The simulations run 1,500 years to simulate the impacts of climate change on alpine treelines. The simulation results shown and discussed below are average results of 20 runs of each set of experiments. Sensitivity tests on the starting points of climate change were also conducted by implementing the rapid or gradual climate change from other specific years that were identified with high and low fractal states of the spatial pattern of the ecotone, which are selected based on existing simulation results. During these tests, a fixed seed random generator was used in repeated runs to make sure the transition probabilities will be in the same sequence in the control and comparison groups.

In the simulation results we expect to see certain forms of breakdown of the scaling properties the dynamics of alpine treeline advance and some considerable deviation from the control group, i.e. the no climate change scenario.

4.3 Impacts of Rapid Climate Change on Alpine Treeline Advance

The simulation results of alpine treeline advance under the three scenarios, no climate change, rapid climate amelioration and rapid deterioration, are shown in Figure 4.2 a, b, c. These three results do not show any significant difference in terms of frequency and overall trend in the dynamics. Visual examination of net tree establishment under the three scenarios does not show any discernable trends: the treeline net rate of increase fluctuates near 120 trees per year. Furthermore, the general pattern of treeline advance before and after the rapid climate warming or cooling around year 800 does not change. Therefore, alpine treeline ecotones as simulated here may not show any discernable signal relevant to detecting a shift of the rate of advance forced by climate change,

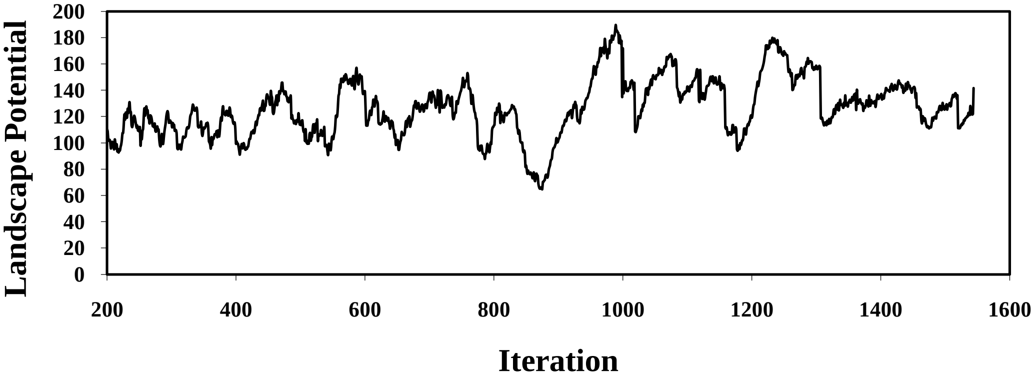


a

b

Figure 4.2. The results of alpine treeline advance dynamics under the three types of scenarios:

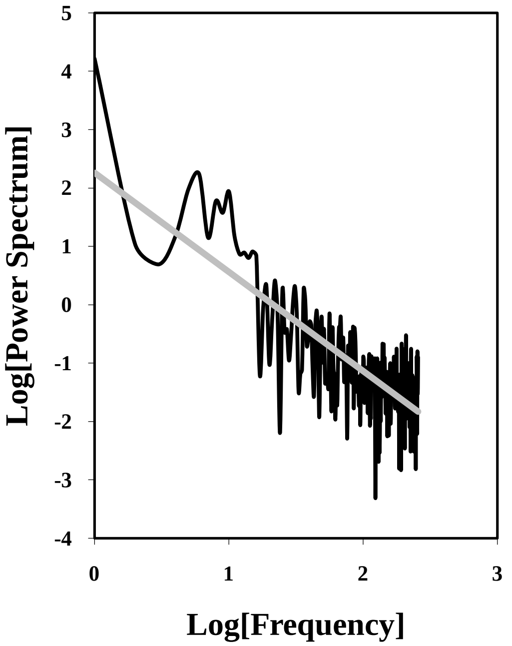
a. no climate change
b. rapid climate amelioration
c. rapid climate deterioration



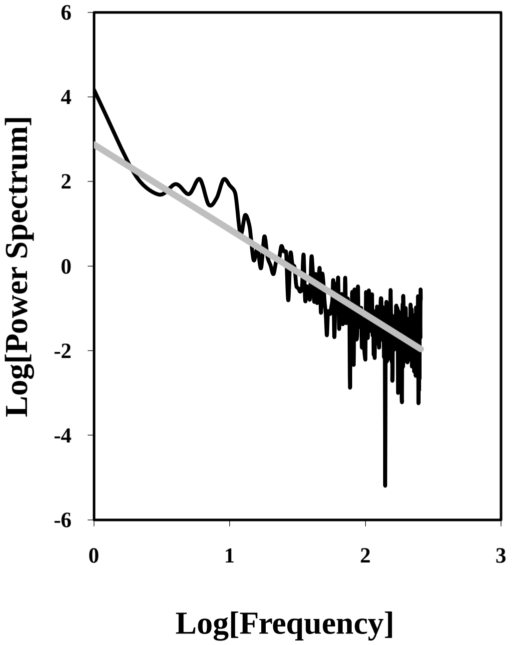
c

Figure 4.2 continued

Next, we examine the temporal and spatial scaling properties of alpine treeline advance dynamics in more detail to see whether there is any structural difference between the temporal and spatial scaling properties under no climate change scenario and rapid warming and cooling scenarios. In particular, we focus on examining whether there is a breakdown of temporal and spatial scaling properties under climate change scenarios, since we already know that there are consistent temporal and spatial scaling properties of alpine treeline dynamics under scenarios of no climate change, i.e. the endogenous dynamics.

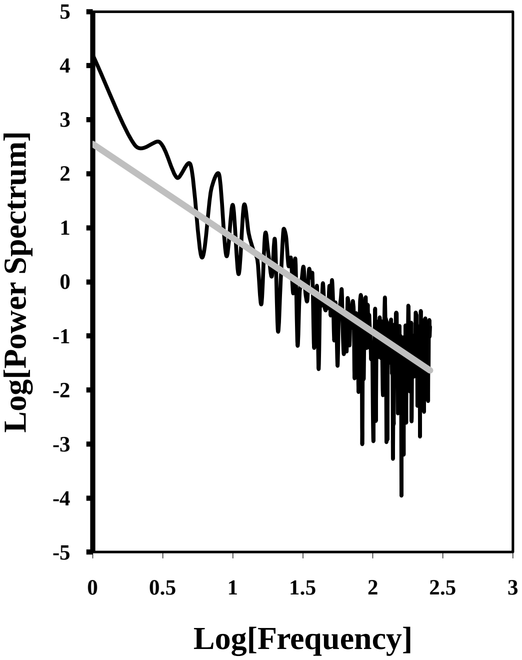


a



b

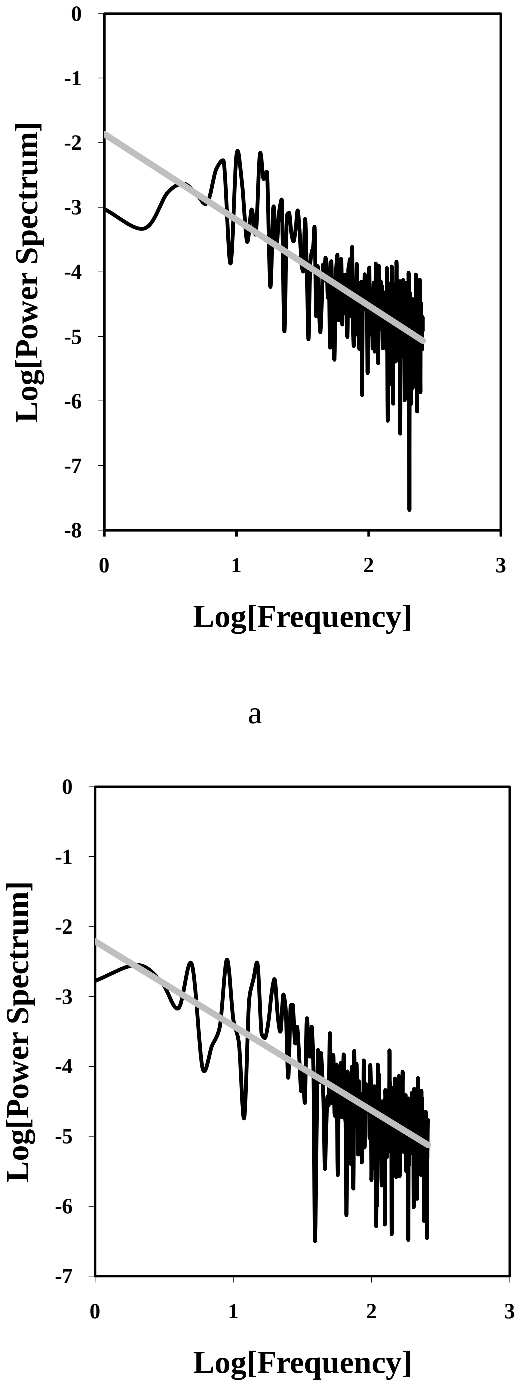
Figure 4.3. Temporal scaling property of alpine treeline dynamics under
a. no climate change
b. rapid climate amelioration
c. rapid climate deterioration



c

Figure 4.3 continued

We can see from Figure 4.3 a, b, and c that the scaling properties show consistent straight lines in the log-log power spectrum – frequency graphs for these three scenarios. With increase of the magnitude of treeline advance rates, the corresponding frequency decrease in a log-log fashion. There is no discernable deviation from the linear regression line and no break points from low to high frequency, although the specific scaling exponents may be slightly different. This indicates that there is breakdown of the scaling property of the temporal dynamics of alpine treeline advance under these three scenarios. The consistent linear relationship across all frequencies means that treelines moving into tundra display all scales of rates of advance.

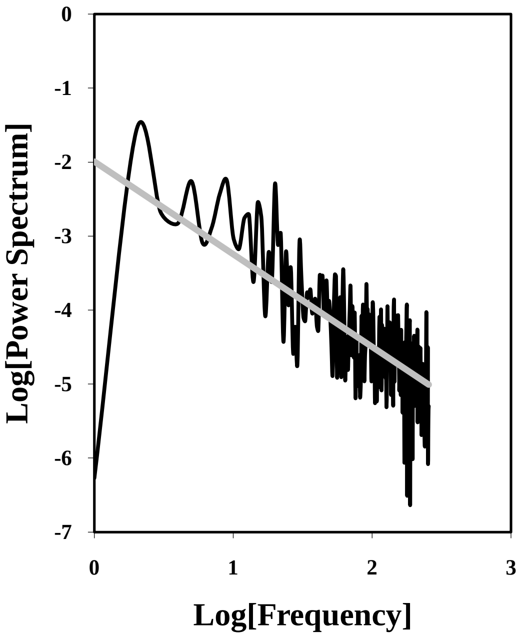


a

b

Figure 4.4. Spatial scaling property of alpine treeline dynamics under

a. no climate change
b. rapid climate amelioration
c. rapid climate deterioration



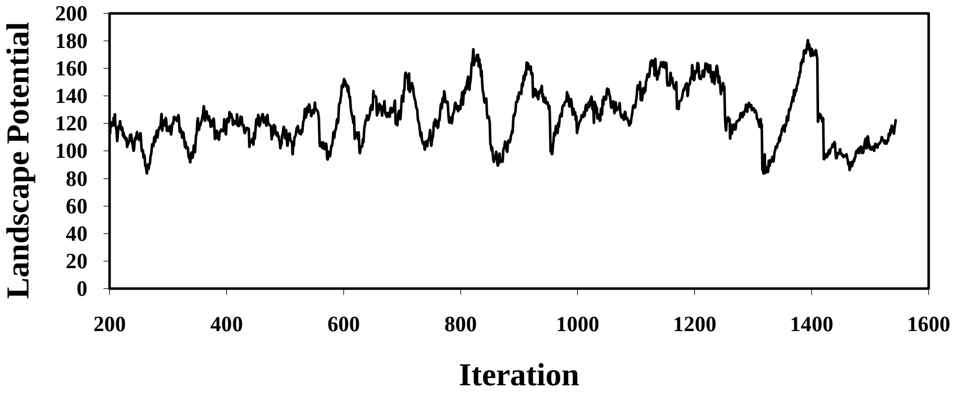
c

Figure 4.4 continued

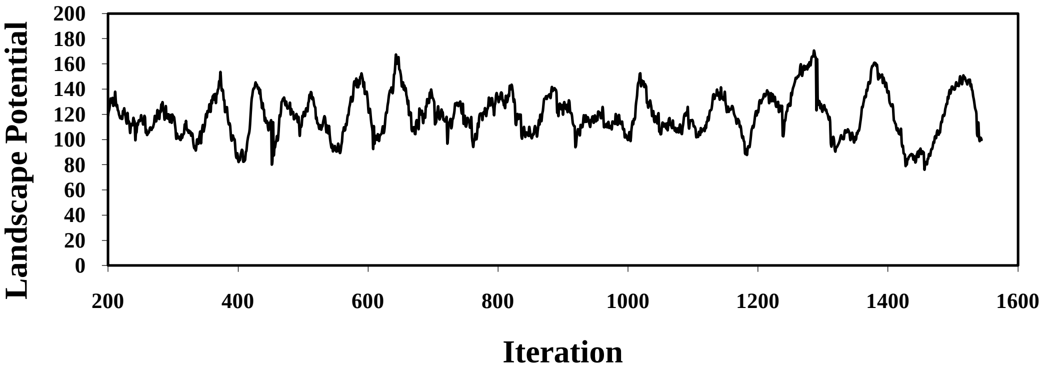
Comparing Figure 4.4 a, b, c, also shows a straight line across all frequencies in the three graphs. No obvious point in the power spectrum deviates considerably from its nearby frequencies and also there is no breakup of the straight line into two or more segments. This suggests that no breakdown of scaling property of the temporal dynamics of alpine treeline advance occurs. This result shows that the evolution of the spatial distribution or patterns of all tree patches or islands in the alpine treeline ecotones exhibits all scales of changes. These changes of spatial pattern under climate change scenarios still contain various high and low fractal states of alpine treeline ecotones and the self-organization of such temporal and spatial changes are still strong enough to maintain the same types of relationships seen in the scenario of no climate change.

4.4 Impacts of Gradual Climate Change on Alpine Treeline Advance

Figure 4.5 a, b, c show the alpine treeline advance dynamics under the another set of three types of scenarios: no climate change, gradual climate amelioration and deterioration. These three dynamics also do not demonstrate any discernable difference in terms of overall trend and distinct treeline advance stages. Essentially, these results from gradual climate change scenarios also are similar to that of rapid climate changes. They indicate that a slow but substantially longer and larger forcing by climate change also fails to change the inherent self-organizing dynamics of alpine treeline ecotones.



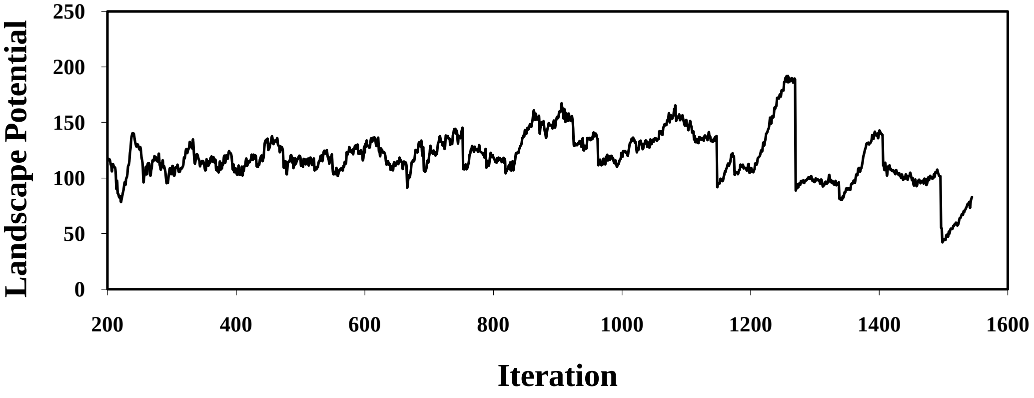
a



b

Figure 4.5. Alpine treeline advance dynamics under the another set of three types of scenarios:

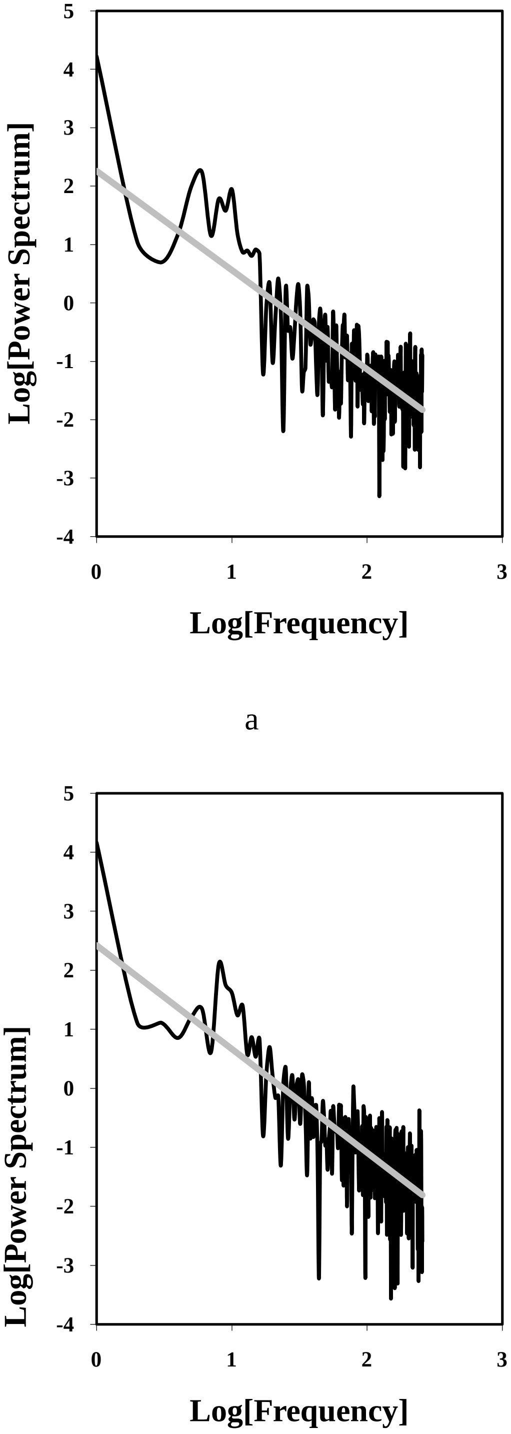
a. no climate change
b. gradual climate amelioration
c. gradual climate deterioration



c

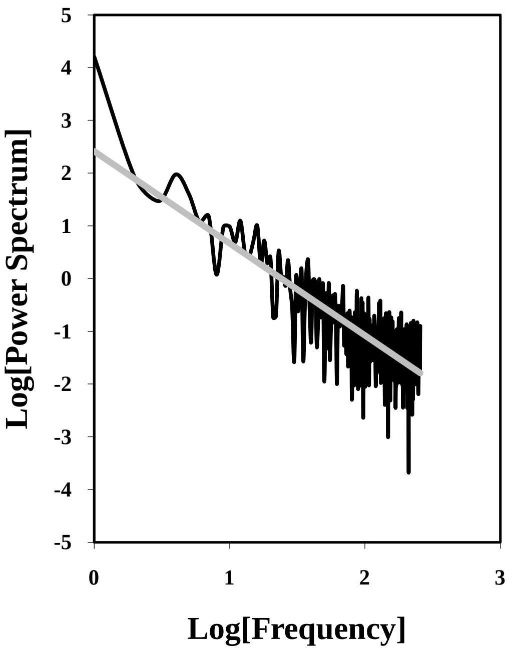
Figure 4.5 continued

Further examination of the scaling property of the temporal dynamics of alpine treeline advance was conducted and the results are shown in Figure 4.6a, b, c. The clear linear pattern in the log-log power spectrum-frequency graphs is maintained and all three scenarios show strong similarity. No breakdown of the scaling property can be discerned in the three types of simulations of alpine treeline dynamics.



b

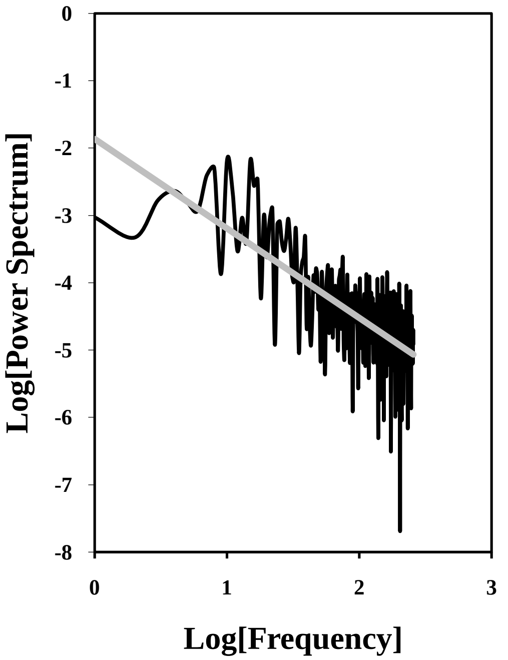
Figure 4.6. Scaling property of the temporal dynamics of alpine treeline advance:
a. no climate change
b. gradual climate amelioration
c. gradual climate deterioration



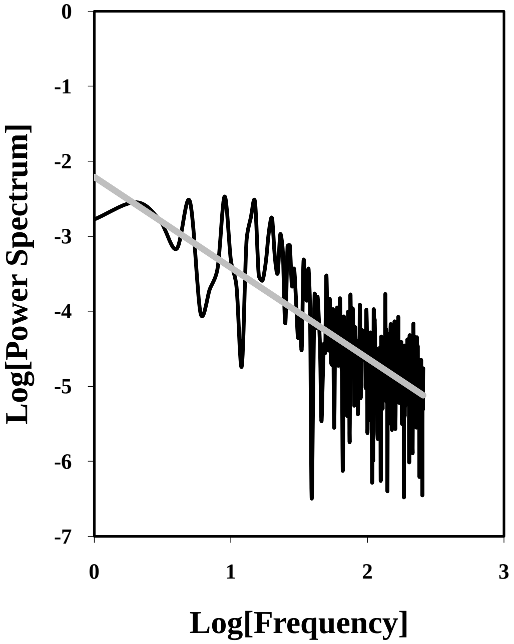
c

Figure 4.6 continued

The scaling properties of spatial pattern dynamics of alpine treeline advance are shown in Figure 4.7 (a) – (c). Still, no breakdown of scaling property is detected and all exhibit the linear pattern in the log-log power spectrum-frequency graphs.

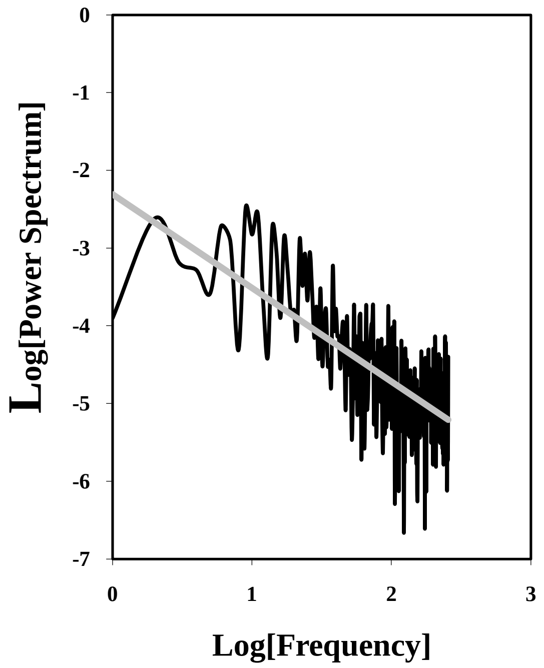


a



b

Figure 4.7. Scaling properties of spatial pattern dynamics of alpine treeline advance:
a. no climate change
b. gradual climate amelioration
c. gradual climate deterioration



c

Figure 4.7 continued

Like the results in the rapid climate change scenarios, these results do not show any form of breakdown of their scaling properties and are not different from the control group, i.e. the no climate change scenario. The hypothesis that climate change has a detectable impact on the dynamics of alpine treeline advance cannot be supported from the results through these simulations.

Sensitivity tests with the climate change initiated at specific high or low fractal states of the spatial pattern also were conducted and show similar spatial and temporal scaling properties in the control (no climate change) scenario and comparison (rapid and gradual climate change) scenarios. The results of sensitivity tests show the robustness of these results through 20 runs of simulation. Whether the climate change is initiated at a low or high fractal state of alpine treeline ecotone does not matter.

4.5 Conclusion

After examining these sets of experiments from both the temporal and spatial aspects of alpine treeline advance, we can conclude that there is no discernable change in the temporal and spatial scaling properties of alpine treeline dynamics caused by rapid or gradual climate changes. This suggests that climate change may not be capable of causing significant changes in temporal and spatial patterns of alpine treeline advance. We do not mean that treelines will not respond to climate change, but that the timing and spatial patterns of their dynamics will be only loosely coupled to the rates and amounts of climate change. This conclusion casts further doubt on suggestions that alpine treeline ecotones can serve as an indicator of climate change and that they can be used for monitoring climate change. Previous critiques of this idea were based on the unpredictability and/or variability of exogenous factors (e.g., Kupfer and Cairns 1995; Holtmeier and Broll 2005). This limitation can be due to endogenous feedbacks and thus apply anywhere and any time. Given that our modeling results depend on assumptions of the relative strengths of exogenous climate change drivers and endogenous feedbacks, more research on the strength of feedback effects and their resultant spatial patterns is needed.

The reason for the insensitivity of alpine treeline ecotone dynamics to external climate changes needs to be further explored. Careful examination of the details in temporal and spatial patterns of alpine treeline advances indicates that the explanation may be in the strength of endogenous positive feedbacks, i.e. the local feedbacks between trees and between trees and their abiotic environments within the alpine treeline ecotones, relative to the effects of climate change. Indeed, many studies demonstrate that facilitation, rather than competition, among trees, is the key for subalpine tree seedlings to survive the very harsh climate and surface conditions in alpine regions (Callaway et al, 2002) and such facilitation in terms of positive feedbacks should be powerful enough to develop tree patches of any size. For example, neighboring subalpine trees ameliorate the microclimate by providing and maintaining snow cover in winter which provides soil moisture in summer. Such strong positive feedbacks also should be nonlinear so that the benefit of facilitation among trees can be amplified to help alpine trees to advance to their ecological limits. This means that the sum of benefits from multiple trees will be greater than the simple addition of the individual benefit of single trees, as indicated in the functions of tree establishment and mortality in this model. As an earlier simulation study (Malanson, 2001) suggested, the strength of feedbacks does affect the responses of alpine treelines to climate change, which may overcome exogenous impacts. In addition, although facilitation as a result of local feedbacks can expand from the immediate vicinities of individual trees to much large areas among tree patches and accelerate the net growth of tree establishment (Zeng and Malanson, 2006) by initiating and maintaining a strong self-organization process. The results of the scaling up of these interactions are the improvement of environment quality for tree establishment across whole landscapes, and the rates and spatial patterns of alpine treeline advance essentially become indistinguishable from the effects that could be caused by external climate change alone. The improvement at certain periods can also be great enough to make additional changes in alpine environment caused by climate changes appear insignificant. For example, in Glacier National Park it appears that the highest patches of tree species that existed prior to the Little Ice Age were quickly reoccupied in the 19th century. No dead material higher than current krummholz patches are found, so scant evidence of significant advance in the 20th century are observed (Butler et al. 1994, Klasner and Fagre, 2002).

The results of this study are qualitatively consistent with the results by Bader et al.'s (2008) mechanistic model for tropical alpine treeline ecotones, but it differs in one respect, i.e. the response of treeline advance rate to climate change. Their results focus on the rate of alpine treeline advance and show a spatial buffer effect of positive feedbacks on responses of treelines to climate change. Our research extends to investigate the impact of climate change on alpine treeline ecotones through exploring both temporal and spatial aspects of the self-organized complexity and its limits, and our explanation focuses on across scale nonlinear interactions within the alpine treeline ecotones. The sensitivity tests in our research which implemented starting points of climate change at high and low fractal states of alpine treeline ecotones do not show discernable difference in treeline advance rate and spatial pattern. This result emphasizes the self-organizing nature of alpine treeline ecotones. In the case of climate warming, at high fractal states, the capacity of site quality in treeline ecotones has already been reached and the potential benefit from climate warming would not be fully utilized by treelines ecosystems; at low fractal states, treeline ecotones do benefit by climate warming and advance and change spatial patterns faster, but the rate of these changes are indistinguishable from that resulted from the fractal nature of their own self-organized movements.

From complexity theory, we expect that a self-organization process can create phenomena of any scale and that strong endogenous feedbacks inside the system make the system flexible or adaptable to the influence of external factors. So, when we consider alpine treeline ecotones as a potential candidate for detecting the signals of climate change, we need to keep in mind that they are complex adaptive systems and their endogenous dynamics may complicate such detection. Climate is an external factor to the alpine treeline ecotone and may be considered as one of the controlling factors of global alpine treelines. Although it seems logical to reason that significant change in one important factor should elicit a corresponding response from the system, this reasoning may carry the danger of misunderstanding the complex self-organization and adaptability of alpine treeline ecotones.

CHAPTER 5

CONCLUSIONS AND SYNTHESIS

The three research projects in this dissertation were carried out from the perspective of complexity theory and the results provide new insights into the dynamics of alpine treeline ecotones (ATE). The simulation and analysis of the spatial complexity at alpine treeline ecotones also contributes to improvement of methodology in landscape ecology, biogeography, and geographical research. There are still limitations in this study, and future research is needed to advance our understanding of alpine treeline ecotones and research methods.

5.1 Summary of Research Results

As a coherent research project, the three research chapters are linked to each other as a sequence to investigate both endogenous and exogenous aspects of complex dynamics of alpine treeline ecotones (ATE). The first project investigates the fundamental features of alpine treeline dynamics, and the following two projects examined the impacts of two exogenous factors on the endogenous dynamics: geomorphic surface features and climate change. The findings from all three research projects provide a fuller picture of alpine treeline dynamics.

In summary, there are seven major findings of this study:

1) A spatial power law distribution in alpine treeline ecotones was revealed. The system dynamics of the simulation exhibit the spatial and temporal characteristics of Self-Organized Complexity (SOC). This supports the proposed self-organization of alpine treeline ecotones by Malanson (1999).

2) A new explanation for such SOC has been proposed that develops a narrative of the evolution of alpine treeline ecotones via across-scale nonlinear feedbacks between trees and between trees and their environments.

3) Spatial processes wholly at a local scale create correlations between spatial pattern and the rate of treeline advance at landscape scale;

4) The temporal and spatial relations of treeline advances in the simulations exhibit dynamics characteristic of SOC.

5) A new landscape metric that quantifies complex space-time patterns of landscape, i.e. power-law slope of patches, was developed based on complexity theory. This enriches the spatial analysis of complex space-time patterns and can be used in other geographic domains.

6) The advance of the alpine treeline ecotones maintains its internal self-organized complexity on a landscape with geomorphic barriers below a threshold. Once geomorphic barriers reach this level, however, they do exert an impact on the dynamics of the alpine treeline ecotones. Signals from the geomorphological features can gradually enter the dynamics of the ecotones and, at some points, break down the pattern-process interactions and thus the scaling properties of ecotones. The break changes the spatial patterns significantly. The scale at which the scaling properties break down is when the geomorphic features are larger than the 3X3 window within which local interaction occurs, and thus it appears that the scale at which self organization breaks down is larger than what is observed for the solifluction patterns that motivated the study.

7) There is no discernable change in scaling properties of alpine treeline dynamics caused by climate change as represented in this simulation research. This insensitivity to climate change impact may be because endogenous positive feedbacks can maintain strong self-organization even with exogenous impacts.

5.2 Synthesis

The alpine treeline patterns at the landscape level could not be derived directly from earlier explanations (e.g., Steven and Fox, 1991). The results from this study offer a new explanation of spatial and temporal characteristics of ecological dynamics at alpine treeline ecotones (ATE) from the perspective of complexity theory. The various nonlinear pattern-process interactions on alpine treeline ecotones were omitted from earlier hypotheses and those nonlinearities at the local neighborhood level are not reducible to the individual tree level and cannot be extrapolated analytically to the landscape level. This is why a spatially explicit simulation that captures the nonlinearity of internal interactions followed by analytical methods aiming at exploring spatial complexity can help generate new explanations of these complex dynamics. Our explanation states that a) individual tree establishment events lead to an acceleration of advance as positive feedback affects a wider number of possible establishment sites, but that b) this change leads to a coalescence of patches that decreases the potential effects of positive feedbacks in the neighborhood of many trees, and so the advance slows. One of findings is that linear relations between spatial pattern and the rate of advance emerge at landscape scale from nonlinear interactions between pattern and process at the local scales. This explanation offers a holistic picture which shows alpine treeline ecotones as a self-organized ecological entity driven by its pattern-process interactions across all scales, which is consistent with the ubiquitous scaling law in ecology.

Various patterns generated from this model also provide a reconciliatory view of the different alpine treeline patterns observed in various places. That is, patterns are not generated from different system mechanisms, but from a unified one. Alpine treeline ecotones evolve with time and exhibit different patterns which are just at various temporal stages. At this landscape level, this view is consistent with the scaling phenomena in nature (West, et al., 1999), and it does not conflict with earlier hypotheses (Stevens and Fox, 1991; Korner 1998). Rather, it complements them to explain the changes in alpine treeline ecotones because the explanation developed in this study is from a different perspective and at multiple scales.

This reasoning also provides a possible explanation for the seeming contradiction that many large scale linear relationships on ecological landscapes where internal vegetation dynamics are apparently nonlinear (Zeng and Malanson, 2006). The specific causes are still unknown, given the fact that the interactions are active and changing constantly through time. The large scale linear relationships may be the result of balancing of various positive and negative feedbacks that control the total entropy of ecosystem evolution in a certain range (Prigogine and Stengers, 1984) and maintain its health. This balancing of feedbacks may also be the result of optimization inherent in ecosystems to develop through various stages as smoothly as possible and to provide maximum ecological functioning.

The question of how robust is the self-organizing complexity of alpine treeline dynamics was addressed by examining the impacts of two major exogenous factors, solifluction pattern and climate change. Solifluction pattern is a spatial exogenous factor, while climate change is a temporal exogenous one. Results show that under conditions that are not at the extremes, the impacts from both exogenous factors are not strong enough to interrupt the self-organizing complexity in alpine treeline dynamics. The strength of endogenous positive feedbacks may be the key to maintain this insensitivity of alpine treelines to exogenous impacts. This point can be supported by results from large scale field experiments on the role of facilitation in maintaining vegetation patterns in environmentally harsh high mountain areas (Callaway et al, 2002). The strength of internal feedbacks should not be a simple sum of various positive feedbacks, but a combined result of all positive and negative feedbacks at a local level. Furthermore, this strength should also be changing through time as the result of interactions between trees and between trees and their environments, as complexity theory predicts. But the measurement and detailed explanation of the strength of positive feedbacks still remain difficult tasks, given the fact that there are many physiological and environmental factors. So, feedback strength is still an umbrella name that captures many unknown local effects.

As the results from the second and third projects show, the self-organizing strength of alpine treeline ecosystems makes them insensitive to external impacts at the landscape scale to certain degree. But individual trees do respond to such disturbances significantly at small spatial and temporal scales. This difference raises new questions about the temporal scale of relationship between vegetation patterns and abiotic factors. If there is usually no significant impact of abiotic factors on the development of vegetation pattern, why are there many types of statistically significant relationships between them reported in the general ecology literature? If we look closely, the time scales of observations of such relationships, usually on the scale of 10^1 years, are much smaller than that of this simulation. Such statistical relationships at landscape scale may be found in a certain stages of an ecosystem but change through time; i.e., we expect correlation patterns to change in ecological succession (e.g., Wang and Malanson 2007). Here we may wish to qualify the nature of previous findings at alpine treeline through statistical modeling. If a statistical model is built which includes all important variables and an analysis is conducted that shows the significance of some of them, the significance of the relationships between the dependent and independent variables should reveal a universally true relationship through time in the sense of hypothesis testing. For example, some research might find a statistically significant relationship between alpine treeline movement, be it rate or position, at landscape scale (e.g., Bader and Ruitjen 2008; Hjort and Luoto 2009). As long known from studies of ecological succession, the limitations on the data length or the collecting period dictates that any finding from these datasets should imply a qualification imposed by the time period of data collection. Since ecosystems are always evolving, it is more desirable to make observations and collect data in their evolutionary stages to construct more robust models to find a more robust relationship. But because of the extremely long time scale of ecosystem evolution at places such as the alpine treeline, it remains a challenge. Where space-for-time substitution has worked well for studying succession in low elevation sites, the range of time since establishment for alpine treeline sites is limited or unknown. Furthermore, because of the interactions or feedbacks within ecosystems, changes in dependent variables may in turn have significant impact on variables that are supposed to be independent in regular statistical models. Such impact loops would distort the statistical relationships and make the hypothesis testing of coefficients unreliable (such endogeneity has been identified as a significant problem in econometrics; Kennedy 2008). One solution may be to construct a statistical model of simultaneous equations to take into account such feedback effects.

5.3 Limitations and Future Research Directions

There are several limitations of this study. First, though the simulation model was developed based on the observational studies by numerous researchers in Glacier National Park in Montana, this model was not fully calibrated and validated because the data that would be needed are impossible to get. The current calibration and validation were rudimentary and were carried out by comparing the resultant spatial patterns and rate of advance of alpine treelines from simulations with the current observed “snapshot’s” of alpine treeline ecotones. Second, the findings from this study are based on a hypothetical simplistic abiotic landscape for the purpose of simplification of the model to reduce uncontrolled external complexity according to the principle of “Occam’s razor”. The main intention is to reveal the endogenous dynamics of alpine treeline ecotones. So, the interpretation of findings should be aware of this fact. Third, the mathematical forms of the local nonlinear feedbacks were developed theoretically based on previous empirical research findings. They should not be considered as empirically calibrated and validated. Fourth, because of the inherent nonlinearity of the feedbacks in any complex model, replication and predictability of exact patterns are often an issue for the modeling community. However, replication and predictability of fundamental characteristics should not be a problem as shown from our repeated runs. This model is no exception.

This research is just an initial step of using complexity theory to simulate and analyze alpine treeline ecotones. From the mentioned above limitations and current state of research on alpine treeline ecotones, there are several possible further steps that can be taken to improve this study. First, more observational studies should be carried out to improve calibration and validation of the simulation model. Improvements would be on the mathematical forms of local feedbacks within the model and then on both the overall resultant patterns and rate of advance of alpine treelines. Second, observational studies from different locations and tree species with similar environments should be used for testing this model and findings to further verify and refine the explanation proposed here. Third, given that other types of simulation models of alpine treelines exist such as a gap model (FORSKA; Bekker, 2005) and a physiologically mechanistic model (ATC-BGC; Cairns and Malanson 1998), is there some way of borrowing some individualistic modeling to improve the local feedback modeling in this model? Fourth, new data sets such as tree rings or other types of dendrological data are needed that can provide long time alpine treeline advances or retreats. This is important for further calibration and validation of the model. Finally, other exogenous factors such as impact of spread of diseases at alpine treeline ecotones (Tomback and Resler 2007) can be considered to see how they interact with endogenous dynamics and other exogenous factors working at the same time, which would further advance our understanding of alpine treeline dynamics. By using a very general model that addresses concepts in as abstract and theoretical a framework as reasonable, this work provides direction for and a way to connect such future research.

In this research, a cellular automaton was constructed to investigate the endogenous spatial dynamics of alpine treeline ecotones and the impacts of exogenous factors, i.e. geomorphic features and climate change, from the perspective of complexity theory. A new explanation of spatial patterns in alpine treeline ecotones was proposed that suggests a Self-Organized Complexity driven by across scale pattern-process interactions which exhibits a scale-free phenomenon. This research provides an alternative theoretical foundation for further computational, statistical and field studies of alpine treeline ecotones and other similar ecotones. The limits discussed above can be addressed to further our understanding of pattern-process interactions in alpine treeline ecotones.

REFERENCES

Alencar, A. M., J. S. Andrade, and L. S. Lucena. 1997. Self-organized percolation. *Physical Review E* 56:R2379-R2382.

Alftine, K. J., and G. P. Malanson. 2004. Directional positive feedback and pattern at an alpine tree line. *Journal of Vegetation Science* 15:3-12.

Alftine, K. J., G. P. Malanson, and D. B. Fagre. 2003. Feedback-driven response to multi-decadal climatic variability at an alpine forest-tundra ecotone. *Physical Geography* 24:520-535.

Allen, P. M. 1982. Evolution, modelling, and design in a complex world. *Environment and Planning B* 9:95-111.

Allen, T. R and S. J. Walsh. 1996. Spatial composition and pattern of alpine treeline, Glacier National Park, Montana. *Photogrammetric Engineering and Remote Sensing* 62:1261-1268.

Armstrong, D. M., J. C. Halfpenny, and C. H. Southwick. 2001. Vertebrates. In: Bowman, W.D., T. R. Seastedt (Eds.). *Structure and Function of an Alpine Ecosystem*. Oxford, UK: Oxford University Press. 128-156.

Bader, M. K, M. Rietkerk, and A. K. Bregt. 2008. A simple spatial model exploring positive feedbacks at tropical alpine treelines. *Arctic, Antarctic, and Alpine Research*, 40(2): 269–278.

Bader, M.Y. and J.J.A. Ruijten. 2008. A topography-based model of forest cover at the alpine tree line in the tropical Andes, *Journal of Biogeography*, 35: 711-723

Bak, P., C. Tang and Wiesenfeld, K., 1987, Self-Organized Criticality: An Explanation of 1/f Noise, *Physical Review Letters*, 59(4):381-384.

Bak, P., C. Tang, and K. Wiesenfeld.1988. Self-organized criticality. *Physical Review A* 38:364-374.

Baker, W. L and P. J. Weisberg.1995. Landscape analysis of the forest-tundra ecotone in Rocky Mountain National Park, Colorado. *Professional Geographer* 47:361-375.

Bekker, M. F. 2002. Effects of Biotic Feedback on the Pattern and Rate of Subalpine Forest Advancement. Doctoral Dissertation, University of Iowa, Iowa City.

Bekker, M.F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, USA. Arctic, Antarctic, and Alpine Research 37(1): 97-107

Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. *Climatic Change* 59: 5-31

Billings, W. D. 1969. Vegetational pattern near timberline as affected by fire-snowdrift interactions. *Vegetatio* 19:192-207.

Bonabeau, E. 2002. Agent-based modeling: Methods and techniques for simulating human systems, *Proc. Natl. Acad. Sci. USA*. 99: no. Suppl 3, 7280-7287

Bowman, W.D., and T. R. Seastedt, (Eds.). 2001. *Structure and Function of an Alpine Ecosystem – Niwot Ridge, Colorado*. Oxford, UK: Oxford University Press.

Bunn, A. G., L. J. Graumlich, and D. L. Urban. 2005. Trends in twentieth-century tree growth at high elevations in the Sierra Nevada and White Mountains, USA. *Holocene* 15: 481-488.

Bunn, A. G, L.A.Waggoner and L.J. Graumlich. 2005. Topographic mediation of growth in high elevation foxtail pine (Pinus balfouriana Grev. et Balf.) forests in the Sierra Nevada, USA
Global Ecology and Biogeography 14: 103-114

Butler, D. R. 1995. *Zoogeomorphology – Animals as Geomorphic Agents*. Cambridge, UK: Cambridge University Press.

Butler, D. R., and G. P. Malanson. 1989. Periglacial patterned ground, Waterton-Glacier International Peace Park, Canada and USA. *Zeitschrift fur Geomorphologie* 33: 43-57.

Butler, D.R., G.P. Malanson and D.M. Cairns.1994. Stability of alpine treeline in northern Montana, USA. *Phytocoenologia* 22:485-500.

Butler, D. R., G. P. Malanson, and L. M. Resler. 2004. Turf-banked terrace treads and risers, turf exfoliation, and possible relationships with advancing treeline. *Catena* 58: 259-274.

Butler, D. R., G. P. Malanson, M. F. Bekker, and L. M. Resler. 2003. Lithologic, structural, and geomorphic controls on ribbon forest patterns. *Geomorphology* 55: 203-217.

Caine, N. 2001. Geomorphic systems of Green Lakes Valley. In: Bowman, W. D. and T. R. Seastedt (Eds.). *Structure and Function of an Alpine Ecosystem*. Oxford, UK: Oxford University Press. 45-74.

Cairns, D.M and G.P. Malanson. 1997. Examination of the carbon balance hypothesis of alpine treeline location in Glacier National Park, Montana. *Physical Geography* 18:125-145.

Cairns, D. M. and G. P. Malanson.1998. Environmental variables influencing carbon balance at the alpine treeline ecotone: A modeling approach. *Journal of Vegetational Science* 9: 679-692

Callaway, R. M. 1998. Competition and facilitation on elevation gradients in subalpine forests of the northern Rocky Mountains, USA. *Oikos*. 82:561-573.

Callaway, R.M., R.W. Brooker, P. Choler, Z. Kikvidze, C.J. Lortie, R. Michalet, L. Paolini, F.L. Pugnaire, B. Newingham, E.T. Aschehoug, C. Armas, D. Kikodze, and B.J. Cook. 2002. Positive interactions among alpine plants increase with stress. *Nature*. 417:844-848.

Camarero, J. J. and E. Gutiérrez. 2004. Pace and patterns of recent treeline dynamics: response of ecotones to climatic variability in the Spanish pyrenees, *Climatic Change* 63: 181-200.

Carpenter, S.R., W.A. Brock and P.C. Hanson. 1999. Ecological and social dynamics in simple models of ecosystem management. *Conservation Ecology* 3(2): 4. Available on the internet: URL: http://www.consecol.org/vol3/iss2/art4.

Cottenie, K. 2005. Integrating environmental and spatial processes in ecological community dynamics, *Ecology Letters*, 8(11): 1175-1182.

Cowan, G.A. Pines, D. and D Meltzer. 1994. *Complexity: Metaphors, Models, and Reality,* Addison-Wesley, Santa Fe.

Daly, C. and D. Shankman. 1985. Seedling establishment by conifers above tree limit on Niwot Ridge, Front Range, Colorado, USA. *Arctic and Alpine Research* 17:389-400.

Daniels, L. D. and T. T. Veblen. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology* 85: 1284–1296.

Davis, M. B. 1989. Lags in vegetation response to greenhouse warming. *Climatic Change* 15: 75-82.

Diaz, H. F., M. Grosjean, and L. Graumlich. 2003. Climate variability and change in high elevation regions: past, present and future *Climatic Change* 59: 1-4.

diCastri, F., A. J. Hansen, and M. M. Holland (Eds.). 1988. A new look at ecotones; emerging international projects on landscape boundaries. *Biology International* 17: 1-163.

Durrett, R. and S.A. Levin. 1994. The importance of being discrete (and spatial). *Theoretical Population Biology* 46:363-394.

Epstein, J. M. 2002. Modeling civil violence: An agent-based computational approach. *Proceedings of National Academy of Science* 99: 7243-7250.

Evans, T. P., A. Manire, F. De Castro, and E. Brondizio. 2001. A dynamic model of household decision-making and parcel level landcover change in the eastern Amazon. *Ecological Modeling* 143: 95-113

Fonstad, M. A. and W.A. Marcus. 2003. Self-organized criticality in riverbank systems. *Annals of the Association of American Geographer* 93(2): 281-296.

Germino, M. J., W. K. Smith., and A. C. Resor. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162:157-168.

Goodall, D. W. 1974. Problems of scale and detail in ecological modeling. *Journal of Environmental Management* 2: 149-157.

Gosz, J. R. 1993. Ecotone hierarchies. *Ecological Applications* 3:369-373.

Hadley, J. L. and W. K. Smith. 1983. Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, USA. *Arctic, Antarctic and Alpine Research* 15: 127-135.

Hagerstrand, T. 1965. A Monte Carlo approach to diffusion. *European Journal of Sociology* 6: 43-67.

Haken, H. 1975. Cooperative phenomena in systems far from thermal equilibrium and in nonphysical systems. *Reviews of Modern Physics* 47:67-121.

Hansen, A. J., F. di Castri, and P.G. Risser. 1988. A new SCOPE project. Ecotones in a changing environment: the theory and management of landscape boundaries. *Biology International* 17:137-163.

Hassell M. P., H. N. Comins, and R.M. May. 1994. Species coexistence and self-organizing spatial dynamics. *Nature* 370, 290 - 292

Hessl, A. E. and W. L. Baker. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. *Arctic, Antarctic and Alpine Research* 29: 173–183.

Hattenschwiler, S. and W. K. Smith. 1999. Seedling occurrence in alpine treeline conifers, a case study from the central Rocky Mountains, USA. *Acta Oecologica* 20:219-224.

Haugland, J. E. 2006. Short-term periglacial processes, vegetation succession, and soil development within sorted patterned ground: Jotunheimen, Norway. *Arctic, Antarctic, and Alpine Research* 38: 82-89.

Haugland, J. E., and S. W. Beatty. 2005. Vegetation establishment, succession and microsite frost disturbance on glacier forelands within patterned ground chronosequences. *Journal of Biogeography* 32: 145-153.

Hessl, A. E. and W. L. Baker. 1997. Spruce and fir regeneration and climate in the forest-tundra ecotone of Rocky Mountain National Park, Colorado, USA. *Arctic and Alpine Research* 29:173-183.

Hiemstra, C. A. A., G. E. Liston, and W. A. Reiners. 2002. Snow redistribution by wind and interactions with vegetation at upper treeline in the Medicine Bow Mountains, Wyoming, USA. *Arctic, Antarctic and Alpine Research* 34:262-273.

Hiemstra, C. A., G. E. Liston, and W. A. Reiners. 2006. Observing, modelling, and validating snow redistribution by wind in a Wyoming upper treeline landscape. *Ecological Modelling* 197: 35–51.

Hjort, J.and M. Luoto. 2009. Interaction of geomorphic and ecologic features across altitudinal zones in a subarctic landscape, *Geomorphology* 112(3-4): 324-333

Holtmeier, F. K. 2003. *Mountain Timberlines: Ecology, Patchiness, and Dynamics*. Kluwer, Dordrecht.

Holtmeier, F. K. 2009. *Mountain Timberlines: Ecology, Patchiness, and Dynamics.* Berlin, Germany: Springer.

Holtmeier, F. K. and G. Broll. 1992. The influence of tree islands and microtopography on pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, USA. *Arctic and Alpine Research* 24:216-228.

Holtmeier, F. K., and G. Broll, 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography* 14: 395-410.

Hoch, G. and C. Korner. 2003. The carbon charging of pines at the climatic treeline: a global comparison. *Oecologia* 135: 10-21.

Hoch, G. and C. Korner. 2009. Growth and carbon relations of treeline forming conifers at constant vs. variable low temperatures. *Journal of Ecology* 97:57-66

Hughes, L. 2000. Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15:56-61.

Jensen, H. J. 1998. *Self-organized criticality--emergent complex behavior in physical and biological systems*. Cambridge, UK: Cambridge University Press.

Jonzen, N., P. Lundberg, E. Ranta, and V. Kaitala. 2002. The irreducible uncertainty of the demography-environment interaction in ecology. *Proceedings of the Royal Society, London, B* 269: 221-225.

Kennedy, P. 1992. *A Guide to Econometrics*. MIT Press, Cambridge, MA

Klasner, F.L. and D.B. Fagre. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, USA. *Arctic, Antarctic and Alpine Research* 34:49-56.

Kohler, T. A. 2000. (editor, with G. Gumerman) *Dynamics in Human and Primitive Societies: Agent-based Modeling of Social and Spatial Presses*. Santa Fe Institute Studies in the Sciences of Complexity, New York, Oxford University Press.

Korner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. *Oecologia* 115:445-459.

Korner, C. 1999. *Alpine plant life: functional plant ecology of high mountain ecosystems,* Springer-Verlag, Berlin.

Korner, C., and J. Paulsen. 2004. A world-wide study of high altitude treeline temperatures. *Journal of Biogeography* 31: 713-732.

Kruckberg, A. R. 2002. *Geology and Plant Life.* Seattle, WA: University of Washington Press.

Kupfer, J.A. and D.M. Cairns. 1996. The suitability of montane ecotones as indicators of global climatic change. *Progress in Physical Geography* 20:253-272.

Lesica, P. 2002. *A Flora of Glacier National Park*. Oregon State University Press, Corvallis.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology* 73:1943-1967.

Levin, S.A. 1999. *Fragile Dominion: Complexity and the Commons*. Cambridge, MA: Perseus Books.

Levis, S., J. A. Foley, V. Brovkin, and D. Pollard. 1999. On the stability of the high-latitude climate-vegetation system in a coupled atmosphere-biosphere model. *Global Ecology and Biogeography* 8: 489-500.

Li, B.L. 2002. A theoretical framework of ecological phase transitions for characterizing tree-grass dynamics. *Acta Biotheoretica* 50:141-154.

Lloyd, A. H. 1997. Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years. *Canadian Journal of Forest Research* 27:936-42.

Lloyd, A. H., L. J. Graumlich. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology* 78: 1199-1210.

Loehle, C., B. L. Li, and R.C. Sundell. 1996. Forest spread and phase transitions at forest-prairie ecotones in Kansas, USA. *Landscape Ecology* 11:225-235.

Ludwig, J. A., D. J. Tongway, and S. G. Marsden. 1999. Stripes, strands or stipples: modelling the influence of three landscape banding patterns on resource capture and productivity in semi-arid woodlands, Australia. *Catena* 37: 257-273.

Macy, M. W.and A. Flache. 2002. Learning dynamics in social dilemmas, *Proc. Natl. Acad. Sci. USA*. 99: no. Suppl. 3, 7229–7236.

Malanson, G. P. 1993. Comment on modeling ecological response to climatic change. *Climatic Change* 23: 95-109.

Malanson, G. P. 1997. Effects of feedbacks and seed rain on ecotone patterns. *Landscape Ecology* 12:27-38.

Malanson, G. P. 1999. Considering complexity, *Annals, Association of American Geographers* 89:746-753.

Malanson, G. P. 2001. Complex responses to Global Change at Alpine Treeline. *Physical Geography* 22(4): 333-342

Malanson, G. P. and D. R. Butler. 1994. Competitive hierarchies, soil fertility gradients, and the elevation of treeline in Glacier National Park, Montana. *Physical Geography* 15:166-180.

Malanson, G.P. and Y. Zeng. 2004. Uncovering spatial feedbacks at alpine treeline using spatial metrics in evolutionary simulations. In *GeoDynamics*, P.M. Atkinson, G. Foody, S. Darby and F. Wu, eds. CRC Press, Boca Raton, FL, 137-150.

Malanson, G. P., D. R. Butler, D. M. Cairns, T. E. Welsh and L. M. Resler. 2002. Variability in a soil depth indicator in alpine tundra. *Catena* 49:203-215.

Malanson, G. P., N. Xiao and K. J. Alftine. 2001. A simulation test of the resource averaging hypothesis of ecotone formation. *Journal of Vegetation Science* 12:743-748.

Malanson, G. P., Y. Zeng, and S. J. Walsh. 2006. Complexity at advancing ecotones and frontiers. *Environment and Planning A* 38 (4): 619-32

Malanson, G. P., D. R. Butler, D. B. Fagre, S. J. Walsh, D. F. Tomback, L. D. Daniels, et al. 2007 Alpine treeline of western North America: Linking organism-to-landscape dynamics. *Physical Geography* 28: 378–396.

Manson, S. M. 2001. Simplifying complexity: a review of complexity theory. *Geoforum* 32 (3): 405-414

Manson, S. M. 2005. Agent-based modeling and genetic programming for modeling land change in the Southern Yucatan Peninsular Region of Mexico. *Agriculture, Ecosystems and Environment* 111(1): 47-62.

Marr, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* 58:1159-1164.

May, R. M. 1976. Simple mathematical models with very complicated dynamics. *Nature* 261: 459-467.

Messina, J.P. and S.J. Walsh. 2001. 2.5D Morphogenesis: Modeling Land Use and Land Cover Dynamics in the Ecuadorian Amazon, *Plant Ecology*, 156(1) 75-88

Milne, B. T., A. R. Johnson, T. H. Keitt, C. A. Hatfield, J. David and P. T. Hraber. 1996. Detection of critical densities associated with pinon-juniper woodland ecotones. *Ecology* 77:805-821

Moir, W. H., S. G. Rochelle and A.W. Schoettle. 1999. Microscale patterns of tree establishment near upper treeline, Snowy Range, Wyoming, USA. *Arctic, Antarctic and Alpine Research* 31:379-388.

Neilson, R. P. 1991. Climatic constraints and issues of scale controlling regional biomes. In: Holland, M.M., P.G. Risser, and R.J. Naiman (eds.) *Ecotones: the role of landscape* *boundaries in the management and restoration of changing environments* 31–51. London, UK: Chapman & Hall.

Noble, I. R. 1993. A model of the responses of ecotones to climate change. *Ecological Applications* 3:396-403.

Nungesser, M. K. 2003. Modelling microtopography in boreal peatlands: hummocks and hollows. *Ecological Modelling* 165:175–207.

Parker, D., and V. Meretsky. 2004. Measuring Pattern Outcomes in an Agent-Based Model of Edge-Erect Externalities Using Spatial Metrics. *Agriculture, Ecosystems, and Environment* 101(2-3): 233-250.

Parrish, J. K., and L. Edelstein-Keshet. 1999. Complexity, Pattern, and Evolutionary Trade-Offs in Animal Aggregation, *Science* 284(5411): 99-101.

Pascual, M. and F. Guichard. 2005. Criticality and disturbance in spatial ecological systems, *Trends in Ecology & Evolution* 20: 88-95

Pascual, M., M. Roy, F. Guichard, and G. Flierl. 2002. Cluster size distributions: signatures of self-organization in spatial ecologies. *Philosophical Transactions of the Royal Society, London, B* 357:657-666.

Payette, S., L. Filion, A. Delwaide and C. Begin. 1989. Reconstruction of tree-line vegetation response to long-term climate change. *Nature* 341:429-432.

Peng, C. K., S. Havlin, H. E. Stanley, and A. L. Goldberger. 1995. Quantification of scaling exponents and crossover phenomena in nonstationary heartbeat time series. *Chaos* 5: 82-7.

Pérez, F. L. 1992. Processes of turf exfoliation (Rasenabschälung) in the high Venezuelan Andes. *Zeitschrift für Geomorphologie* 36: 81– 106.

Phillips, J.D. 1999. Divergence, convergence, and self-organization in landscapes. *Annals, Association of American Geographers* 89:466-488.

Phillips, J. D. 2001. The relative importance of intrinsic and extrinsic factors in pedodiversity. *Annals, Association of American Geographers* 91: 609-621.

Phillips, J.D. 2004. Laws, contingencies, irreversible divergence, and physical geography. *Professional Geographer* 56:37-43.

Phillips, J. D. 2006. Evolutionary geomorphology: thresholds and nonlinearity in landform response to environmental change. *Hydrology and Earth System Sciences* 10: 731-742.

Phipps, M. 1989. Dynamical behavior of cellular automata under the constraint of neighborhood coherence. *Geographical Analysis* 21:197-215.

Prigogine, I. and I. Stengers, 1984. *Order Out of Chaos*. New York: Bantam Books.

Rietkerk, M., M.C. Boerlijst, F. van Langvelde, R. HilleRisLambers, J. van de Koppel, L. Kumar, H.H.T. Prins and A.M. de Roos. 2002. Self-organization of vegetation in arid ecosystems. *American Naturalist* 160:524-530.

Resler, L. M., D. R. Butler, and G. P. Malanson. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. *Physical Geography* 26: 112-125.

Rind. R.1999. Complexity and Climate. *Science* 284(5411): 105-107.

Risser, P.G. 1995. The status of the science examining ecotones. *BioScience* 45:318-325

Rochefort, R.M. and Peterson, D.L. 1996. Temporal and spatial distribution of trees in subalpine meadows of Mount Rainier National Park. *Arctic and Alpine Research*. 28: 52-59.

Rochefort, R.M., R.L. Little, A. Woodward and D.L. Peterson .1994. Changes in the distribution of subalpine conifers in western North America: a review of climate and other factors. *Holocene* 4:89-100.

Roulet, N., and T. Moore. 2000. Modelling and analysis of peatlands as dynamical systems. *Journal of Ecology* 88: 230–242.

Rupp, T.S., F.S. Chapin III, and A.M. Starfield. 2001. Modeling the Influence of Topographic Barriers on Treeline Advance in the Forest-Tundra Ecotone in Northwestern Alaska. *Climatic Change* 48, 399-416.

Seastedt, T. R. 2001. Soils. In: Bowman, W. D., and T. R. Seastedt (Eds.). *Structure and Function of an Alpine Ecosystem.* Oxford, UK: Oxford University Press 157-173.

Sharp, R. P., and A. F. Glazner. 1997. *Geology Underfoot in Death Valley and Owens Valley*. , Missoula, MT: Mountain Press Publishing.

Sheppard, E.S. 1985. Urban system population dynamics: incorporating nonlinearities. *Geographical Analysis* 17:47-53.

Smith, W.K., M.J. Germino, T.E. Hancock and D.M. Johnson. 2003. Another perspective on altitudinal limits of alpine treelines. *Tree Physiology* 23:1101-1112.

Sole, R.V., and S.C. Manrubia. 1995. Are rainforest self-organized in a critical state? *Journal of Theoretical Biology* 173:31-40.

Sole, R.V., S.C. Manrubia, M. Benton, S. Kauffman, and P. Bak. 1999. Criticality and scaling in evolutionary ecology. *Trends in Ecology and Evolution* 14, 156-160).

Sornette, D. and A. Helmstetter. 2003. Endogenous versus exogenous shocks in systems with memory. *Physica A* 318:577-591.

Sprugel, D. G. 1976. Dynamic structure of wave-regenerated *Abies balsamea* forests in the north-eastern United States. *Journal of Ecology* 64: 889-911.

Stallins, J. A. 2001. Soil and vegetation patterns in barrier-island dune environments. *Physical Geography* 22: 79-98.

Stallins, J. A. 2006. Geomorphology and ecology: Unifying themes for complex systems in biogeomorphology. *Geomorphology* 77: 207-216.

Stallins, J. A, A. J. Parker. 2003. The influence of complex systems interactions on barrier island dune vegetation pattern and process. *Annals, Association of American Geographers* 93: 13-29.

Stevens, G.C. and J.F. Fox. 1991. "The causes of treeline." *Annual Review Ecology and Systematics* 22:177-191.

Straussfogel, D. 1991. Modeling suburbanization as an evolutionary system dynamic. *Geographical Analysis* 23:1-24.

Sturm, M., J.P. McFadden, G.E. Liston, F.S. Chapin, C.H. Racine, and J. Holmgren. 2001. Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *Journal of Climate* 14:336-344.

Thorn, C. E. 1978. A preliminary assessment of the geomorphic role of pocket gophers in the alpine zone of the Colorado Front Range. *Geografiska Annaler 60A*: 181-187.
Valentin, C., J. M. d'Herbes, and J. Poesen. 1999. Soil and water components of banded vegetation patterns. *Catena* 37: 1-24.

Tilman, D., and P. Kareiva. 1997. *Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions.* Princeton, New Jersey: Princeton University Press.

Tomback, D.F. and L.M. Resler. 2007. Invasive pathogens at alpine treeline: Consequences for treeline dynamics, *Physical Geography* 28(5): 397-418

Tranquillini, W. 1979. *Physiological Ecology of the Alpine Timberline*. New York: Springer-Verlag.

Turcotte, D.L. 1990. Implications of chaos, scale-invariance, and fractal statistics in geology. *Global Planetary Change* 89:301-308.

Turcotte, D. L. and J. B. Rundle. 2002. Self-organized complexity in the physical, biological, and social sciences. *Proceedings of the National Academy of Sciences, USA* 99:2463-2465.

Turcotte, D., B. D. Malamud, G. Morein and W. I. Newman. 1999. An inverse-cascade model for self-organized critical behavior. *Physica A* 268:629-643.

Valentin, C., J. M. d'Herbès and J. Poesen. 1999. Soil and water components of banded vegetation patterns. *Catena* 37:1-24.

Virah-Sawmy, M., L. Gillson and K.J. Willis. 2009. How does spatial heterogeneity influence resilience to climatic changes? Ecological dynamics in southeast Madagascar, *Ecological Monographs*, 79(4): 557-574

Walker, D. A., W. D. Billings and J. G. deMolenaar. 2001. Snow-vegetation interactions in tundra environments. Pages 266-324 *in* H. G. Jones, J. W. Pomeroy, D. A. Walker and R.W. Hoham, eds. *Snow Ecology*, Cambridge University Press, Cambridge.

Walker, D. A., J. C. Halfpenny, M. D. Walker and C. A. Wessman. 1993. Long-term studies of snow-vegetation interactions. *BioScience* 43:287-301.

Walker S., J. B. Wilson, J. B. Steel, G. L. Rapson, B. Smith, W. M. King and Y. H. Cottam. 2003. Properties of ecotones: Evidence from five ecotones objectively determined from a coastal vegetation gradient. *Journal of Vegetation Science* 14:579-590.

Walsh, S. J., L. Bian, S. McKnight, D. G. Brown, and E. S. Hammer. 2003b. Solifluction steps and risers, Lee Ridge, Glacier National Park, Montana, USA: a scale and pattern analysis. *Geomorphology* 55: 381-398.

Walsh, S. J., D. R. Butler, G. P. Malanson, K. A. Crews-Meyer, J. P. Messina, and N. Xiao. 2003. Mapping, modeling, and visualization of the influences of geomorphicprocesses on the alpine treeline ecotone, Glacier National Park, Montana, USA. *Geomorphology* 53: 129-145.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan, T. J. C. Beebee, J. M. Fromentin, O. Hoegh-Guldberg and F. Bairlein. 2002. Ecological responses to recent climate change. *Nature* 416:389-395.

Wang, Q. and G.P. Malanson. 2007. Patterns of correlation among landscape metrics. *Physical Geography* 28: 170-182.

Watts, A. S. 1947. Pattern and process in the plant community. Journal of Ecology 35:1-22.

Werner, B.T. 1999. Complexity in Natural Landform Patterns. *Science* 284(5411): 102-104

West, G. B., J. H. Brown, and B. J. Enquist. 1999. The fourth dimension of life: fractal geometry and allometric scaling of organisms. *Science* 284(5420): 1677-1679

Wiegand T, JJ. Camarero, N. Ruger, and E. Gutierre. 2006. Abrupt population changes in treeline ecotones along smooth gradients. *Journal of Ecology* 94: 880-892.

Wiens, J. A., C. S. Crawford and J. R. Gosz. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* 45:421-7.

Wilmking, M., G. P. Juday, V. A. Barber, and H. S. J. Zald. 2004. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology* 10: 1724-1736

Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* 23:263-336.

Wolfram, S. 1984. Cellular automata as models of complexity. *Nature* 311:419-424.

Wootton, J. T. 2001. Local interactions predict large-scale pattern in empirically derived cellular automata. *Nature* 413:841-844.

Wu, Y. G., N. M. Wang, K. Rutchey. 2006. An analysis of spatial complexity of ridge and slough patterns in the Everglades ecosystem. *Ecological Complexity* 3: 183-192.

Zeng, Y., and G. P. Malanson. 2006. Endogenous fractal dynamics at alpine treeline ecotones. *Geographical Analysis* 38: 271-287.

Zeng, Y., G. P. Malanson, and D.R. Butler. 2007. Geomorphic limits to self organization in alpine forest-tundra ecotone vegetation. *Geomorphology* 91: 378-392.

APPENDIX

Statistics Tables of Power Law Regression Models in the Corresponding Graphs

a. Fig. 2.3 b

SUMMARY

Regression Statistics	
Multiple R	0.917707
R Square	0.842186
Adjusted R Square	0.841565
Standard Error	0.361322
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	176.9636	176.9636	1355.488	8.00E-104
Residual	254	33.16058	0.130553		
Total	255	210.1242			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	3.621573	0.109648	33.02919	6.51E-94	3.405639
X Variable 1	-1.99491	0.054185	-36.817	8.00E-104	-2.10162

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
3.837508	3.405639	3.837508
-1.88821	-2.10162	-1.88821

b. Fig. 2.3 c

SUMMARY

Regression Statistics	
Multiple R	0.801612
R Square	0.642582
Adjusted R Square	0.641175
Standard Error	0.508485
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	118.071	118.071	456.653	1.12E-58
Residual	254	65.67358	0.258557		
Total	255	183.7446			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-1.64238	0.154306	-10.6436	4.06E-22	-1.94626
X Variable 1	-1.6295	0.076254	-21.3694	1.12E-58	-1.77967

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.3385	-1.94626	-1.3385
-1.47933	-1.77967	-1.47933

c. Fig. 3.4 a

SUMMARY

Regression Statistics	
Multiple R	0.791771
R Square	0.626901
Adjusted R Square	0.62617
Standard Error	0.549529
Observations	512

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	258.778	258.778	856.9305	2.90E-111
Residual	510	154.0111	0.301983		
Total	511	412.7891			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.486703	0.132862	18.71644	6.85E-60	2.225679
X Variable 1	-1.67828	0.057331	-29.2734	2.90E-111	-1.79091

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.747727	2.225679	2.747727
-1.56564	-1.79091	-1.56564

d. Fig. 3.4 b

SUMMARY

Regression Statistics	
Multiple R	0.797289
R Square	0.635669
Adjusted R Square	0.634955
Standard Error	0.542857
Observations	512

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	262.2262	262.2262	889.826	6.70E-114
Residual	510	150.2939	0.294694		
Total	511	412.5201			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.659413	0.131249	20.26239	2.08E-67	2.401558
X Variable 1	-1.68942	0.056635	-29.83	6.70E-114	-1.80069

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.917268	2.401558	2.917268
-1.57816	-1.80069	-1.57816

e. Fig. 3.4 c

SUMMARY

Regression Statistics	
Multiple R	0.749645
R Square	0.561968
Adjusted R Square	0.561109
Standard Error	0.600627
Observations	512

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	236.0402	236.0402	654.2983	1.80E-93
Residual	510	183.9841	0.360753		
Total	511	420.0243			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.611429	0.145216	17.98306	2.32E-56	2.326134
X Variable 1	-1.60285	0.062662	-25.5793	1.80E-93	-1.72596

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.896725	2.326134	2.896725
-1.47974	-1.72596	-1.47974

f. Fig. 3.5 a

SUMMARY

Regression Statistics	
Multiple R	0.614345
R Square	0.37742
Adjusted R Square	0.372479
Standard Error	0.546004
Observations	128

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	22.7715	22.7715	76.38351	1.23E-14
Residual	126	37.56319	0.298121		
Total	127	60.33469			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-2.33832	0.205902	-11.3565	5.13E-21	-2.74579
X Variable 1	-1.03867	0.118845	-8.73977	1.23E-14	-1.27386

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.93084	-2.74579	-1.93084
-0.80348	-1.27386	-0.80348

g. Fig. 3.5 b

SUMMARY

Regression Statistics	
Multiple R	0.801208
R Square	0.641935
Adjusted R Square	0.639047
Standard Error	0.46674
Observations	126

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	48.42842	48.42842	222.3055	1.97E-29
Residual	124	27.01294	0.217846		
Total	125	75.44136			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-1.32616	0.201959	-6.5665	1.27E-09	-1.7259
X Variable 1	-1.7246	0.115668	-14.9099	1.97E-29	-1.95354

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-0.92643	-1.7259	-0.92643
-1.49566	-1.95354	-1.49566

h. Fig. 3.5 c

SUMMARY

Regression Statistics	
Multiple R	0.691447
R Square	0.478099
Adjusted R Square	0.473957
Standard Error	0.577244
Observations	128

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	38.46091	38.46091	115.4253	1.64E-19
Residual	126	41.98451	0.33321		
Total	127	80.44542			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-2.42773	0.217682	-11.1526	1.63E-20	-2.85851
X Variable 1	-1.34987	0.125644	-10.7436	1.64E-19	-1.59852

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.99694	-2.85851	-1.99694
-1.10123	-1.59852	-1.10123

i. Fig. 3.5 d

SUMMARY

Regression Statistics	
Multiple R	0.741734
R Square	0.55017
Adjusted R Square	0.5466
Standard Error	0.555966
Observations	128

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	47.63381	47.63381	154.1056	1.32E-23
Residual	126	38.94642	0.309099		
Total	127	86.58023			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-2.34958	0.209658	-11.2067	1.20E-20	-2.76449
X Variable 1	-1.50225	0.121013	-12.4139	1.32E-23	-1.74173

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.93467	-2.76449	-1.93467
-1.26277	-1.74173	-1.26277

j. Fig. 3.7 c

SUMMARY

Regression Statistics	
Multiple R	0.727257
R Square	0.528903
Adjusted R Square	0.525165
Standard Error	0.599118
Observations	128

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	50.77635	50.77635	141.4611	2.47E-22
Residual	126	45.22672	0.358942		
Total	127	96.00307			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-1.77786	0.225931	-7.86902	1.41E-12	-2.22497
X Variable 1	-1.55101	0.130405	-11.8937	2.47E-22	-1.80908

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.33075	-2.22497	-1.33075
-1.29294	-1.80908	-1.29294

k. Fig. 4.3 a

SUMMARY

Regression Statistics	
Multiple R	0.772952
R Square	0.597455
Adjusted R Square	0.59587
Standard Error	0.583344
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	128.284	128.284	376.9846	4.18E-52
Residual	254	86.43361	0.34029		
Total	255	214.7176			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.258033	0.177023	12.7556	3.95E-29	1.909414
X Variable 1	-1.69851	0.08748	-19.4161	4.18E-52	-1.87079

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.606653	1.909414	2.606653
-1.52623	-1.87079	-1.52623

l. Fig. 4.3 b

SUMMARY

Regression Statistics	
Multiple R	0.812984
R Square	0.660943
Adjusted R Square	0.659609
Standard Error	0.601302
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	179.0239	179.0239	495.1376	1.36E-61
Residual	254	91.83723	0.361564		
Total	255	270.8611			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	2.869139	0.182473	15.72367	2.29E-39	2.509787	3.228491	2.509787	3.228491
X Variable 1	-2.00649	0.090173	-22.2517	1.36E-61	-2.18407	-1.82891	-2.18407	-1.82891

m. Fig. 4.3 c

SUMMARY

Regression Statistics	
Multiple R	0.751045
R Square	0.564069
Adjusted R Square	0.562352
Standard Error	0.639761
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	134.5189	134.5189	328.6604	1.07E-47
Residual	254	103.9608	0.409295		
Total	255	238.4797			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	2.553286	0.194144	13.15153	1.77E-30	2.17095	2.935622	2.17095	2.935622
X Variable 1	-1.7393	0.09594	-18.129	1.07E-47	-1.92824	-1.55036	-1.92824	-1.55036

n. Fig. 4.4 a

SUMMARY

Regression Statistics	
Multiple R	0.707968
R Square	0.501218
Adjusted R Square	0.499255
Standard Error	0.555347
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	78.71887	78.71887	255.2409	3.03E-40
Residual	254	78.33616	0.30841		
Total	255	157.055			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	-1.86409	0.168527	-11.0611	1.79E-23	-2.19598	-1.53221	-2.19598	-1.53221
X Variable 1	-1.33052	0.083281	-15.9763	3.03E-40	-1.49453	-1.16651	-1.49453	-1.16651

o. Fig. 4.4 b

SUMMARY

Regression Statistics	
Multiple R	0.700178
R Square	0.490249
Adjusted R Square	0.488242
Standard Error	0.603877
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	89.08168	89.08168	244.2824	4.86E-39
Residual	254	92.62538	0.364667		
Total	255	181.7071			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-1.69669	0.183254	-9.25871	9.00E-18	-2.05759
X Variable 1	-1.41539	0.090559	-15.6295	4.86E-39	-1.59373

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.3358	-2.05759	-1.3358
-1.23705	-1.59373	-1.23705

p. Fig. 4.4 c

SUMMARY

Regression Statistics	
Multiple R	0.693407
R Square	0.480813
Adjusted R Square	0.478769
Standard Error	0.544511
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	69.74276	69.74276	235.2264	5.04E-38
Residual	254	75.309	0.296492		
Total	255	145.0518			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*	*Upper 95%*	*Lower 95.0%*	*Upper 95.0%*
Intercept	-1.9924	0.165239	-12.0577	8.96E-27	-2.31782	-1.66699	-2.31782	-1.66699
X Variable 1	-1.25237	0.081656	-15.3371	5.04E-38	-1.41318	-1.09156	-1.41318	-1.09156

q. Fig. 4.6 a

Same as 4.4 a

r. Fig. 4.6 b

SUMMARY

Regression Statistics	
Multiple R	0.760506
R Square	0.578369
Adjusted R Square	0.576709
Standard Error	0.627115
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	137.0252	137.0252	348.4221	1.52E-49
Residual	254	99.89151	0.393274		
Total	255	236.9167			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.42119	0.190306	12.72261	5.11E-29	2.046412
X Variable 1	-1.75543	0.094044	-18.6661	1.52E-49	-1.94063

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.795969	2.046412	2.795969
-1.57022	-1.94063	-1.57022

s. Fig. 4.6 c

SUMMARY

Regression Statistics	
Multiple R	0.800109
R Square	0.640174
Adjusted R Square	0.638757
Standard Error	0.547319
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	135.369	135.369	451.896	2.62E-58
Residual	254	76.08767	0.299558		
Total	255	211.4566			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	2.412088	0.166091	14.52271	3.36E-35	2.084998
X Variable 1	-1.74478	0.082077	-21.2578	2.62E-58	-1.90642

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
2.739179	2.084998	2.739179
-1.58315	-1.90642	-1.58315

t. Fig. 4.7 a

Same as 4.4 a

u. Fig. 4.7 b

SUMMARY

Regression Statistics	
Multiple R	0.672117
R Square	0.451741
Adjusted R Square	0.449583
Standard Error	0.557092
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	64.95186	64.95186	209.2847	5.26E-35
Residual	254	78.82932	0.310352		
Total	255	143.7812			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-2.21113	0.169057	-13.0792	3.12E-30	-2.54406
X Variable 1	-1.20859	0.083543	-14.4667	5.26E-35	-1.37311

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.87819	-2.54406	-1.87819
-1.04406	-1.37311	-1.04406

v. Fig. 4.7 c

SUMMARY

Regression Statistics	
Multiple R	0.677938
R Square	0.4596
Adjusted R Square	0.457472
Standard Error	0.546417
Observations	256

ANOVA

	df	*SS*	*MS*	*F*	*Significance F*
Regression	1	64.49804	64.49804	216.0222	8.33E-36
Residual	254	75.83713	0.298571		
Total	255	140.3352			

	Coefficients	*Standard Error*	*t Stat*	*P-value*	*Lower 95%*
Intercept	-2.31072	0.165817	-13.9354	3.60E-33	-2.63728
X Variable 1	-1.20436	0.081942	-14.6977	8.33E-36	-1.36573

Upper 95%	*Lower 95.0%*	*Upper 95.0%*
-1.98417	-2.63728	-1.98417
-1.04299	-1.36573	-1.04299